1984

Inheritance of Plant Height and Other Agronomic Traits in Nine Crosses of Sunflower (Helianthus annuus L.)

Saif Ur Rehman Khan

Recommended Citation

Khan, Saif Ur Rehman, "Inheritance of Plant Height and Other Agronomic Traits in Nine Crosses of Sunflower (Helianthus annuus L.)" (1984). *Electronic Theses and Dissertations*. 4216.
https://openprairie.sdstate.edu/etd/4216

INHERITANCE OF PLANT HEIGHT AND OTHER AGRONOMIC TRAITS IN NINE CROSSES OF SUNFLOWER (*HELIANTHUS ANNUUS* L.)

By

SAIF UR REHMAN KHAN

A thesis submitted
in partial fulfillment of the requirements for the
degree Master of Science
Major in Agronomy
South Dakota State University

1984

INHERITANCE OF PLANT HEIGHT AND OTHER AGRONOMIC TRAITS IN NINE CROSSES OF SUNFLOWER (HELIANTHUS ANNUUS L.)

This thesis is approved as a creditable and independent investigation by a candidate for the degree, Master of Science, and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

Charles L. Lay
Thesis Adviser

6/6/84
Date

Maurice L. Horton
Head, Plant Science, Dept.

6/6/84
Date

ACKNOWLEDGEMENTS

The author wishes to express sincere gratitude to his major professor and thesis adviser, Dr. Charles L. Lay for his advice and council throughout the period of this study and guidance in conducting the statistical analysis and writing this manuscript.

Appreciation is extended to Mr. Paul D. Evenson and Dr. Martin L. Carson for their help in statistical problems and to Dr. Arvid A. Boe for reviewing the manuscript and valuable suggestions.

The author is indebted to Dr. Maurice L. Horton, Dr. Chen H. Chen for their cooperative spirit, advice and encouragement throughout the course of the study.

Many thanks to Mr. Soloman Tuwafe and his family for their friendship and sharing unforgettable memories during stay at South Dakota State University. Appreciation is extended to Mrs. Marilyn Eighmy for her help in typing.

Sincere appreciation is expressed to my wife, Sabiha, without whose patience, encouragement and immense help this thesis would never have seen the light of day.

Finally, the author is grateful for financial assistance provided by the Government of Pakistan through a loan agreement with the United States Department of Agriculture to complete this study.

SRK

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF TABLES (continued)

INTRODUCTION

Sunflower, a member of the Compositae, belongs to the genus Helianthus, a word derived from the Greek "Helios" meaning sun and "anthus" which means flower (2). This is because of the characteristic turning of the plant head towards the sun during day-light.

Sixty-five out of 100 known species of Helianthus are native to North and South America (2). Although the early literature mentioned Peru as the place of origin, modern authorities believe that sunflower is native to North America, probably southwest US. Archaeological explorations have found evidence of sunflower cultivation at many sites in Arizona and New Mexico as early as 3000 B.C. (2).

The USSR is the world leader in production of sunflower seeds harvesting about 4 to 4.5 million hectares per year with production remaining fairly stable since 1960. The US and Argentina rank second and third having planted about 1.6 and 1.3 million hectares during 1981 respectively. Spain, China, Romania, Bulgaria, Australia, and Canada follow in importance. The total amount of land devoted to sunflower production in the world increased from 8.4 million hectares in the 1960's to more than 11.6 million in 1981 (36).

Sunflower became a commercial crop in the US during the late 1960's. Production during the 1970's increased from a few thousand to 2.1 metric tons due to the establishment of markets in Europe and also the development of hybrids, which were higher in yield and oil content (35). Sunflower is commercially important because it produces more oil per unit land than any other crop in many areas. The seed contains 40% of high quality oil on a dry weight basis, which is free of toxic constituents. The crude meal obtained after removal of the oil has a protein content of 38-40%, making it a valuable protein supplement for poultry, sheep, swine, and cattle. The hulls and heads which remain after the seed is removed can be processed to yield pectin (2).

Some large seed is used whole and roasted seed much like peanuts, whereas some seed is dehulled and the kernels sold as confectionary "nuts". Smaller whole seed is used in rations for pet birds and small animals, as well as in home feeders for wild birds (26).

Although sunflower has gained importance as an oil seed crop, genetic information is still lacking on many aspects of the plant. Breeding programs should be based on sound genetic principles. Estimates of genetic variability and heritability, type of gene action, and the number of genes associated with a trait provide useful guidelines to determine the value of source populations and appropriate procedures to use in a breeding program.

Genetic variation of characters associated with plant growth, morphological or physiological differences may serve as a basis for development of inbred lines and hybrids with improved agronomic traits. Variability of traits such as plant height, flowering, and maturity can be particularly useful because it allows for development of types adapted to an array of environments and agronomic regions.

Plant height is an important characteristic in sunflower production. Yields of tall hybrids can be reduced due to lodging. Lodging as high as 80% was observed in a test of 56 hybrids planted at White, South Dakota, in 1983 (15), emphasizing the importance of short hybrids. Early hybrids can also overcome yield losses caused by flowering during hot dry weather and early frost. Variation among other traits, such as leaf number and internode length, seems to have less apparent value. However these traits may be correlated with those of more direct economic importance.

This research was conducted to study the mode of inheritance of plant height, leaf number, internode length, flowering, and their relationship in crosses of two short inbred lines of sunflower selected from PI 386323 and PI 386316 with a number of inbred lines commonly used in production of sunflower hybrids.

REVIEW OF LITERATURE

Inheritance of plant characteristics like plant height, days to flowering, number of leaves, and internode length have been extensively studied in a number of crop species. However, with sunflower being relatively a new crop in terms of genetic research, detailed information regarding the inheritance of many aspects of the plant is still lacking.

Both multigene and single gene control of rather large differences in plant height have been reported in the literature. Gundaev (12) reported a range of 0.5 to 4 m for plant height in sunflower. Types up to 12 m in height have been reported by Cockrell (6). Unrau (37), in a study of single crosses from four inbred lines from 'Mennonite', two Russian lines and the variety 'Sunrise', observed that crossing plants of different heights usually produced F1 plants exceeding the tallest parent. Heterosis for plant height and blooming time was also evident in a diallel study, including lines CM 5, CM 49, CM 121, CM 119, CM 53, CM 54, CM 91, CM 30, CM 85 and 5-37-388 conducted by Putt (27).

Stoyanova, Ivanov and Georgiev (34) studied plant height in 140 F1 hybrids developed from 192 inbred lines. Heterosis averaged 27% in the F1 hybrids for plant height. In another study with seven inbred lines, Velkov (38) reported strong heterosis for plant height in the F1 mainly due to dominant genes. Clement and Diehl (5) studied a cross between dwarf sunflower and 'B-65-40', a tall variety and observed segregation in F2, which suggested that tallness is dominant over shortness and controlled by many genes. Fick (10) observed that lines differing in leaf number and plant height showed largely a continuous distribution in the F2 generation, suggesting quantitative inheritance of these traits.

Single gene control of plant height has also been reported by Rodin (30,31), Enns (9), and Fick (10). Rodin (30) observed F1s intermediate in height from crosses between short and tall varieties. The F2 segregation resulted in tall, intermediate and short plants in a 1:2:1 ratio. The intermediate plants continued to segregate into three groups in the F3, suggesting shortness was controlled by a single gene with incomplete dominance. Additional studies of Rodin (31) showed that some of the tall hybrid plants did not segregate in subsequent generations. The short plants either segregated for height or were stable. This later group differed from the others in having dark green rugose leaves.

Enns (9) found that dwarf character of the inbred line 77AB was controlled by single recessive gene. A similar result has been observed by Fick (10), in a cross of RHA 273 and a line isolated from the Romania hybrid H 590.

Unrau (37), in his study of F1 hybrids developed from lines with different flowering time, observed that all F1 hybrids were earlier than their parents with the exception of crosses involving 'Saratov', an extremely early line, which produced hybrids intermediate in flower. This suggested dominance and partial dominance for early flowering over late flowering. Putt (26), in his diallel study of 10 lines also observed heterosis for blooming time. Fick (10) isolated an inbred line from the cultivar 'Volar', which showed a recessive gene controlling early flowering.

Rao and Singh (28), in a diallel cross of seven inbred lines, including CM 303, CM 312, CM 319, CM 358, CM 360, CM 392 and CM 400 observed a significant dominant component for days to 75% flowering. Manjunath and Goud (18) studied 25 crosses among ten Canadian inbred lines viz; CM 303, CM 324, CM 378, CM 379, CM 384, CM 391, CM 392, CM 408, CM 409 and CM 69-2, their F1s including reciprocals, F2s, B1 and B2 generations. They observed epistatic effects for number of days to flowering.

Miller, Hammond and Roath (22) and Rao and Singh (28) observed significant additive genetic variance for plant height in sunflower. Velkov (38) studied inheritance of stem height in F1, F2, B1 and B2 generations from crosses of four inbred lines of sunflower. The results of the study indicated that additive gene action was three times weaker than dominance effects. Epistatic effects were non-significant in most cases, however the interaction between additive and dominant genes was expressed.

Marinkovic (20) in a diallel cross with six inbred lines viz; cms-HA 99, M-6/4, S-59, R-251, R-287 and R-222 studied the mode of inheritance of leaf number and plant height. His results indicated that additive and non-additive components were equally important in the inheritance of plant height. For leaf number, the non-additive components, dominance and epistasis, were more important than the additive component. Analysis of components of genetic variance and regression analysis showed the presence of super-dominance in the inheritance of plant height and leaf number. Marinkovic also found that dominant genes were more frequent than recessive genes for plant height but the reverse was true for leaf number.

Manjunath (17) estimated the components of variance for seventeen quantitative characters of sunflower and observed that for days to flowering and leaf number, dominance x dominance gene action was of prime importance followed by dominance. Whereas for plant height dominance gene action was more important than dominance x dominance. He reported that, in general, overdominance was in operation and that dominant genes outnumbered recessive genes controlling plant height.

Estimates of heritability for plant height, number of days to flowering, and leaf number of sunflower have been obtained by different research workers. Pathak (24), Kloczowski (13) and Shabana (32) reported broad sense heritability estimates of 20, 49 and 90% respectively for plant height. From a plant height study of seven inbred lines, Velkov (38) obtained a range of 47 to 86% for broad sense and -0.17 to 80% for the narrow sense heritability estimates. Fick (10) reported a wide range of 4 to 85% for the broad sense heritability for plant height in nine crosses of short and tall inbred lines. He further reported that narrow sense heritability estimates ranged from 20 to 38% for the three crosses with broad sense heritabilities of 80%. Shabana (32), from a study of four Russian varieties, one Novisad's new selected strain and five Novisad's inbred lines obtained broad sense heritability estimates of 98 and 94% for number of days to flowering and leaf number respectively. Oka and Campos (23) reported in a study with sunflower varieties 'Arrowhead' and 'Armavirec' that estimates of heritability and regression coefficients were high for plant height and number of days to flowering. They also observed a positive significant phenotypic correlation between plant height and number of days to flowering.

Pathak (24), in his study of yield components in sunflower, reported a significant correlation of 0.45 between days to flowering and plant height. Moreover significant positive correlations between leaf number and days to flowering, leaf number and plant height, plant height and days to flowering were reported by Shabana (32) in a diallel cross of four lines of sunflower. Kovacik and Skaloud (14) reported that growth rate was correlated with plant height.

MATERIALS AND METHODS

This study was conducted near White, South Dakota, on Vienna loam, udic haploborolls, fine loamy, mixed type soil (40). Eight inbred lines of sunflower (Helianthus annuus L.) were chosen as parents. Selfed seed of S2 plants from PI 386323 and PI 386316 were the short parents. Original seed lots of both of these parents obtained from the USDA Helianthus collection at Ames, Iowa, were very uniform for plant height and will therefore, be considered inbred lines. The other inbred lines were HA 89, HA 124, HA 290, HA 301, HA 302 and CM 408. Table 1 lists the crosses and their pedigrees used to investigate the inheritance of plant height, days to flowering, leaf number, and internode length.

Field and greenhouse facilities were used to develop the various generations. Standard field plot and greenhouse cultural methods were applied during development of genetic material. Plants approaching flowering were covered with "DelNet"[1] synthetic bags to prevent out-crossing. Crosses were made by following the procedure described by Dedio and Putt (7). Two methods were used to break seed dormancy when necessary. A portion of the seed from each cross was treated at 60°C for about 5 hours, placed in dessicator to cool and then germinated. The other part was treated with 0.05% Ethrel (15). Both treatments were effective. Sprouted seeds were planted into vermiculite in 10 cm^2 pots, and after 10 days transplanted to soil beds or 25 x 31 cm glazed pots.

