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A DIALLEL ANALYSIS OF CELERY SHOOT AND LEAF PRODUCTION AND THE INHERITANCE OF A DWARF MUTANT IN CELERY

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Michael William McCaffery

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Eugene Hoerner
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A DIALLEL ANALYSIS OF CELERY SHOOT AND LEAF PRODUCTION AND THE INHERITANCE OF A DWARF MUTANT IN CELERY

By

Michael William McCaffery

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ABSTRACT

A DIALLEL ANALYSIS OF CELERY SHOOT AND LEAF PRODUCTION AND THE INHERITANCE OF A DWARF MUTANT IN CELERY

By

Michael William McCaffery

A diallel analysis of basal shoot, heart shoot and leaf production was performed with four celery (Apium graveolens L., Dulce Group) cultivars. Significant general and specific combining abilities were exhibited for all traits. The individual specific combining ability estimates suggest the presence of hybrid vigor or complementary genes for all traits. Potence ratio and graphical analysis suggested dominance for increased basal shoot production, decreased heart shoot production, and decreased leaf number. Minimum phenotypic correlations were observed between the characters. No genotypic correlations were noted.

The dwarf phenotype, first identified in a Michigan State University massed breeding line, appeared to be controlled by a monogenic recessive.

To my parents, Ralph and Laura McCaffery, who loved and encouraged me from gleam to geneticist.

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INTRODUCTION

Lateral shoots in celery (Apium graveolens L., Dulce Group) are generally removed prior to packing for shipment and sale. Removal of the shoots is a time consuming and costly operation for the grower. Therefore, the development of celery cultivars with reduced lateral shoot number would benefit the celery grower.

For the purpose of this investigation, the lateral shoots produced by the celery plant were classified into two types (Figure 1). The first type, 'basal shoots', are shoots that lack a subtending leaf and are located below the oldest leaf on the stem. These shoots are the largest of the lateral shoots, and possess several well developed leaves. The second type, 'heart shoots', are axillary shoots. These shoots are generally smaller, ranging from visible yet unexpanded buds to small shoots with a few leaves. While varietal differences for lateral shoot production in celery have been noted, studies on the mode of gene action or inheritance have not been reported.

Correlation between the number of axillary shoots produced and the number of leaves or nodes produced in Nicotiana tabacum L. have been cited by Matsuda and Sato (1981) and in Brassica oleracea L., Gemmifera Group by

Figure 1. Diagram of sectioned celery plant.

B: Basal shoot

L: Leaf

H: Heart shoot

Hodgkin (1978). Since such a study has not been reported for celery, an analysis of the inheritance of leaf number and its relationship to lateral shoot production was conducted.

The objectives of the study were:

1. To determine the gene action controlling lateral shoot production.

2. To determine the gene action controlling leaf number.

3. To determine the relationship between number of leaves and number of lateral shoots.

LITERATURE REVIEW

Celery

Celery is a diploid (2n = 22) (Hore, 1972), outcrossing species and may exhibit 10-50% selfing (Allard, 1960; Welsh, 1981; Orton, 1984). Most commercial celery breeding has been based on mass selection (Orton, 1984), although inbreeding has also been used (Honma, 1958).

Lateral shoots

The number of axillary shoots (often called tillers in cereals) produced by a plant is related to the number of axils or nodes and the amount of growth per axil or node. Adventitious shoots, however, may arise from any part of the plant body. The production and growth of axillary and adventitious buds is dependent upon many factors, including nutrient competition and hormone balances (Esau, 1981; Waring and Phillips, 1983).

Axillary bud production in tomato (*Lycopersicon esculentum* Mill.) has been studied by Tucker (1976). From biochemical and morphological comparisons of isogenic lines of the tomato cultivar Craigella lateral suppressor (*ls*), Craigella blind (*bl*) and normal Craigella, Tucker tenatively concluded that inhibition of axillary bud formation in lateral suppressor type plants is due to a reduction in

peroxidase activity which allows accumulation of normally oxidized indoleacetic acid, suppressing bud and shoot development. This inhibition may be mediated by abscissic acid and cytokinin since lateral suppressor type plants had lower levels of these two hormones as compared to blind type and normal plants.

Increased tillering in maize (Zea mays L.) due to basal branching has been noted in the andromonoecious dwarfs, d1, d2, d3 and d5 (Coe and Neuffer 1977). McCune (1961) noted differences in peroxidase electrophorograms of maize dwarfs, d1, d3, d5, D8, and normals. Auxin control of tillering has been postulated for the monogenic recessive uniculm mutant in barley (Hordeum sp.) (Kirby 1973). The mutant produces no visible tillers and the phenotype is similar to that resulting from applied 2,4-D.

Axillary shoot production in tobacco (Nicotiana tabacum L.) appears to be primarily controlled by varying amounts of additive and dominance effects, depending upon the population stidied (Matsuda and Sato , 1982ab; Matzinger et al., 1962). Signifiant heterosis for increased axillary shoot production was noted by Matzinger et al. (1962). Heterosis for decreased axilllary shoot production was noted by Matsuda and Sato (1982a). Environmental influences on axillary shoot production were small (Matzinger et al., 1962).

Matsuda and Sato (1981) classified the axillary shoots produced by the tobacco plant into two groups; ground

suckers - those occuring in the 8th - 15th leaf above the cotyledon, and upstalk suckers - those occuring in the 1st - 8th leaf from the top, four days after removal of the inflorescence. They noted that some varieties produced different amounts of ground and upstalk suckers, although the overall correlation between the two was significant. Mann and Chaplin (1957) concluded that groundstalk and upstalk sucker production were controlled differently. Matsuda and Sato (1982b) reported that the number of effective factors controlling ground sucker production ranged from 0.688 to 5.188 and varied, along with amount and direction of heterosis, with the cross.

Inheritance of axillary shoot production (branching) in sunflower (Helianthus annuus L.) is complex with four or more genes regulating this trait (Luczkiewicz, 1975; Hockett and Knowles, 1970; Putt, 1964). Hockett and Knowles (1970) reported four genes controlling branching: Br2, a dominant gene that conditions branching on the top one half of the stem with a large capitulum; Br2Br3, duplicate dominant genes that condition top branching or branching at almost every node and b2b3 duplicate recessive genes that condition branching at almost every node with a reduced capitulum. The phenotype conditioned by b2b3 is similar to the phenotype conditioned by the single recessive (b) reported by Putt (1964). Digenic dominant epistasis conditioned for a fully branched phenotype in X-ray induced mutants of sunflower (Luczkiewicz, 1975). Basal branching, appearing in non-branched types, appeared to be controlled by modifiers

(Hockett and Knowles, 1970).

Axillary bud formation in Brussels sprouts (Brassica oleracea Gemmifera Group) showed significant general combining ability in a ten parent half diallel (Hodgkin, 1980). One or a few major recessive genes and modifiers of varying effects conditioned axillary head formation in cabbage (Brassica oleracea Capitata Group) (Akratanakul and Baggett, 1977).

Tillering in maize x teosinte hybrids was reported to be partially dominant to no tillering (Rogers, 1950). An eight parent diallel experiment conducted by Rood and Major (1981) showed that high tillering was partially dominant to low tillering. Heterosis for increased tillering was noted in crosses between single-stalked parents. The presence of specific combining ability was dependent upon inbreeding depression in the parents.

Several single gene mutants, with radically altered phenotypes, exhibit increased tiller production (Coe and Neuffer, 1977).

Tillering in wheat (Triticum aestivum L.) appears to be controlled by varying amounts of additive, dominance and epistatic effects (Nanda et al., 1982; Soomro, 1977; Ketata et al., 1976). Important additive x additive and dominance x dominance effects, possibly inflating the 36% heritability for this trait, were reported by Ketata et al. (1976). Soomro (1977) estimated heritabilities for tillering in a five parent diallel cross of common wheat by several

methods. Analysis of variance methods yielded a broad sense heritability of 56% and a narrow sense heritability of 46%. Parent-offspring regression yielded a similar estimate of 36%. Variance components analysis gave an estimate of 66%.

Nanda et al. (1982) observed that additive effects were predominant in crosses involving tall, semi-dwarf and dwarf wheats. Significant dominance effects and heterosis for increased tillering were observed in a tall x semi-dwarf cross while other crosses showed negative heterosis. Additive x additive and dominance x dominance interactions were reported for some crosses.

An average broad sense heritability estimate of 41.6% and a very low narrow sense heritabilty estimate were obtained for tillering in pearl millet (Pennisetum sp.) (Lal and Singh, 1970). A 52.6% genetic advance was also reported. Analysis of a six parent diallel indicated that tillering was controlled by dominance and epiststic effects with few tillers completely dominant to many tillers (Ahluwalia et al., 1962). They also reported that both general and specific combining ability were significant with specific combining ability being more important. Similar results were obtained by Gupta and Nanda (1968). They reported that partial dominance and complementary epistasis were major effects controlling tillering in a six parent diallel.

Leaf Number

Leaf number may be determined by a number of factors: rate of growth, duration of the vegetative phase, length of

growing period and other environmental factors (Prasad and Prasad, 1981; Thurling and Vijendra Das, 1979; Hodgkin, 1978; Mann and Chaplin, 1957). Analysis of a ten parent half diallel of Brussels sprouts cultivars revealed that final node number and rate of node production are highly correlated and highly heritable (Hodgkin, 1978). Significant general combining ability was shown for both traits. Dominant genes for high and low final node number were found in separate cultivars. Thurling and Vijendra Das (1979) reported that leaf number at anthesis in Brassica napus L. was controlled by partial dominance and affected by the length of time to flowering. Different photoperiod and temperature regimens, corresponding to different sowing times altered the dominance relationships of the parents and influenced the very high narrow and broad sense heritabilities for this trait. Genic interactions and correlated gene distributions among the parents were also noted.

Analysis of leaf number in 21 carrot (Daucus carota L.) cultivars yielded a heritabilty esimate of 72.9% A study of 14 radish (Raphanus sativus L.) cultivars indicated that leaf number was moderately heritable (56.37%) and partially controlled by non-additive effects (Prasad and Prasad, 1978). Prasad and Prasad (1981) reported in turnip a leaf number heritability estimate of 32.00% in a ten variety study.