---

[1] Hercules Inc. plastic products, 910 Market Street, Willmington, Delaware 19899.

TABLE 1. Pedigrees of 9 sunflower (*Helianthus annuus* L) crosses used to study plant height, days to flowering, number of leaves and internode length at White, South Dakota, in 1983.

GENERATION	PEDIGREE
P1	PI 386323
P2	HA 290
F1 and F2	PI 386323/HA 290
B1	PI 386323//PI 386323/HA 290
B2	HA 290//PI 386323/HA 290
P1	PI 386323
P2	HA 302
F1 and F2	HA 302/PI 386323
B1	PI 386323//HA 302/PI 386323
B2	HA 302//HA 302/PI 386323
P1	PI 386316
P2	HA 301
F1 and F2	PI 386316/HA 301
B1	PI 386316//PI 386316/HA 301
B2	HA 301//PI 386316/HA 301
P1	PI 386316
P2	CM 408
F1 and F2	CM 408/PI 386316
B1	PI 386316//CM 408/PI 386316
B2	CM 408//CM 408/PI 386316
P1	PI 386323
P2	HA 89
F1 and F2	PI 386323/HA 89
B1	PI 386323//PI 386323/HA 89
B2	HA 89//PI 386323/HA 89
P1	PI 386323
P2	HA 124
F1 and F2	PI 386323/HA 124
B1	PI 386323//PI 386323/HA 124
B2	HA 124//PI 386323/HA 124
P1	PI 386323
P2	HA 301
F1 and F2	PI 386323/HA 301
B1	PI 386323//PI 386323/HA 301
B2	HA 301//PI 386323/HA 301
P1	PI 386316
P2	HA 89
F1 and F2	PI 386316/HA 89
B1	PI 386316//PI 386316/HA 89
B2	HA 89//PI 386323/HA 89
P1	PI 386316
P2	HA 124
F1 and F2	PI 386316/HA 124
B1	PI 386316//PI 386316/HA 124
B2	HA 124//PI 386316/HA 124

F1 crosses were made in the field and greenhouse during 1981. Parental and F1 plants were selfed to produce parental and F2 populations of each cross. B1 was produced by crossing the F1 with the short parent while B2 was produced by crossing the F1 with the tall parent.

All generations including parents, F1s, F2s, and backcrosses were planted in the field on June 3, 1983. Due to shortage of seed of the original S2 selection of PI 386316 used in crosses, seed from a sister selection was used as the parent in the field study. A split plot design with two replications was used with crosses as main plots. There were six subplots in each main plot, consisting of two parents, F1, F2 and backcross generations. Each subplot was composed of variable number of 7 m rows depending upon expected amount of genetic variation. Parents and F1s consisted of 1 row plots, backcrosses were 2 row plots and F2s were 11 row plots. Rows were planted on 76 cm centers with hills spaced 23 cm within a row.

All plants were thinned to one plant per hill 28 days after planting. Poor stands were observed in some plots due to seed dormancy from greenhouse produced seed and downey mildew (Plasmapara halstedii (Far) Berl & de Toni). Trifluralin was applied at the rate of 0.84 kg per hectare before planting and hand weeding was done during the growing season to control weeds. Head clipper (Haploxynehites aemeus) appeared at late bud stage. Insecticides, Permethrin, at the rate of 25 ml per 3.8 liters of water, was hand sprayed and Parathion, at the rate of 0.56 kg per hectare, was applied to protect the plants.

Data on plant population, number of days to flowering, plant height and number of leaves were recorded on each plant in the populations. Internode length was calculated for each plant using data on leaf number and plant height. The procedure used to record observations on each trait was:

Population - Healthy plants in each population.

Flowering date - Number of days from planting to opening of first row of disc flowers on a plant.

Plant height - Distance from soil surface to the center of head held in a vertical position after flowering.

Leaves per plant - Leaves from the base to the top of the stem after flowering. Small leaves on the back of the head and cotyledonary leaves at the base were not considered.

Internode length was calculated for each plant by dividing plant height by number of leaves.

Statistical Analysis:

Means, standard deviations, variances and correlations were calculated for each population on a single plant basis. Methods described by Steel and Torrie (33) were utilized for analysis of variance to establish levels of significance between crosses and among generations in each cross using plot means.

Estimation of Heterosis:

Percent heterosis, either positive or negative, of the F1 over the mid-parent (MP) values for each character was calculated using the methods of Marani (19). The parental means, calculated on the basis of total number of plants of each parent in all the crosses, were used to estimate heterosis, potence ratio, F2, and backcross deviations.

Percent heterosis = (F1 - MP)/MP x 100

where F1 = mean of the F1 generation

MP = (mean of parent 1 + mean of parent 2)/2.

Estimation of the Types of Gene Action:

The strength of dominance expressed by each trait was calculated by the potence ratio method (25) using the following formula.

Potence ratio = (F1 - MP)/(HP - MP) x 100

where MP = calculated mid-parental mean

HP = mean of the parent with high value.

F2 and backcross deviations were calculated as an estimate of epistatic effects in the inheritance of the characters under investigation. F2 deviation was calculated as the percentage decrease of the observed F2 performance from the average of F1 and mid-parental performance. Backcross deviation was calculated as the percentage decrease of the observed backcross performance from the average performance of F1 and the recurrent parent. F-tests were calculated, to test the significance of these effects, based on error terms from analysis of variance (19).

The importance of genetic effects in inheritance of traits included in this study was also determined by generation mean analysis. Data from all plots containing the same generation within replicates were pooled to obtain mean values for plant height, number of days to flowering, number of leaves and internode length. Means were then fitted by unweighted multiple regression to the genetic model of Mather and Jinks (21). The significance of additive and dominance genetic effects plus residuals was determined by fitting the following additive-dominance model to the data (4).

$$\bar{y} = m + a_1 d + a_2 h$$

where $\bar{y}$ = generation mean.

m = slope intercept

d = pooled additive genetic effect

h = pooled dominance genetic effect

a_1 and a_2 = coefficients of the additive and dominance genetic effects.

Estimation of Heritability:

Heritability may be defined as the proportion of the total variation in a population that has a genetic basis. Heritability percentage estimated from the total genetic variance is referred to as broad sense heritability. If heritability is expressed as a percent of the total additive variance, it is known as narrow sense heritability (8).

Broad and narrow sense heritabilities for plant height, number of days to flowering, number of leaves, and internode length were calculated. Estimates of the environmental component of the phenotypic variance were made from the F1 variances (3), average of the parental variances (16) and the average of F1 and parental variances (1). It was assumed that there was equal environmental variance in segregating and non-segregating or homogeneous populations. Estimates of genetic variances for each segregating population were obtained by subtracting the variance of the homogeneous population from the variance of the segregating populations. Parental variances, calculated on the basis of total number of plants of each parent in all crosses were used to estimate heritabilities.

Broad sense heritabilities (h^2) were calculated by the following methods.

1. Mahmud and Kramer (16): $h^2 = VF2-(VP1 \cdot VP2)^{\frac{1}{2}}/VF2$
2. Burton (3): $h^2 = (VF2 - VF1)/VF2$
3. Allard (1): $h^2 = [VF2 - 1/3(VF1+VP1+VP2)]/VF2$

where h^2 is the coefficient of heritability and VP1, VP2, VF1 and VF2 are phenotypic variances for parent 1, parent 2, F1 and F2 respectively.

Narrow sense heritabilities were estimated using Warner's method (39). The additive variance was determined by multiplying F2 variance by two, and subtracting the value from the summed variance of the two backcross populations and then dividing by total phenotypic variance of the F2 population.

$h^2 = [2VF2 - (VB1 + VB2)]/VF2$

where VB1 and VB2 are the variances for backcross populations.

Estimation of Genotypic Correlations:

Genotypic correlations were obtained by using the method of Petr and Frey (25). F2 data were utilized to calculate all possible genotypic correlations among the four traits under study for each cross. F2 genotypic variance for each character was obtained by subtracting the parental variance from the total F2 variance. Similarly genotypic covariances were obtained by subtracting the parental covariance from the observed F2 covariance. The negative parental covariance obtained in some of the crosses presented a problem in calculating the correlations. In such a case, the numerator and denominator were multiplied by -1 to obtain the estimate of correlation (15). The formula used to calculate the genotypic correlations is as follows:

$$rg = [COVF2_{xy} - (COVP1_{xy} \times COVP2_{xy})^{\frac{1}{2}}]/[VF2_{x} - (VP1_{x} \times VP2_{x})^{\frac{1}{2}}(VF2_{y} - (VP1_{y} \times VP2_{y})^{\frac{1}{2}}]^{\frac{1}{2}}$$

Where COV and V represent covariance and variance, respectively, x and y represent the traits being correlated and the P1 and P2 are the parents of the cross.

$COVF2_{xy}$ = total F2 covariance between the characters x and y.

$COVP1_{xy}$, $COVP2_{xy}$ = the covariance between characters x and y of parent 1 and parent 2 respectively.

$VF2_{x}$, $VF2_{y}$ = total F2 variance observed in characters x and y respectively.

$VP1_{x}$, $VP2_{x}$, $VP1_{y}$, $VP2_{y}$ = observed variance of parent 1 and parent 2 in characters x and y respectively.

EXPERIMENTAL RESULTS

Parental Means

Analysis of variance of each trait for the parents is presented in Table 2. There were significant differences among the parents for plant height, number of days to flowering, leaf number, and internode length. Further statistical evaluation of parental means is given in Table 3. Parental means were grouped in three categories based on plant height. Group 1, the short parents, consisted of PI 386316 and PI 386323 with plant heights of 86 and 94 cm, respectively. HA 89, with a plant height of 107 cm and HA 301 with 111 cm, were included in the medium height group. The tallest group consisted of CM 408, HA 124, HA 290 and HA 302 with plant heights of 122, 129, 134, and 136 cm, respectively.

On the basis of significant differences among the parents for days to flowering, parents were grouped in two categories. HA 290, HA 301, HA 302, CM 408, PI 386323, and HA 89 were considered as early flowering parents with flowering dates ranging from 69 to 72 days to flowering. The late flowering group consisted of PI 386316 and HA 124 with 76 and 77 days to flowering, respectively.

HA 124 had the highest leaf number at 37 per plant, whereas HA 290 and HA 301 had the lowest leaf number at 22 and 24 leaves per plant, respectively. There was no significant difference in leaf number among the remaining parents.

The short parents, PI 386316 and PI 386323 had the shortest internode length. The tall parents, HA 290, and HA 302, had the

TABLE 2. Analysis of variance of 4 agronomic traits of sunflower in 8 inbred lines grown at White, South Dakota, in 1983.

		Mean Squares			
Source	df	Plant height	No. of days to flowering	No. of leaves	Internode length
Rep	1	70.56	0.53	0.36	0.07
Genotype	7	676.74**	15.45*	38.40**	2.25**
Error	7	42.33	3.17	1.47	0.03

*Significantly different at the 5% level of probability.
**Significantly different at the 1% level of probability.

TABLE 3. Means and variances for plant height, number of days to flowering, number of leaves and internode length for 8 inbred lines of sunflower grown at White, South Dakota, in 1983.

Inbred lines	No. of Plants	Plant height (cm)		No. of days to flowering		No. of leaves		Internode length (cm)	
		Mean[1]	Variance	Mean[1]	Variance	Mean[1]	Variance	Mean[1]	Variance
PI 386316	77	86.3 d	104.9	75.8 ab	7.3	27.9 b	4.2	3.1 e	0.21
PI 386323	46	93.8 cd	77.5	71.6 bc	3.9	28.3 b	4.4	3.3 e	0.10
HA 89	56	107.4 bc	104.6	72.0 abc	8.0	27.3 b	6.1	4.0 d	0.12
HA 301	27	110.7 b	67.3	70.6 c	13.6	24.4 cd	3.8	4.2 cd	0.15
CM 408	19	121.7 ab	129.4	70.8 c	7.3	27.9 b	3.6	4.4 c	0.21
HA 124	12	129.1 a	444.2	76.6 a	4.8	36.8 a	22.3	3.5 e	0.10
HA 290	19	133.6 a	23.0	69.9 c	4.4	21.6 d	2.4	6.2 a	0.26
HA 302	20	135.8 a	299.2	69.8 c	6.8	25.7 bc	13.6	5.3 b	0.51

[1] means followed by the same letter are not significantly different based on Waller at K-ratio = 100.

longest internodes. However, HA 124, which was one of the tall parents, had one of the shortest internode lengths due to its higher number of leaves.

Crosses

Analysis of variance combined over all crosses for plant height, number of days to flowering, number of leaves per plant and internode length is presented in Table 4. Crosses were significantly different for all traits except days to flowering. Generations within crosses were significantly different for all characters as was the interaction of crosses and generations.

Analysis of variance of individual crosses is presented in Table 5. Generations were significantly different for plant height and internode length in all crosses. There was no difference in flowering between generations of all crosses except PI 386323 x HA 290 and PI 386316 with HA 301 and HA 124. In the case of leaf number per plant, PI 386323 x HA 290 and PI 386316 x HA 124 were the only crosses in which there was a significant difference among generations.

Means for F1s and Segregating Generations

Mean values of the characters studied for the various generations within a cross are presented in Table 6. There was no significant difference between the parents in the crosses PI 386323 x HA 124 and PI 386316 x HA 89. Mean plant height of the F1 generation ranged from a low of 126 cm for the cross PI 386323 x HA 89 to a high to 157 cm for PI 386316 x HA 301. All F1s were taller than the tallest parent. F2 populations were shorter than the F1 tending toward the midparent value.

TABLE 4. Mean squares for plant height, number of days to flowering, leaf number and internode length combined over 9 sunflower (Helianthus annuus L) crosses grown at White, South Dakota, in 1983.

		Plant height	No. of days to flowering	No. of leaves	Internode length
Source	df	Ms	Ms	Ms	Ms
Cross	8	961.28*	19.45	53.96**	1.98**
Rep	1	389.38	2.74	3.70	0.95*
Cross X Rep	8	265.67	8.35	3.31	0.13
Gen[1]	5	6521.79**	14.74**	18.14**	5.97**
Cross X Gen	40	201.24**	5.62*	10.44**	0.40**
Error (b)	45	68.88	2.93	2.72	0.05

* = significantly different at the 5% level of probability.
** = significantly different at the 1% level of probability.

[1] Gen = Parent 1 (P1), Parent 2 (P2), F1, F2, B1 and B2.

TABLE 5. Mean squares for plant height, number of days to flowering, leaf number and internode length of 9 individual sunflower crosses grown at White, South Dakota, in 1983.

		MS			
Source	df	Plant height	No. of days to flowering	No. of leaves	Internode length
		Crosses with PI 386323			
PI 386323 x HA 290					
Gen[1]	5	684.08*	4.40*	24.09*	2.34*
Rep	1	9.52	2.52*	0.62*	0.09
Gen x Rep	5	28.16	0.22	0.09	0.05
HA 302 x PI 386323					
Gen	5	1163.27*	1.46	6.02	1.77*
Rep	1	337.52	35.49	15.97	0.01
Gen x Rep	5	90.95	7.77	3.96	0.08
PI 386323 x HA 89					
Gen	5	235.09*	1.65	2.42	0.16*
Rep	1	51.10	3.38*	0.01	0.06
Gen x Rep	5	19.02	0.62	0.57	0.02
PI 386323 x HA 124					
Gen	5	922.22*	6.03	19.82	0.31*
Rep	1	886.28	5.28	0.84	0.72*
Gen x Rep	5	151.97	6.15	11.71	0.02
PI 386323 x HA 301					
Gen	5	938.83*	3.05	2.61	0.89*
Rep	1	0.51	0.01	2.51	0.05
Gen x Rep	5	67.42	1.99	1.50	0.03
		Crosses with PI 386316			
PI 386316 x HA 301					
Gen	5	1160.08*	21.16*	11.23	1.41*
Rep	1	669.04*	3.33	5.75	0.32*
Gen x Rep	5	49.57	1.60	3.05	0.02
CM 408 x PI 386316					
Gen	5	1155.92*	6.00	2.79	0.96*
Rep	1	432.39*	4.64	0.53	0.70*
Gen x Rep	5	22.49	3.05	0.85	0.01
PI 386316 x HA 89					
Gen	5	726.80*	5.63	5.72	0.70*
Rep	1	5.70	10.43	0.01	0.02
Gen x Rep	5	140.22	3.11	1.47	0.14
PI 386316 x HA 124					
Gen	5	1165.41*	10.37*	26.97*	0.65*
Rep	1	123.02	4.66	3.92	0.01
Gen x Rep	5	50.14	1.87	1.27	0.07

* = significantly different at the 5% level of probability.

[1] Gen = Parent 1 (P1), Parent 2 (P2), F1, F2, B1 and B2.

TABLE 6. Means and variances for plant height, number of days to flowering, leaf number and internode length of parents, F1s, midparental values[1] and segregating generations in 9 sunflower crosses grown at White, South Dakota, in 1983.

		Agronomic Traits							
	Number	Plant height (cms)		No. of days to flowering		No. of leaves		Internode length (cms)	
Crosses/Generations	of plants	Mean[2]	Variance[3]	Mean[2]	Variance[3]	Mean[2]	Variance[3]	Mean[2]	Variance[3]
		Crosses with PI 386323							
PI 386323 x HA 290									
P1	14	100 e	55	72 a	3	28 bc	2	3.6 d	0.1
B1	29	114 d	332**	71 b	8*	31 a	8**	3.7 d	0.4*
MP		117 cd		70 cd		25 d		4.9 c	
F1	39	155 a	36	68 e	3	28 b	3	5.5 b	0.1
F2	407	128 bc	151**	70 cd	7*	27 c	9**	4.7 c	0.5**
B2	44	129 b	85**	70 bcd	6	23 e	11**	5.7 b	0.4*
P2	19	134 b	23	69 de	4	22 ef	2	6.2 a	0.3
HA 302 x PI 386323									
P1	5	90 c	11	71 a	3	29 a	7	3.1 c	0.1
B1	22	113 b	793**	71 a	12	31 a	5	3.7 bc	0.6
MP		113 b		71 a		27 a		4.3 b	
F1	13	150 a	158	71 a	12	28 a	9	5.4 a	0.3
F2	304	145 a	241	71 a	7	30 a	13	4.9 a	0.6
B2	9	92 bc	335	74 a	15*	25 a	14	3.8 b	0.1
P2	20	135 a	299	70 a	7	26 a	14	5.3 a	0.5
PI 386323 x HA 89									
P1	7	95 d	9	72 b	2	28 c	1	3.4 b	0.0
B1	34	115 b	243**	74 a	8*	29 bc	11**	3.9 ab	0.2**
MP		104 cd		72 b		28 bc		3.6 ab	
F1	22	126 a	123*	72 ab	6	31 a	5**	4.1 a	0.1
F2	322	121 ab	147**	71 b	6*	30 ab	12**	4.1 a	0.3**
B2	38	115 b	190**	73 ab	7*	28 bc	13**	4.1 a	0.5**
P2	26	112 bc	61	71 b	4	29 bc	2	3.9 ab	0.1
PI 386323 x HA 124									
P1	11	94 d	92	71 a	4	30 a	2	3.2 d	0.1
B1	23	100 cd	72	70 a	8	28 a	3	3.7 bc	0.2
MP		102 cd		73 a		31 a		3.3 d	
F1	25	154 a	75	71 a	3	34 a	2	4.5 a	0.1
F2	183	127 abc	292	73 a	6	34 a	21	3.8 b	0.3*
B2	35	138 ab	182	74 a	6	37 a	9	3.7 bc	0.1
P2	4	110 bcd	887	75 a	9	33 a	34	3.3 d	0.1
PI 386323 x HA 301									
P1	9	86 de	66	73 a	6	28 a	12	3.1 d	0.0
B1	19	82 e	249**	71 a	11**	28 a	7*	3.0 d	0.1*
MP		96 cd		72 a		27 a		3.5 c	
F1	23	129 a	170	70 a	5	29 a	3	4.5 a	0.2
F2	173	117 ab	188**	71 a	9	29 a	7	4.1 ab	0.3**
B2	47	125 ab	106**	72 a	9	29 a	5	4.3 ab	0.1
P2	13	107 bc	28	72 a	12	27 a	2	4.0 b	0.0
		Crosses with PI 386316							
PI 386316 x HA 301									
P1	19	92 d	58	76 a	7	28 bc	4	3.3 d	0.2
B1	5	105 c	812**	75 ab	32*	32 a	13*	3.3 d	0.4
MP		104 cd		73 bc		27 bc		3.9 c	
F1	37	157 a	78	69 d	3	30 ab	1	5.3 a	0.1
F2	464	135 b	305**	70 cd	12	29 abc	8*	4.7 b	0.4**
B2	52	136 b	171**	69 d	8	28 bc	5	4.8 b	0.2
P2	14	116 c	66	69 d	10	26 c	6	4.5 b	0.1
CM 408 x PI 386316									
P1	18	88 d	86	76 a	8	28 b	5	3.2 d	0.2
B1	29	140 b	887**	72 ab	13	30 ab	7	4.7 b	0.7**
MP		105 d		73 ab		28 b		3.8 c	
F1	20	150 a	213*	72 ab	10	31 a	6	4.9 a	0.2
F2	438	141 ab	332**	73 ab	12*	30 ab	14**	4.8 a	0.6**
B2	58	145 ab	213**	72 ab	10	30 a	6	4.8 a	0.4*
P2	19	122 c	129	71 b	7	28 b	4	4.4 b	0.2
PI 386316 x HA 89									
P1	12	75 c	101	77 a	9	28 abc	4	2.7 c	0.1
B1	43	110 ab	407**	74 ab	12	29 abc	15**	3.8 ab	0.5**
MP		90 c		75 ab		27 bc		3.4 bc	
F1	12	132 a	369**	72 ab	7	31 a	3	4.3 ab	0.6**
F2	232	122 a	318**	72 b	11	28 abc	12*	4.4 a	0.5**
B2	52	123 a	288**	72 ab	8	29 ab	7	4.2 ab	0.3**
P2	30	105 abc	123	72 ab	12	26 c	6	4.0 ab	0.1
PI 386316 x HA 124									
P1	28	89 e	73	75 ab	7	28 e	4	3.2 d	0.2
B1	56	130 c	651**	73 bc	14**	31 d	15**	4.3 ab	0.4**
MP		113 d		77 a		33 bc		3.4 d	
F1	20	155 a	379**	72 c	4	33 bcd	10*	4.7 a	0.1
F2	73	132 c	540**	72 bc	10*	32 cd	15**	4.2 bc	0.5**
B2	40	154 ab	290**	73 bc	12*	35 b	6	4.4 ab	0.2
P2	8	137 bc	38	78 a	1	39 a	7	3.6 cd	0.1

---

[1] MP = calculated midparental value.

[2] means followed by the same letter are not significantly different based on Waller at K-ratio = 100.

[3] variances followed by *, ** are significantly different from a pooled parental variance at the 5% and 1% level of probability, respectively.

Significant decrease in F2 was observed in PI 386323 x HA 290 and crosses of PI 386316 with HA 301 and HA 124. Backcrossing to the short parent reduced the mean plant height below that observed for the F2 but not as short as the recurrent parent except PI 386323 x HA 124 and PI 386323 x HA 301, while backcrossing to the tall parent showed similar heights as in F2s but tended to increase the height above the tall parent. Exceptions to these trends were observed for the crosses of PI 386323 with HA 290, HA 302 and HA 89 and PI 386316 x HA 124.

There was a 4 day range for number of days to flowering, from 68 to 72 days for the F1 generation. Mostly, the F1s were as early or earlier in flowering than the early parent. Generally, the F2s were similar to the F1s in flowering except for PI 386323 x HA 290 in which the F2 was later than the F1. Backcrossing to the early parent produced populations as early flowering as the recurrent parent. Backcrossing to the late parent tended to increase the number of days to flowering above the F2 but lower than the late parent for crosses made with PI 386316.

The average number of leaves per plant of the F1 generation ranged from a low of 28 for the crosses of PI 386323 with HA 290 and HA 302 to a high of 34 leaves for PI 386323 x HA 124. The F1s were equal or higher in leaf number than the parent with the most leaves except for PI 386316 x HA 124 in which the observed number of leaves of the F1 was close to the midparent value. F2 populations reacted like the F1s relative to the parents for all crosses except PI 386323 x HA 290 and PI 386316 x HA 89. Backcrossing to the parent with less number of leaves decreased leaf number below the F2 population but not below the recurrent parent in most crosses. Whereas backcrossing to the parent with higher number of leaves tended to increase leaf number above the F2 and recurrent parent except for cross PI 386316 x HA 124.

Average internode length of the F1 generation ranged from a low of 4.1 cm for the cross PI 386323 x HA 89 to a high of 5.5 cm for the cross PI 386323 x HA 290. The F1s produced internode lengths as long or longer than either parent. F2s were similar to F1s for this trait in most crosses. Backcrossing to the parent with shortest internode decreased the internode length below that observed for F2s in six out of nine crosses. Backcrossing to the parent with longer internode produced BC populations similar to F2s and longer than the recurrent parent in most crosses except PI 386323 x HA 290 and HA 302 x PI 386323.

Variances

Variances for plant height, number of days to flowering, leaf number and internode length are also presented in Table 6. Higher variances for plant height were observed in F1s than their parents in most crosses. The F2 populations exhibited higher variances than their respective F1s for all crosses. Variances of the backcrosses to the short parent were higher than backcrosses to the tall parent except for cross PI 386323 x HA 124. The backcrosses made with PI 386316 showed higher variances than crosses with PI 386323.

Data in Table 6 on days to flowering indicated that variances of the F1s were not significantly different from the pooled parental variance. The F2s had comparatively higher variances than F1s in most crosses. Backcrosses made with the late parent of a cross exhibited a higher variance than backcrosses to the early flowering parent. Data in Table 6 further reveal that backcrosses with PI 386316, which was the latest parent in terms of days to flowering, showed higher variances than the backcrosses made with PI 386323.

Variances of the different generations for leaf number demonstrate that in most crosses F1s did not show significantly different variances from their pooled parental variance. The magnitude of the F2 variances was higher than the F1s. Variances were higher for the backcrosses made with the parents with fewer number of leaves compared to backcrosses with parents with more leaves for crosses, PI 386323 x HA 290 and PI 386316 x HA 124.

For internode length, the variances of the F1s were not significantly different from their pooled parental variance but lower than the F2 generations. Higher variances were demonstrated on backcrossing with the short parents (Table 6).

Frequency Distributions

Frequency distributions of plants for each generation of the individual crosses for plant height, number of days to flowering, leaf number and internode length are presented in Tables 7, 8, 9 and 10, respectively. For plant height, skewness towards tallness was observed in all F2 populations. The F2 generations had a wider distribution of individuals for plant height than any other generation suggesting genetic variation for this trait (Table 7). Transgressive segregates were observed in the F2 and backcross generations.

TABLE 7. Frequency distributions for plant height (cm) of 9 sunflower crosses including parents F1, F2 and both backcross populations grown at White, South Dakota, in 1983.

POPULA-TIONS	Class Midpoints																													X̄
	57.5	62.5	67.5	72.5	77.5	82.5	87.5	92.5	97.5	102.5	107.5	112.5	117.5	122.5	127.5	132.5	137.5	142.5	147.5	152.5	157.5	162.5	167.5	172.5	177.5	182.5	187.5	192.5	194.5	
PI 386323							2	1	2	5	3	1																		100
B1							1	5	12		3	5	2	1																114
F1																		4	7	5	21	2								155
F2					1		1	1	1	5	13	27	$\underline{32}$	73	74	69	51	37	9	8	2			1			1		1	128
B2													10	7	12	3	7	3	2											129
HA 290															2	10	4	3												134
PI 386323						1			2	1	1																			90
B1			1			4	1	4		2				2	1	1		2	1	2	1									113
F1														1			1	2	2	4	1	1	1							150
F2							1			4	2	$\underline{\quad}$	9	13	14	30	41	32	37	29	33	30	19	5	3	1	1			145
B2			1	1	1	1			1	2	1			1																92
HA 302										1	1	1	3		1	1	3	3	2		3	1								135
PI 386323								5		2																				95
B1								3	1	10	1	2	5	1	7	1	2					1								115
F1										2		1	3	2	4	2	8													126
F2						1	1	2	8	$\underline{17}$	27	29	46	62	48	46	20	10	3	1							1			121
B2								1	4	4	8	5	2	6	1	3	3			1										115
HA 89									3	1	4	7	10																	112
PI 386323				1			2	1	4	2	1																			94
B1						2		3	3	7	6	1	1																	100
F1																	2	3	1	6	7	4	2							154
F2				1		1		4	5	$\underline{11}$	10	6	17	19	16	35	25	15	11	2	2		1				1		1	127
B2								1				1	1	3	1	4	5	5	10	2		1	1							138
HA 124						2										1	1													110
PI 386323			1		1	1	2	3	1																					86
B1	3	1		3		1	1	4	6																					82
F1								1		2		3	2	6	6	2	1													129
F2						1	2	4	$\underline{10}$	12	20	22	25	29	19	15	5	5	2		1			1						117
82										1	3	5	4	7	8	9	8	2												125
HA 301										6	1	6																		107
PI 386316					1	3	3	5	4	2	1																			92
B1							1	2	1											1										105
F1																	1	3	4	5	8	8	6	2						157
F2							2	4	14	$\underline{17}$	12	14	30	20	35	40	61	77	48	38	30	10	8	3			1			135
B2										1	1	2	2	2	6	8	5	11	4	7	3									136
HA 301											5	2	3	1	1	2														116
PI 386316				2	3	2	2	5	3	1																				88
B1					1	2	2	2		1	3	2	8	6	1	1														140
F1														1	1	1	3	3	2	4	3						1			150
F2									4	$\underline{9}$	12	11	23	24	22	35	46	58	50	45	35	30	16	6	5	2	1	3	1	141
B2											2		2	2		8	5	7	8	8	10	3	1		2					145
CM 408										2		2	3	5	2	3	1		1											122
PI 386316	1		2	4	1	2	1		1																					75
B1			2	1		1	1	5	3	5	5	4	3	3	1	5		2	2											110
F1										1	2	1					1	2	4	1										132
F2				1	5	2	3	$\underline{7}$	6	18	9	24	16	36	28	25	11	23	5	6	7									122
B2								2	4	3	5	1	9	5	4	3	6	5	2	3										123
HA 89				1	1	1			2	6	7	9	2	1																105
PI 386316		1	1			4	8	8	3	3																				89
B1							4	2	4	6	2	3	3	1	1		6	5	11	4	2	2								130
F1											1		1	2	1			5		2	4	3		1						155
F2						1	1	6	2	2	4	$\underline{3}$	2	2	3	8	7	4	10	5	6	4	2	1						132
B2											1	1	1		1	1	2	1	3	8	3	6	5	4	2	1				154
HA 124															1	1	3	2	1											137

Class midpoints containing midparental values are underlined in F2 populations.

TABLE 8. Frequency distributions for number of days to flowering of 9 sunflower crosses including parents, F1, F2 and backcross populations grown at White, South Dakota, in 1983.

POPULATIONS	Class Midpoints																			X̄
	61.5	62.5	63.5	64.5	65.5	66.6	67.5	68.5	69.5	70.5	71.5	72.5	73.5	74.5	75.5	76.5	77.5	78.5	79.5	
PI 386323								1	2	2	3	5			1					72
B1	1				2		3		13		5		4		1					71
F1				1	11	9	7	3	5	1	1	1								68
F2		1	2	3	7	34	37	72	67	57	44	19	35	12	9	4	4			70
B2					2	9	7	4	7	3	5	4		3						70
HA 290					5		8		4		1		1							69
PI 386323							1			2	2									71
B1					5		5		5		2		2		3					71
F1			1		1		3				5		1		2					71
F2				1	4	16	29	40	47	41	25	24	38	17	14	8				71
B2			1								1		5		2					74
HA 302					2		9		2		6		1							70
PI 386323									2	2		3								72
B1							1		5	3	2	4	6	2	3	6	2			74
F1							1	3	4	1	2	3	5	2	1					72
F2						2	7	22	46	56	52	35	32	30	27	3	9		1	71
B2						1		2	5	6	6	5	3	4	3	2	1			73
HA 89								3	8	6	4		3	1		1				71
PI 386323							2	2	1	1	3	1	1							71
B1					2		7		8		4				1		1			70
F1							2	6	4	7	3	1	1		1					71
F2						1	2	8	19	18	21	26	27	20	25	11	4	1		73
B2								1	2	2	3	5	5	3	8	4	2			74
HA 124										1			1		1		1			75
PI 386323								1	2	1			2	3						73
B1			2		2		2		7				6							71
F1					2		9		8		3				1					70
F2			1	2	7	9	10	18	26	23	17	20	7	14	12	6		1		71
B2						1	2	3	12	3	2	7	5	2	5	3	2			72
HA 301					1		3		2		1		4		2					72
PI 38616									2		2		3		7		5			76
B1			1										1		1		2			75
F1					1	5	11	9	5	2	3			1						69
F2		6	4	11	21	33	50	67	40	52	52	26	23	25	20	8	18	7	1	70
B2				1	8	3	12	11	4	7	1		2			3				69
HA 301			3		3		2		3		2		1							69
PI 386316									1		3		1		5		8			76
B1					2		6		8		2		5		5		1			72
F1					2		4		5		3		2		4					72
F2				1	1	10	16	32	28	51	28	27	41	44	48	28	50	19	14	73
B2					1	2	6	3	9	8	2	9	3	4	4	4	3			72
CM 408					2		3		8		2		3		1					71
PI 386316									1		1		2		2		5		1	77
B1					1		1	6	2	5	2	1	3	7	5	5	3	2		74
F1								2	2		3	1	1		3					72
F2	1			1	7	13	10	28	31	29	19	23	17	17	15	11	6	4		72
B2					1	1	2	6	5	3	7	10	5	5	5	1		1		72
HA 89					1		3	7	4	1		1	5	2	2	4				72
PI 386316									1	1	4	2	1	2	7	1	7	2		75
B1					1	4	4	6	4	2	5	8	3	1	6	4	6	2		73
F1								2	4	4	4	1	2	2	1					72
F2							8	9	13	4	6	10	2	2	9	6	3	1		72
B2						2	1	5	7		3	6	2	3	4	3	3	1		73
HA 124																4	3	1		78

Class midpoints containing midparental values are underlined in F2 populations.

TABLE 9. Frequency distributions for number of leaves of 9 sunflower crosses including parents, F1, F2 and backcross populations grown at White, South Dakota, in 1983.

Class Midpoints

POPULATIONS	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	x̄
PI 386323												1		2	8	1	1	1																			28
B1														1	4	3	2	5	4	2	2	2	4														31
F1												4	2	4	10	12	6				1															28
F2				1				7	16	20	33	32	42	63	49	45	36	25	21	6	5	4	1	1													27
B2				1	6	7	7	4	2	3	1	4	5	1	3																				23
HA 290					1	4	5	4	3	1	1																								22
PI 386323													1		2				2																			29
B1													1		7		7		5		1		1															31
F1								1		1		4		2		3		2																			28
F2							1	7	6	5	21	15	20	33	17	30	46	33	28	16	8	9	4	2	3											30
B2						2		1		2		2		1		1																				25
HA 302				1	1		1		2		2	6	3		1	1	1		1																		26
PI 386323														1	3	3																						28
B1										3		7		10		7		4		2						1										29
F1														3	2	1	1	4	5	4	2																31
F2					1	1		1	7	11	14	16	20	37	27	35	43	34	29	22	9	6	3	5	1										30
B2				1		1				4		7		11		10		1		2				1											28
HA 89										1		1	3	3	10	6	2																			29
PI 386323														2		1	5	3																				30
B1												3	3	6	6	2		3																				28
F1																				4	2	5	12	1		1												34
F2								1		3		7		26		22		25		36		32		16		5		4		5					1	34
B2																			3		5		9		13		3		1						1		37
HA 124														2									1		1												33
PI 386323								2				1		3		2		1																			28
B1								2		3		1		8		4		1																			28
F1														6	4	6	3	3		1																29
F2							1	1		7	9	12	17	26	32	22	21	8	9	4	3	1														29
B2								1				1	1	5	9	6	8	8	5	2	1																29
HA 301													7	1	3	2																					27
PI 386316												2	4	5	1	3	2	1	1																			28
B1													1				2				1		1														32
F1														1	2	13	10	10	1																			30
F2						3		4	5	17	20	47	59	73	71	57	39	27	18	14	5	4			1										29
B2								1		2	3	5	6	7	14	9	2	1	1	1																	28
HA 301								3		2		5		3		1																					26
PI 386316								1		1		6		7		2		1																			28
B1										1	1		5	2	4	4	6	2	1	2	1															30
F1													3		4		5		6		1		1															31
F2			1		1	2	3	4	7	10	27	18	37	38	43	42	53	42	40	24	20	14	7	1	1	1	2								30
B2								1				1		5	9	5	9	8	9	6	4		1															30
CM 408										2		2	2	7	2	3	1																					28
PI 386316												1	2	2	5			1	1																			28
B1						2		1	1	1	2	2	3	7	5	4	5	5	1	1			3														29
F1															2			6	2	1	1																	31
F2				1		2	3	8	6	11	12	21	35	31	28	17	18	17	9	7	1	2	2		1												28
B2										2	3	7	7	5	3	7	6	8	4																		29
HA 89		1				1				6		14		7		1																					26
PI 386316										1	1	5	7	5	3	2	2	2																			28
B1								1	2	3	3	1	1	3	6	4	9	6	4	7	2	1	2	1													31
F1												2		2		1		4		7		4															33
F2							1		1	1		4	1	6	5	6	8	6	9	6	5	4	6	2	1	1										32
B2															2		1	2	5	3	9	9	4	2	1	1	1										35
HA 124																							2		5						1						39

Class midpoints containing midparental values are underlined in F2 populations.

TABLE 10. Frequency distributions for internode length (cm) of 9 sunflower crosses including parents, F1, F2 and backcross populations grown at White, South Dakota, in 1983.

	Class Midpoints																															
POPULATIONS	2.1	2.3	2.5	2.7	2.9	3.1	3.3	3.5	3.7	3.9	4.1	4.3	4.5	4.7	4.9	5.1	5.3	5.5	5.7	5.9	6.1	6.3	6.5	6.7	6.9	7.1	7.3	7.5	7.7	7.9	8.1	8.3	$\bar{X}$
PI 386323						2		7	3	1	1																						3.6
B1			1		1	4	4	4	2	2	4		3	2	2																		3.7
F1												1				5	9	10	9	3		2											5.5
F2				1			4		34			107		124			89		33			11		2		1						1	4.7
B2														1	4	5	2	7	7	4	4	2	3	2	1	2							5.7
HA 290																	2		2	1	3	2	2	5	1	1							6.2
PI 386323					2		3																										3.1
B1			1	1	3	2	2	3			3	2	3		2																		3.7
F1													1	2		2	2	2	1	1	2												5.4
F2				1			1	3	14	16	29	31	27	23	27	22	22	24	14	19	13	11	3	1	2	1							4.9
B2						1	1	1	1	4	1																						3.8
HA 302									2					2		1	2	8		1	2	1	1										5.3
PI 386323						1	3	3																									3.4
B1						1	5	4	2	5	7	6	2			1	1																3.9
F1								1	1	5	7	5	2	1																			4.1
F2			1		4	8	19	31	42	49	46	30	29	20	19	13	5	3			2	1											4.1
B2							3	4	6	4	5	6	5	2			1			1					1								4.1
HA 89						1	2		4	9	7	1	1	1																			3.9
PI 386323		1			1	1	4	3	1																								3.2
B1				2			3		13		5																						3.7
F1										2	4	3	7	5	1	3																	4.5
F2			1	2	4	9	25	28	29	31	29	13	4	1	5						1								1				3.8
B2					2		5	2	14	5	4	2		1																			3.7
HA 124						2			1	1																							3.3
PI 386323				1	1	3	4																										3.1
B1		2	3	1	1	6	4	2																									3.0
F1								1	3			4	13			2																	4.5
F2					2		11	20	18	19	39	27	17	7	6	2	3			1							1						4.1
B2									1	8	12	12	7	6		1																	4.3
HA 301									1	7	3	2																					4.0
PI 386316			1		3	5	3	2	2	2	1																						3.3
B1					2	2						1																					3.3
F1													2	2	3	5	9	9	6	1													5.3
F2					1	4	3	8	12	23	33	46	48	74	63	44	48	23	15	13	3	1	1	1									4.7
B2										1	2	7	6	5	8	11	6	6															4.8
HA 301										2	1	4	1	3	2	1																	4.5
PI 386316			1	4	1	2	3	3	4																								3.2
B1					1	1		4			3		7			8		5															4.7
F1											3	7				7		3															4.9
F2					3		8	6	16	21	45	51	37	52	49	39	36	25	12	10	8	7	1	2	3	3	1	1	1	1			4.8
B2							1	1	1	1	1	6	8	13	8	5	4	4	4							1							4.8
CM 403								1	1	1	4	1	4	2	3	2																	4.4
PI 386316		3	1	4	1	3																											2.7
B1			1		3	4	6	4	4	6	1	6	1	1	4		1	1															3.8
F1							4						2	4			2																4.3
F2		1		4	2	6	5	14	13	24	25	29	27	16	26	17	7	7	2	3	2	1	1										4.4
B2							1	5	4	5	14	5	7	4	3	1	1	1		1													4.2
HA 89					1			3	1	7	6	10	1	1																			4.0
PI 386316	1	1	1	1	3	6	5	5	3	1	1																						3.2
B1				2	1		1	4	7	2	6	6	6	10	5	3	3																4.3
F1										1		2	4	3	7	3																	4.7
F2				1	1	4	9	2	6	4	11	6	8	8	7	3	1		1				1										4.2
B2						1		1	4	2	3	7	6	6	3	6	1																4.4
HA 124						1	2		4	1																							3.6

Class midpoints containing midparental values are underlined in F2 populations.

Data on frequency distributions for days to flowering presented in Table 8 showed the occurrence of considerable segregation in the F2 generations with individuals exceeding both early and late parents in the crosses with PI 386323. However, in crosses of PI 386316 with HA 89 and HA 124, transgressive segregates were observed only for earliness. Although the amount of segregation in backcross generations is quite high, the maximum segregation was observed in F2 generations, showing genetic variation in the segregating populations for days to flowering.

Frequency distributions of the parents, F1, F2 and backcross generations for number of leaves per plant presented in Table 9 demonstrate that the maximum plant to plant variation again occurred in F2 populations. Segregates with higher number of leaves than either parent were observed in F2 populations.

Data presented in Table 10 demonstrate highest amount of variability in the F2 populations for internode length. Short internode parental types were recovered in the F2 and B1 populations.

Heterosis and Potence Ratio Values

Heterosis and potence ratio values were positive for plant height, number of leaves per plant, and internode length in all crosses (Table 11). The magnitude for leaf number, and internode length was lower than that observed for plant height. This is to be expected for internode length since it is a calculated value based on plant height and leaf number. Crosses with PI 386323 tended to give lower levels of heterosis for plant height than crosses with PI 386316. The lowest level of heterosis for plant height was observed in crosses of PI 386323

TABLE 11. Percent Heterosis and Potence Ratio calculated for plant height, number of days to flowering, leaf number and internode length of 9 sunflower crosses grown at White, South Dakota, in 1983.

CROSSES	Plant height		No. of days to flowering		No. of leaves		Internode length	
	Heterosis	Potence Ratio	Heterosis	Potence Ratio	Heterosis	Potence Ratio	Heterosis	Potence Ratio
				Crosses with PI 386323				
PI 386323 x HA 290	36	208	-4	-180	13	100	15	51
HA 302 x PI 386323	30	165	1	68	5	98	23	100
PI 386323 x HA 89	26	380	0	159	11	300	12	130
PI 386323 x HA 124	37	239	-5	-138	5	43	31	900
PI 386323 x HA 301	26	314	-2	-215	10	132	18	151
				Crosses with PI 386316				
PI 386316 x HA 301	59	479	-6	-160	14	210	44	284
CM 408 x PI 386316	49	260	-2	-70	9	-[1]	32	188
PI 386316 x HA 89	36	332	-2	-76	13	700	20	161
PI 386316 x HA 124	44	220	-6	-900	2	11	43	721

Percent Heterosis = (F1-MP)/MP x 100   Potence Ratio Percent = (F1-MP)/(HP-MP) x 100

where F1 = mean of the F1 generation
MP = midparental value
HP = mean of the parent with high value
[1] = no difference between the high parent and midparent

with HA 89 and HA 301. Potence ratio values were highly variable ranging from 11 to 700% for leaf number and from 51 to 900% for internode length. Crosses with the lowest level of heterosis had the lowest potence ratio values for both traits. However, crosses with higher levels of heterosis did not always have higher potence ratio values.

F2 and Backcross Deviations

F2 and backcross deviations for the traits studied in all crosses are presented in Table 12. F2 deviation was calculated as the percentage decrease of F2 performance from the average of F1 and mid-parental performance. Backcross deviation was calculated as the percentage decrease of backcross performance from the average performance of F1 and the recurrent parent. F2 performance would be expected to be near the average of F1 and mean parental performance if epistasis is not effective. A significant F2 deviation from this average indicates epistatic gene action. Similarly, when no effects of epistasis are assumed, backcross performance should be expected to be near the average of F1 and recurrent parent performance (19).

In most crosses the F2s were taller than the average of the F1 and the midparent values. A significant F2 deviation for plant height was observed in the cross CM 408 x PI 386316. Significant B1 and B2 deviations were observed for plant height in PI 386323 x HA 290, PI 386323 x HA 124 and CM 408 x PI 386316. Generally there were no significant Fs, B1, or B2 deviations observed for any of the other traits. The data suggest lack of epistasis for the traits studied in these crosses.

TABLE 12. F2 and backcross deviation percentage for plant height, number of days to flowering, number of leaves and internode length of 9 sunflower crosses grown at White, South Dakota, in 1983.

	Plant height			No. of days to flowering			No. of leaves			Internode length		
Crosses	F2	B1	B2	F2	B1	B2	F2	B1	B2	F2	B1	B2
						Crosses with PI 386323						
PI 386323 x HA 290	5	9	10*	-1	-2	2	-3	-8*	8	8	16	2
HA 302 x PI 386323	-10	8	36	0	1	-5	-8	-8	0	-1	16*	31
PI 386323 x HA 89	-7	-4	2	1	-3	-1	-2	1	3*	-5	-6*	-1
PI 386323 x HA 124	5	19*	2	-1	1	-1	-1	12	-10	5	6	7
PI 386323 x HA 301	1	26	-4	-1	0	-3	-5	3	-10	1	24	2**
						Crosses with PI 386316						
PI 386316 x HA 301	-6	13	-2	2	-3	1	3	-11	-4	-6	22*	-2
CM 408 x PI 386316	-11*	-18	-7*	1	2	-1	3	-2	-4	-10	-16	-3
PI 386316 x HA 89	-6	0	-2	2**	1	0	4	2	1	-11	-3	-2
PI 386316 x HA 124	-1	-8	-9	2*	2	2	2	0	-1	-4	-9	-8

F2 Deviation Percentage = $[\frac{1}{2}(F1 + MP)-F2]/\frac{1}{2}(F1 + MP) \times 100$ - *,** indicates significance at the 5% and 1% level of probability from the average of the F1 and MP values.

B1 Deviation Percentage = $[\frac{1}{2}(F1 + P1)-B1]/\frac{1}{2}(F1 + P1) \times 100$ - *,** indicates significance at the 5% and 1% level of probability from the average of F1 and P1.

B2 Deviation Percentage = $[\frac{1}{2}(F1 + P2)-B2]/\frac{1}{2}(F1 + P2) \times 100$ - *,** indicates significance at the 5% and 1% level of probability from the average of F1 and P2.

where P1 = mean of low parent
P2 = mean of high parent
MP = calculated midparental value
B1 = mean of the backcross with low parent
B2 = mean of the backcross with high parent

Generation Mean Analysis

Analysis of variance of generation means for plant height, days to flowering, leaf number and internode length is presented in Table 13. Only additive and dominance effects were included in the model. Significant additive and dominance gene effects for plant height were observed in all crosses except for PI 386323 x HA 124 and PI 386316 x HA 89, in which only the dominance effect was significant. A significant residual effect was expressed for crosses of PI 386323 with HA 290, HA 302, HA 301 and CM 408 x PI 386316. Generally dominance genetic effects were of a higher magnitude than additive genetic effects with the exception of PI 386323 x HA 301 and PI 386316 x HA 124. For number of days to flowering, significant additive and dominance effects were observed for crosses, PI 386323 x HA 290 and PI 386316 x HA 301 and additive effect for CM 408 x PI 386316. A significant residual effect was observed only in the cross PI 386323 x HA 290.

Data in Table 13 for leaf number indicate a highly significant additive effect for crosses PI 386323 x HA 290 and PI 386316 x HA 124, while significant dominance effects were observed for crosses PI 386323 x HA 290, PI 386323 x HA 89, CM 408 x PI 386316 and PI 386316 x HA 89. A significant residual effect was present only for the cross PI 386323 x HA 290. Generally significant additive and dominance effects were observed for internode length. Five out of nine crosses were also significant for residual effects.

Percent of the total genetic variation contributed by each component for plant height, number of days to flowering, number of

TABLE 13. Analysis of variance of generation means for plant height, number of days to flowering, number of leaves and internode length in 9 crosses of sunflower grown at White, South Dakota, in 1983.

Source of Variation	PI 386323 x HA 290	HA 302 x PI 386323	PI 386323 x HA 89	PI 386323 x HA 124	PI 386323 x HA 301	PI 386316 x HA 301	CM 408 x PI 386316	PI 386316 x HA 89	PI 386316 x HA 124
					Plant height				
Block	9.52	337.52	51.10	886.28	0.15	669.04*	432.39**	5.70	123.02
Generations									
Additive	1319.09**	1491.61**	255.43*	967.94	1761.57**	1149.20**	1393.84**	925.56	2973.62**
Dominance	1620.33**	1614.73**	816.18**	2627.65**	1359.65**	4151.23**	3846.54**	2506.81**	2654.24**
Residual	160.06*	903.34*	34.61	338.51	524.31*	133.32	179.74*	67.22	66.40
Error	28.16	90.95	19.02	151.97	67.42	49.57	22.49	140.22	50.14
					Number of days to flowering				
Block	2.52*	35.49	3.38	5.28	0.01	3.33	4.64	10.43	4.46
Generations									
Additive	10.77*	4.00	0.69	21.21	0.95	79.52**	21.97*	17.45	4.56
Dominance	7.18*	1.08	1.87	0.92	7.94	15.97*	4.84	6.55	40.33**
Residual	1.34*	0.74	1.90	2.67	2.12	3.43	1.06	1.38	2.32
Error	0.22	7.77	0.62	6.15	1.99	1.60	3.05	3.11	1.87
					Number of leaves				
Block	0.62*	15.97	0.01	0.84	2.51	5.75	0.53	0.01	3.92
Generations									
Additive	85.31**	11.23	0.02	46.27	0.79	16.75	0.18	3.49	132.14**
Dominance	17.94**	4.36	8.02*	17.61	6.36	19.94	11.95*	22.65**	1.01
Residual	5.73**	4.83	1.36	11.74	1.96	6.49	0.61	0.83	0.57
Error	0.09	3.96	0.57	11.71	1.50	3.05	0.85	1.47	1.27
					Internode length				
Block	0.09	0.01	0.06	0.72*	0.05	0.32*	0.70*	0.02	0.01
Generations									
Additive	10.47**	3.92**	0.33**	0.04	2.00**	3.27**	1.66**	1.80*	0.17
Dominance	0.28	1.08*	0.38**	1.27**	0.90**	2.40**	2.62**	1.23*	2.93*
Residual	0.32*	1.29*	0.03	0.08	0.48**	0.47**	0.17**	0.15	0.06
Error	0.05	0.08	0.02	0.02	0.03	0.02	0.01	0.14	0.07

*significantly different at 5% level of probability.
**significantly different at 1% level of probability.

leaves and internode length is presented in Table 14. It is shown in Table 14 that dominance effects for plant height were higher than the additive effects and ranged from 28% for HA 302 x PI 386323 to 69% for PI 386323 x HA 89. Additive gene effects were highest for PI 386316 x HA 124 at 39% and lowest for PI 386323 x HA 124 at 21%. Residual effects for crosses made with PI 386323 ranged from 9% for PI 386323 x HA 89 to 47% for HA 302 x PI 386323. The highest contributions to genetic variability for plant height were from dominance effects. The residual effects were minimum except for crosses of PI 386323 with HA 302, HA 124 and HA 301. Crosses with PI 386316 resulted in higher dominance effect than the crosses with PI 386323.

Percentage of variation which contributed to total genetic variation for number of days to flowering (Table 14) showed that contribution of 49, 75 and 75% from the additive effects were observed for the crosses PI 386323 x HA 290, PI 386316 x HA 301 and CM 408 x PI 386316 respectively. The highest contribution of 98% from additive effect to the total genetic variability for leaf number was demonstrated for cross PI 386316 x HA 124. High contributions of 66, 86 and 79% from dominance effect resulted in crosses, PI 386323 x HA 89, CM 408 x PI 386316 and PI 386316 x HA 89 respectively. Residual contributions tended to be smaller than either dominance or additive effects. However, crosses made with PI 386323 have exhibited higher values of residual effects as compared to crosses made with PI 386316.

For internode length, the additive effects ranged from a high of 89% for PI 386323 x HA 290 to a low of 2% of the total genetic variation

TABLE 14. Percentage of genetic variation due to additive or dominance gene action plus the residual for plant height, number of days to flowering, number of leaves and internode length among generation means of 9 sunflower crosses grown at White, South Dakota, in 1983.

	PI 386323 x HA 290	HA 302 x PI 386323	PI 386323 x HA 89	PI 386323 x HA 124	PI 386323 x HA 301	PI 386316 x HA 301	CM 408 x PI 386316	PI 386316 x HA 89	PI 386316 x HA 124
				Plant height					
Additive	39	26	22	21	38	20	24	25	51
Dominance	47	28	69	57	29	73	67	69	46
Residual	14	47	9	22	33	7	9	6	3
				Number of days to flowering					
Additive	49	55	8	70	6	75	73	62	9
Dominance	33	15	23	3	52	15	16	23	78
Residual	18	32	69	27	42	10	11	15	13
				Number of leaves					
Additive	71	37	0	47	6	30	1	12	98
Dominance	15	15	66	18	49	36	86	79	1
Residual	14	48	34	36	45	34	13	9	1
				Internode length					
Additive	89	44	41	2	46	46	35	52	5
Dominance	2	12	47	83	21	34	55	35	90
Residual	8	44	12	17	33	20	10	13	5

for PI 386323 x HA 124. Cross PI 386323 x HA 124 has demonstrated the highest dominance effect of 90% while the lowest value of 2% was recorded for PI 386316 x HA 124. High residual effects of 44 and 33% were recorded for crosses HA 302 x PI 386323 and PI 386323 x HA 301 respectively. The remaining crosses exhibited low residual effect for the inheritance of internode length.

Heritabilities

Estimates of broad sense heritabilities based on three different methods of calculation and narrow sense heritabilities are presented in Table 15. Average broad sense heritability values for plant height ranged from 29% for cross PI 386323 x HA 89 to 73% for crosses PI 386323 x HA 290 and PI 386316 x HA 301. HA 301 showed highest heritability value when crossed with PI 386316 as compared to cross with PI 386323. The estimates of broad sense heritability were similar in crosses of HA 89 and HA 301 with the both short parents. Observed narrow sense heritability estimates were highly variable ranging from a low of 10 to a high of 113. The average broad sense heritabilities for days to flowering ranged from 3% for cross PI 386323 x HA 89 to 50% for cross PI 386316 x HA 124. Narrow sense heritabilities were very low as compared to broad sense heritabilities for this trait.

The broad sense heritabilities for leaf number were again generally higher than estimates of narrow sense heritability. Data in Table 15 on internode length indicate high broad sense heritability estimates for most of the crosses. High narrow sense heritability estimates obtained for PI 386323 crosses with HA 302, HA 124 and HA 301

TABLE 15. Estimates of percent heritability for plant height, number of days to flowering, leaf number and internode length of 9 sunflower crosses grown at White, South Dakota, in 1983.

	Plant Height (cm)					Days to Flowering				
CROSSES	I	II	III	$\bar{X}$	IV	I	II	III	$\bar{X}$	IV
CROSSES with PI 386323										
PI 386323 x HA 290	72	76	70	73	-76	39	49	42	43	-11
HA 302 x PI 386323	37	34	26	32	-269	29	-64	-4	29	-162
PI 386323 x HA 89	39	16	31	29	-95	4	5	1	3	-42
PI 386323 x HA 124	37	74	32	48	113	29	43	33	35	-31
PI 386323 x HA 301	61	9	44	38	10	20	48	18	29	-11
CROSSES with PI 386316										
PI 386316 x HA 301	72	74	73	73	-122	19	74	35	43	-123
CM 408 x PI 386316	65	36	55	52	-131	40	16	32	29	8
PI 386316 x HA 89	67	-16	39	53	-19	28	34	30	31	13
PI 386316 x HA 124	60	30	43	44	26	43	59	47	50	-49
	Number of Leaves					Internode Length (cm)				
CROSSES with PI 386323										
PI 386323 x HA 290	66	67	65	66	2	67	73	67	69	49
HA 302 x PI 386323	40	33	31	35	55	63	57	52	57	90
PI 386323 x HA 89	56	55	55	55	2	68	79	72	73	-26
PI 386323 x HA 124	52	90	54	65	141	67	57	63	62	100
PI 386323 x HA 301	42	62	49	51	28	58	41	52	50	124
CROSSES with PI 386316										
PI 386316 x HA 301	49	85	61	65	-33	51	64	55	57	44
CM 408 x PI 386316	72	55	65	64	102	64	61	63	63	27
PI 386316 x HA 89	56	74	62	64	7	68	-14	40	54	46
PI 386316 x HA 124	36	30	18	28	60	70	80	72	74	67

I - Broad Sense Heritability Method I: $h^2 = [VF2 - (VP1 \times VP2)^{1/2}]/VF2 \times 100$
II - Broad Sense Heritability Method II: $h^2 = (VF2 - VF1)/VF2 \times 100$
III - Broad Sense Heritability Method III: $h^2 = [VF2 - 1/3\ (VP1 + VP2 + VF1)]/VF2 \times 100$
$\bar{X}$ - Average of Methods I, II and III.
IV - Narrow Sense Heritability: $h^2 = [2VF2 - (VB1 + VB2)]/VF2 \times 100$
where VP1, VP2, VF1, VF2, VB1 and VB2 are the variances of parent 1, Parent 2, F1, F2, B1 and B2 populations respectively.

indicate the importance of additive gene action for the inheritance of internode length in these crosses.

Correlations

The phenotypic and genotypic correlations among the characters studied are presented in Tables 16 and 17 respectively. Genotypic correlations were generally higher than the phenotypic correlations. In some crosses positive phenotypic correlations became negative genotypic correlations. Genotypic correlations among different traits in crosses of PI 386323 with HA 124, HA 301 and in some other crosses were erratic due to the negative values of parental covariances.

Highest positive phenotypic and genotypic correlations among the characters studied were found between plant height and internode length, whereas highest negative correlations were observed between leaf number and internode length. Strong positive correlations were obtained between plant height and leaf number with the exception of crosses, PI 386316 x HA 301 and PI 386323 x HA 290, in which significant positive correlation values became negative values for genotypic correlation. Number of days to flowering was significantly negatively correlated with leaf number and plant height for cross PI 386323 x HA 290. However, significant positive phenotypic correlations were observed for PI 386316 crosses with HA 302, CM 408, HA 89 and HA 124. Cross PI 386323 x HA 124 showed significant negative phenotypic correlation between days to flowering and internode length.

TABLE 16. Phenotypic correlations of 4 agronomic traits in 9 sunflower crosses grown at White, South Dakota, in 1983.

Crosses/ Generations	No. of observations	Flower vs. leaf no.	Flower vs. height	Flower vs. internode length	Leaf no. vs. height	Leaf no. vs. internode length	Height vs. internode length
			Crosses with PI 386323				
PI 386323 x HA 290							
PI 386323	14	-0.44	-0.19	0.12	0.47	-0.21	0.77**
HA 290	19	-0.15	-0.23	0.03	-0.19	-0.91**	0.57**
F2	407	-0.14**	-0.19**	-0.04	0.13**	-0.70**	0.60**
HA 302 x PI 386323							
PI 386323	5	-0.73	-0.25	0.66	0.32	-0.92*	0.08
HA 302	20	-0.13	-0.23	-0.04	0.47*	-0.64**	0.36
F2	304	-0.14*	-0.08	0.05	0.04	-0.74**	0.64**
PI 386323 x HA 89							
PI 386323	7	0.29	0.28	0.02	-0.30	-0.77*	0.84*
HA 89	26	0.10	-0.21	-0.22	-0.01	-0.63**	0.78**
F2	322	0.04	-0.05	-0.07	0.16**	-0.71**	0.56**
PI 386323 x HA 124							
PI 386323	11	-0.21	-0.38	-0.25	0.11	-0.36	0.88**
HA 124	4	0.82	0.86	0.91	0.99**	0.97*	0.99*
F2	183	0.26**	0.09	-0.17*	0.48**	-0.45**	0.55**
PI 386323 x HA 301							
PI 386323	9	-0.15	-0.34	-0.14	0.88**	-0.70*	-0.29
HA 301	13	0.70**	0.63*	0.01	0.54	-0.40	0.56*
F2	173	-0.04	-0.06	-0.03	0.28**	-0.47**	0.71**
			Crosses with PI 386316				
PI 386316 x HA 301							
PI 386316	19	-0.20	-0.09	0.06	-0.22	-0.72**	0.83**
HA 301	14	-0.64*	-0.12	0.63*	0.54*	-0.69**	0.23
F2	464	0.08	0.09	0.03	0.42**	-0.34**	0.71**
CM 408 x PI 386316							
PI 386316	18	0.04	-0.08	-0.08	0.03	-0.63**	0.76**
CM 408	19	0.59**	0.47*	0.01	0.21	-0.50*	0.74**
F2	438	0.46**	0.28**	-0.13	0.26**	-0.60**	0.60**
PI 386316 x HA 89							
PI 386316	12	0.45	-0.06	-0.39	0.59*	0.04	0.83**
HA 89	30	-0.18	-0.40	-0.25	0.63**	-0.38**	0.47**
F2	232	0.24**	0.31**	0.09	0.29**	-0.49**	0.68**
PI 386316 x HA 124							
PI 386316	28	0.44*	-0.45*	-0.52*	-0.48**	-0.81**	0.89**
HA 124	8	-0.24	-0.68	-0.21	-0.14	-0.84	0.65
F2	73	0.09	0.26*	0.20	0.48**	-0.25*	0.72**

* Significantly different at 5% level of probability.

** Significantly different at 1% level of probability.

TABLE 17. Genotypic correlations between 4 agronomic traits in 9 sunflower crosses grown at White, South Dakota, in 1983.

Crosses	Flower vs. Leaf Number	Flower vs. Plant Height	Flower vs. Internode Length	Leaf Number vs. Plant Height	Leaf Number vs. Internode Length	Plant Height vs. Internode Length
				CROSSES with PI 386323		
PI 386323 x HA 290	-0.38	-0.44	-0.11	-0.08	-1.07	0.57
HA 302 x PI 386323	-1.13	-0.31	0.04	-0.31	-2.82	0.82
PI 386323 x HA 89	0.01	0.18	0.13	0.34	-0.92	0.51
PI 386323 x HA 124	0.04	38.18	6.85	2.31	2.23	-0.06
PI 386323 x HA 301	1.73	1.22	-0.16	0.04	-1.02	-0.78
				CROSSES with PI 386316		
PI 386316 x HA 301	-0.47	0.09	-0.17	-0.54	-1.47	0.86
CM 408 x PI 386316	0.77	-0.38	0.28	0.35	-1.15	0.54
PI 386316 x HA 89	-0.31	1.14	-0.24	0.09	0.78	0.72
PI 386316 x HA 124	-0.01	0.21	0.16	0.57	-0.74	0.73

DISCUSSION

The main objective of this study was to investigate the inheritance of plant height plus the related agronomic characteristics, days to flowering, leaf number and internode length in sunflower crosses. Eight inbred lines were chosen and used to develop nine crosses, their F1, F2 and backcross populations, included in this study. The parental lines represented a wide range in plant height, number of days to flowering, leaf number and internode length and were significantly different for all traits (Tables 2,3). PI 386316 and PI 386323 were shorter than the other inbred lines averaging 86 cm and 94 cm respectively. These lines also had the shortest internode length but differed in days from planting to flowering with PI 386323 being four days earlier than PI 386316 which was one of the latest flowering parents in this study. HA 124 was the tallest and latest in flowering plus it had the highest number of leaves resulting in internode lengths similar to PI 386316 and PI 386323. HA 290 was also a tall parent based on average plant height and earliest in terms of days to flowering with the fewest number of leaves. Similarly there were significant differences among the crosses for all traits except number of days to flowering and among generations within a cross for all traits (Table 4).

All F1s were taller than their tallest parent. The range in height among the F1s was from 157 cm for PI 386316 x HA 301 to 126 cm for PI 386323 x HA 89. HA 89, HA 301 and HA 124 were used in crosses with both PI 386316 and PI 386323. F1s of the three crosses with PI 386316 as the common parent averaged 148 cm while those with

PI 386323 averaged 136 cm. A commercial hybrid was not included in this study. However, in a test consisting of 49 commercial hybrids seeded two days earlier, the range in height was from 178 cm to 130 cm with an average of 155 cm. Hybrid 894, which is from the cross cms HA 89 x RHA 274 averaged 142 cm (15). It appears that both PI 386316 and PI 386323 can be used to produce hybrids which are as short or shorter than those currently available.

Another concern with the production of short hybrids is with a loss in leaf number thus reducing the total leaf area. Data in Table 3 which is based on observations of all plants of each parent in the study indicated that for PI 386316 and PI 386323, the average number of leaves per plant was midway between HA 124, which produced 37 leaves per plant and HA 290 which produced 22 leaves per plant. Plants of PI 386316 and PI 386323 were shorter because of a reduced internode length rather than a loss of leaves. The crosses in which there was a significant difference between F1 and one of the parents (Table 6), leaf number of the F1 equaled or exceeded the parent with the most leaves. The only exception was the cross PI 386316 x HA 124 in which the F1 had the same number of leaves as the midparent value.

Flowering date is another important consideration in the development of commercial sunflower hybrids. It is important to have a range in flowering dates to fit various production situations. PI 386323 was short in plant height and early in flowering while PI 386316 was late in flowering as compared to most other parents in this study. In crosses of HA 89, HA 124 and HA 301 with PI 386323 the average flowering date of the F1 was 71 days and ranged from 70 to 72 days after seeding (Table 6). There was no significant difference between F1 and either parent in these crosses. In crosses with PI 386316, which averaged 4 days later than the PI 386323, the mean and range in F1s was similar to that of crosses with PI 386323. These results may have been due to the type of weather conditions experienced during flowering. Higher than normal temperatures may have shortened the flowering period and reduced the observed variation. It appears from these data, however, that it may be somewhat difficult to obtain late flowering short hybrids. Additional testing will be required to confirm these results.

Heterotic effects were observed for all four traits studied but the magnitude was higher for plant height and internode length (Table 11). Crosses with PI 386316 tended to give higher values of heterosis for all traits than crosses with PI 386323. HA 89 showed the lowest heterotic effect for plant height in crosses with the both short parents, where as HA 301 resulted in the highest heterosis on crossing with PI 386316 but the lowest effect on crossing with PI 386323. The same observation can be made by comparing F1 means presented in Table 6. The shortest F1 in crosses with PI 386316 and PI 386323 involved HA 89. By contrast HA 301 x PI 386323 produced a short F1 of about the same height as PI 386323 x HA 89. However the cross PI 386316 x HA 301 produced one of the tallest F1 in crosses with PI 386316. Data in Table 3 suggest that even though PI 386316 and PI 386323 were the shortest parents, HA 89 and HA 301 were also relatively short. It appears that

HA 89 has genes in common with PI 386316 and PI 386323 controlling reduced plant height. The data also suggest that HA 301 has genes in common with PI 386323 for reduced plant height but not with PI 386316. A lower magnitude of the F2 variance observed in crosses of PI 386323 with HA 89 and HA 301 as compared to crosses of PI 386316 with these parents (Table 6) is also supportive of the above result. However, additional studies will be necessary to confirm this observation. The heterotic effects observed in this study are similar to those of Stoyanova (34), Putt (27) and Velkov (38).

Potence ratio is the ratio of two differences and has been denoted as (h)/(d) by Mather and Jinks (21), where (d) is the sum of the departures of all the genes adding or subtracting from the character in the true breeding parental line with the greater expression of the trait from the mid-parent value. Whereas (h) is the sum departures of all the relevant genes controlling a trait of an F1 from the mid-parent of the true breeding lines of the cross.

Mather and Jinks pointed out that although h/d provides a measure of dominance for a single gene difference, h/d does not provide a corresponding measure of dominance when more than one gene is considered. (h)/(d) may be very small simply because some of the h's are positive and others negative, so leading to a small value for (h) even though none of the individual h's are small. Equally (h)/(d) may be large because the genes are so distributed between the parental lines that they tend to balance out one anothers effects resulting in a small (d). Thus (h)/(d) cannot depart from zero unless one or more of the genes show dominance.

Potence ratio values presented in Table 11 suggest that there is some degree of dominance controlling plant height and internode length in these crosses. Crosses with PI 386316 tended to give higher values than crosses with PI 386323.

The continuous pattern of frequency distributions of plants in the F2 generations for plant height, days to flowering, leaf number and internode length indicate multigenic inheritance of these traits. The F2 frequency distributions for plant height were found skewed towards taller parents in varying degrees, depending on the crosses, resulting deviations from normal distribution. The possible reasons of skewness could be dominance and heterosis observed in all crosses for this trait. The wider distribution of individuals observed in F2 populations indicate genetic variation for the trait studied.

Backcross population means generally tended towards those observed in the recurrent parent (Table 6). An exception was in the cross HA 302 x PI 386323 in which backcrossing to tall parent, HA 302, reduced plant height below that observed from backcrossing to the short parent (Table 6). These results could be due to small population size, resulting in a poor estimate of the true population mean or some other unknown reason.

Results obtained from generation mean analysis (Tables 13,14) demonstrate that dominance genetic effects were relatively more important in the inheritance of plant height in most crosses. These results agree with those of Velkov (38). The higher estimates of dominance genetic effects resulted from generation mean analysis could be biased due to the heterotic effects observed for this trait. Higher additive genetic effects than the dominance effects were observed for crosses, PI 386323 x HA 301 and PI 386316 x HA 124.

Additive genetic effects were more pronounced than dominance effects in most crosses for internode length, leaf number and number of days to flowering. It has been reported by Gamble (11) and Robinson et al. (29) that characters showing greater additive gene effects have probably less complex inheritance, whereas greater contribution of the dominance gene effects suggest more complex inheritance of the trait.

Additive dominance genetic model was found adequate for all the traits studied in most crosses. Deviation from the additive dominance model as was observed in several crosses for plant height and internode length (Table 13) could be due to the nonfulfillment of certain assumptions about the genetic material used in this study. Normal Mendelian segregation of alleles, absence of selection favoring certain gametes or zygotes and absence of mutation are usually assumed in quantitative genetic models (21). Mather and Jinks (21) further mentioned that lack of isodirectional distribution of alleles between the two parental lines can change the genetic expectation of the means and backcross generations. These effects could be confounded with episatic effects.

Significant residual effects for plant height, indicating deviation from the additive dominance model, were observed in crosses of PI 386323 with HA 290, HA 302, HA 301 and CM 408 x PI 386316. Data in

Table 12 would support epistasis as a cause in the crosses PI 386323 x HA 290 and CM 408 x PI 386316. The epistatic effects not detected from the generation mean analysis in some of the crosses may have introduced bias in the estimates of additive and dominance effects (4).

F2 variances for plant height and internode length exceeded those of the pooled parental variances in all crosses involving PI 386316 and in three of the five crosses involving PI 386323. In the two crosses in which there was no difference between the F2 variance and the pooled parental variance, the variance for plant height of the tall parent equaled or exceeded the observed F2 variance. However, the magnitude of the F2 variance was similar to those observed in other crosses.

The test units in this study were individual plants in segregating and nonsegregating populations. In a nonsegregating homogenous population such as an inbred line, any plant to plant variation is considered to be environmental, because for all practical purposes each plant is a genetic duplicate of the other. The precision of the measurement is dependent on the number of plants observed. In several of these crosses the number of parental plants was less than 10 and because of stand problem these plants were not bordered. This situation could have resulted in an inflated estimate of the parental variance. By contrast a population of F2 plants derived by crossing two homozyzous lines, is both heterozygous and heterogenous. It is possible for every F2 plant to be genetically distinct depending on the number of genes involved and population size. The plant to plant variation in an F2 is due to genetic, environmental and genotype by environmental interaction. The environmental effects are assumed to be the same in the segregating and nonsegregating populations. Since an F2 plant is unique and cannot be duplicated, except by asexual means, there is no way of estimating the impact of the environment or the genotype by environment interaction on an estimate of genetic variances. The effect of a significant genotype by environment interaction on a genetic variance is usually to be biased it upward (8). In addition the genetic variance contains the additive, dominance, epistatic plus their interactions. For these reasons the observed variances of the segregating populations should be considered as maximum values. In addition the observed variance of the backcross populations are questionable because of the small number of plants.

Estimates of broad sense heritability calculated by three methods for plant height, days to flowering, leaf number and internode length are presented in Table 15. The estimates vary from one method to the other for individual crosses due to differences in variances of the non-segregating populations. Lower estimates obtained in some crosses by Method I (16) are due to high parental variance. While high F1 variance obtained in some crosses resulted in lower estimates of heritability calculated by Method II (3). In situations where the non-segregating generations exhibit a high degree of environmental variance, as observed in this study, the method proposed by Allard (1) should be the better estimate because it utilizes F1 and parental plants to estimate the environmental variance.

Broad sense heritability for plant height averaged over crosses was about 45 percent for crosses with PI 386323 and about 55 percent for crosses using PI 386316. Broad sense heritabilities of individual crosses ranged from 29 to 73 percent, 3 to 50 percent, 28 to 66 percent and 50 to 74 percent for plant height, days to flowering, leaf number and internode length respectively. Similar ranges for the estimates of broad sense heritability for plant height have been reported by Velkov (38) and Fick (10) from studies of short and tall inbred lines. The estimates reported by Shabana (32) for plant height, number of days to flowering and leaf number are comparatively higher than those obtained in this study.

Narrow sense heritability estimates obtained for plant height, number of days to flowering and leaf number are erratic and in some crosses have no value. However, the estimates obtained for internode length are comparable to broad sense heritability estimates. A very low magnitude of narrow sense heritability estimates for plant height have also been reported by Fick (10). Lower estimates obtained in this study are due to higher backcross variances observed in most crosses, whereas the method involving F2 and backcross variances require a comparable range of heterozygosity in the F2 and backcross populations (3).

Phenotypic and genotypic correlations presented in Tables 16 and 17 revealed that genotypic correlations were generally higher than the phenotypic correlations. Low phenotypic correlations may be due to masking or modifying effects of the environment on expression of genetic association between the characters (41). Genotypic correlations among different traits in crosses of PI 386323 with HA 124, HA 301 and in some other crosses were erratic due to the negative values of parental covariances. Such results indicate the need of better control of environmental variance and/or genotypic environmental interations.

Positive phenotypic and genotypic correlations between plant height and internode length, plant height and leaf number and negative correlations between leaf number and internode length suggested that selection for short internode could be practiced to reduce plant height without reducing the leaf number. Positive phenotypic correlations observed between plant height and days to flowering in crosses involving PI 386316 suggest that selection of early flowering short individuals would be possible in these crosses.

When this study was initiated it was hoped that the short plant height of PI 386323 and PI 386316 was due to few number of dominant genes, perhaps even one. The data suggest that tallness is quantitatively controlled with relatively strong dominance effects and heterosis. However, relatively few genes could be involved because of the ease with which the short recurrent parent is recovered with one backcross. To use these inbred lines in the production of short hybrids it will be necessary to incorporate genes controlling plant height into three lines; the cytoplasmic male sterile, the maintainer or B-line and the restorer. It appears from data on backcross populations (Table 6) that this will be possible by successive backcrosses. However, it may be easier to continue looking for a genetic source of short plant height controlled by a dominant gene. It may also be possible to develop even shorter plant types by intercrossing PI 386323, PI 386316, HA 89 and HA 301. Future studies will be necessary to confirm this possibility.

SUMMARY

Parental lines, F1s, F2s and backcross populations in nine sunflower crosses were used to study the inheritance of plant height, number of days to flowering, leaf number and internode length. Results from this study showed heterosis for tallness, early flowering, greater number of leaves and longer internodes.

The F2 generations had a wider distribution of individuals than any other generation for plant height and other traits, suggesting genetic variation for these traits. The continuous frequency distributions of plants of the segregating generations also suggested multigenic inheritance. Generation mean analysis indicated a higher magnitude of dominance effects than additive effects for plant height, whereas a varying response to these effects was observed in different crosses for the other traits. The backcross means were tending towards the recurrent parent indicated that there were relatively few genes controlling plant height and that the desired characters could be incorporated by successive backcrossing.

Highly significant positive correlations between internode length and plant height, leaf number and plant height and highly significant negative correlation between leaf number and internode length revealed effectiveness of selection for short internode length to reduce plant height.

A wide range of broad sense heritabilities obtained for the traits under study also indicated greater amount of genetic variability

in the segregating populations, which suggested the possibility of selection for desirable genotypes.

Inbred line HA 89 showed minimum heterosis and lowest F1 means in crosses with PI 386316 and PI 386323. Similar response was shown by HA 301 on crossing with PI 386323, which indicated the prospects of using these parents to develop short and early flowering hybrids.

LITERATURE CITED

1. Allard, R. W. 1960. Principles of plant breeding. John Wiley and Sons, Inc., NY.

2. Beard, B. H. 1981. The Sunflower crop. Scientific American 244:150-161.

3. Burton, G. W. 1951. Quantitative inheritance in pearl millet (Pennisetum glaucum). Agron. J. 43:409-417.

4. Carson, M.L. and A. L. Hooker. 1981. Inheritance of resistance to stalk rot caused by Colletro-trichum graminicola. Phytopathology 71:1190-1196.

5. Clement, Y., and E. Diehl. 1968. Contribution to the study of some characteristics. Sunfl. C. R. Acad. Agric. Fr. 54:853-859. Cited by Fick, G.N. 1978.

6. Cockerell, T. D. A. 1915. Specific and varietal characters in Annual Sunflower. Am. Nat. 49:609-622.

7. Dedio, W., and E. D. Putt. 1980. Sunflower. p. 631-644. In W. R. Fehr and H. H. Hadley (ed.) Hybridization of crop plants. Am. Soc. of Agron. Madison, Wis.

8. Dudley, J. W., and R. H. Moll. 1969. Interpretation and use of estimates of heritability and genetic variances in plant breeding. Crop Sci. 9:257-262.

9. Enns, H. 1959. A study of the inheritance and expressivity of some seedling characters in the Sunflower (Helianthus annuus L.). M.S. Thesis, Univ. Manitoba, Winnipeg. Cited by Fick, G. N., 1978.

10. Fick, G. N. 1978. Breeding and Genetics. p. 279-328. In Carter, Jack F., (ed.) Sunflower Science and Technology. Am. Soc. of Agronomy. Madison, Wis.

11. Gamble, E. E. 1962. Gene effects in Corn (Zea Mays L). II Relative importance of gene effects for plant height and certain component attributes of yield. Can. J. Plant Sci. 42:349-358.

12. Gundaev, A. I. 1971. Basic principles of sunflower selection. p. 417-465. In Genetic principles of plant selection, Nauka, Moscow. (Trans.) Dept. of the Secretary State, Ottawa, Canada 1972. Cited by Fick, G.N. 1978.

13. Klaczowski, Z. 1975. Studies on some Features of oil sunflower and their significance in breeding that plant in Poland (in Polish). Howowla Rosl. Aklim, Nasienn. 19:89-131. Cited by Fick, G. N. 1978.

14. Kovacik, A., and V. Skaloud. 1972. The proportion of the variability component caused by the environment and the correlations of economically important properties and characters of the sunflower (Helianthus annuus L.). Sci. Agric. Bohemoslov. 4:249-261.

15. Lay, C. L. 1983. Personal communication.

16. Mahmud, I., and H. H. Kramer. 1951. Segregation for yield, height and maturity following a soybean cross. Agron. J. 43:605-609.

17. Manjunath, A. 1978. Genetics of seed yield, oil content and other quantitative characters in sunflower (Helianthus annuus L.). Mysore J. Agric.. Sci. 12:667-668.

18. _____ and J. V. Goud. 1978. Genetics of quantitative characters in sunflower (Helianthus annuus L.) I. Suitability of diallel crosses. Genet. Iber., 30-31:249-256.

19. Marani, A. 1968. Heterosis and Inheritance of quantitative characters in interspecific crosses of cotton. Crop Sci. 8:299-303.

20. Marinkovic, R. 1982. Inheritance of plant height and leaf number in diallel crossing of sunflower inbreds. p. 232-233. In Proc. 10th Int. Sunflower Conf. (Surfers Paradise, Australia).

21. Mather, K., and J. L. Jinks. 1971. Biometrical genetics. Cornell Univ. Press, Ithaca, NY.

22. Miller, J. F., J. J. Hammond and W. W. Roath. 1980. Comparison of inbred vs. single cross testers and estimation of genetic effects in sunflower. Crop Sci. 20:703-706.

23. Oka, H. I., and I. F. Campos. 1974. Breeding behavior and genetic variations of sunflower observed in Central Luzon. SABRAO J. 6:61-67. Central Luzon State Univ., Nueva Ecija, Phillippines. (Plant. Breed. Abstr. 44:7979, 1974).

24. Pathak, R. S. 1974. Yield components in sunflower p. 271-281. In Proc. 6th Int. Sunflower Conf. (Bucharest, Romania).

25. Petr, F. C. and K. J. Frey. 1966. Genotypic correlations, dominance, and heritability of quantitative characters in oats. Crop Sci. 6:259-262.

26. Putt, E. D. History and present world status. p. 1-29. In Carter, Jack F. (ed.) Sunflower Science and Technology. Am. Soc. of Agron. Madison, Wis.

27. Putt, E. D. 1966. Heterosis combining ability and predicted synthetics from a diallel cross in sunflowers (*Helianthus annuus* L.). Can. J. Plant Sci. 46:59-67.

28. Rao, N. M., and B. Singh. 1977. Inheritance of some quantitative characters in sunflower (*Helianthus annuus* L.), Pantnagar J. Res. 2:144-146.

29. Robinson, H. F., R.E. Comstock, and P. H. Harvey. 1949. Estimates of heritability and the degree of dominance in Corn. Agron. J. 41:353-359.

30. Rodin, V. F. Production of short forms of sunflower uniform in height. Selektsiya; Semenovdstvo (1978) No. 4, 37-39 (Ru). (Pl. Breed. Abstr. 48:11928, 1978).

31. _____, Inheritance of short stem in sunflower. Byul, nauch.-tekhn informatsii po/maslich/. kul'turam (1976) No 2, 8-12 (Ru). (pl. Breed. Abstr. 50:633, 1980).

32. Shabana, R. 1974. Genetic variability of sunflower varieties and inbred lines p. 263-269. In Proc. 6th Int. Sunflower Conf. (Bucharest, Romania).

33. Steel, R. G. D. and J. H. Torrie. 1980. Principles and procedures of statistics. McGraw Hill, Book Co., Inc., New York.

34. Stoyanova, Y., P. Ivanov and I. Georgiev. 1971. Inheritance of certain features in F1. in Sunflower. Genet. Sel. 4:3-14.

35. U. S. Department of Agriculautre *Agricultural statistics*. 1982. Washington, D.C. Govt. Printing Office 1982.

36. United Nations. Food and Agriculature organization. *FAO production yearbook*. 1981 Rome. Food and Agriculture organization of the U.N. 35:130.

37. Unrau, J. 1947. Heterosis in relation to sunflower breeding. Sci. Agri. 27:414-427.

38. Velkov, V. N. 1970. Inheritance of stem height in sunflower. Genet. Sel. 3:393-401.

39. Warner, J. N. 1952. A Method For estimating heritability. Agron J. 44:427-430.

40. Westin, F. C. 1959. Soil survey, Brookings County, South Dakota U.S. Soil Conservation Service, Soil Survey, ser. 1955, no. 3. U.S. Govt. Printing office.

41. Weber, C. R. and B. K. Moorthy. 1952. Heritable and non heritable relationships and variability of oil content and agronomic characters in F2 generations of soybean crosses. Agron. J. 44:202-209.