Leaf number in tobacco appears to be controlled by

additive effects in some varieties (Robinson et al., 1954) and additive and dominance effects in others (Matzinger et al., 1960). General combining ability effects for leaf number were predominant in an eight parent diallel and subsequent F_2 population analyzed by Matzinger et al. (1962). Analysis of a four parent diallel by Murty et al. (1962) indicated that mostly additive effects controlled tobacco leaf number. Heterosis and dominance for reduced leaf number were also noted. The short day conditiong mammoth gene (m) increased leaf number by increasing the duration of the vegetative phase under long days (Mann and Chaplin, 1957). The leaf shape allele (Pt) increased leaf number by altering the growth habit of the tobacco plant (van der Veen and Bink, 1961). No correlation between rate of growth and total leaf number was observed.

A six parent diallel analysis of maize conducted by Bonaparte (1977) revealed that leaf number was controlled by partially dominant genes with highly significant additive and dominance effects. Additive variances were larger than dominance variances and no interactions were noted.

Additive, dominance, additive x additive and dominance x dominance effects controlled leaf number in sorghum crosses analyzed by Indi and Gaud (1981). Inheritance of leaf number in pearl millet was shown to depend on two to ten effective factors with arithmetic and geometric interactions (Burton, 1951). Low heritability was also noted. A diallel analysis of leaf number in nine pearl millet cultivars indicated highly significant general combining ability and

significant specific combining abilty with an average degree of dominance of 0.85 (Phul et al., 1973). Broad sense heritability was estimated at 98.50% and narrow sense heritability was estimated at 56.71%.

MATERIALS AND METHODS

Eleven breeding lines selfed for a minimum of five generations and the inbred commercial cultivar Golden Spartan were visually selected to represent the range of lateral shoot production in this investigation. This material was obtained from the collection of commercial and experimental lines grown at the Michigan State University Muck Soils Research Center near Bath, Michigan in 1984. After making a visual selection of lines, plants of each line were stripped and counts of the leaves and total number of axillary shoots for each plant were recorded. The quotient: shoots/leaves, was used as a measure of lateral shoot production. The data were arcsin transformed and an analysis of variance performed. Differences in the axillary shoot production of each of the lines were noted. The lines with their respective means and standard deviations are shown in Table 1. Plants exhibiting the extremes of lateral shoot production are shown in Figure 2.

Four lines with approximately equal intervals of lateral shoot production from high to low were selected from the original twelve. The four lines choosen were Michigan State University experimental lines 83-631, 84-56, 84-83, and Golden Spartan. These lines are henceforth referred to as

Table 1. Means and variances of shoot production by selected lines in 1984.

Line	Mean	Variance
84-47	12.72	205.10
83-631*	16.10	100.88
83-613	19.20	139.16
83-610	20.76	117.20
85-56*	23.83	49.47
84-7	26.17	82.23
Golden Spartan*	34.32	133.66
83-74	35.47	83.74
84-107	41.01	97.25
83-69	48.29	107.72
84-83*	49.27	61.18
84-42	54.33	444.20

* selected for analysis

Figure 2. **Stripped plants showing extremes of shoot production.**

Left: profuse shoot production

Right: reduced shoot production

Figure 2.

lines 1, 2, 3 and 4 respectively. Golden Spartan is homozygous for the monogenic recessive character of yellow petiole color (Townsend, et al., 1946). This allowed detection of the selfs produced in Golden Spartan x green petioled crosses.

Three plants from each of the four selected lines were lifted from the field, pruned and potted in 25 cm pots filled with muck soil. The plants were placed in a lath house for two weeks prior to moving them to a lighted 5 C chamber for ten weeks to vernalize the plants. The plants were then moved to a 19 C greenhouse with supplemental lighting providing 14 hour days. After two weeks, the temperature of the house was raised to 22 C to hasten flower stalk development. The plants began to flower in February, 1985.

A four parent full diallel design, including the parental selfs, was used for the genetic analysis of shoot production and leaf number. Hybridization was performed according to the method described by Honma (1959). The umbels of the female parent were pollinated by brushing them with a pollen bearing umbel of the male parent. A polyethylene cheese cloth bag was placed over the umbels after pruning and pollination and left on the plants until seed harvest. The number of seeds obtained from each cross ranged from 0 to over 100.

The seeds were sown in vermiculite and the flats were placed on a timed heating pad. The use of the heating pad

provided a minimum soil temperature of 22 C during the day and a night temperature of about 15 C (ambient) that enhanced germination (Knott, 1980). The seedlings at the one true leaf stage were transplanted into flats containing a sterilized mixture of 3:1 muck soil:sand. The eight week old seedlings were then transplanted to the field for the 1985 growing season at the MSU Muck Soils Research Center in June.

The plot was arranged as a completely randomized block design with 3 replicates. An equal number of plants of each genotype were grown in each replicate. The number of plants of each genotype varied due to the number of seed produced for each genotype. The rows were 81 cm apart and the plants were spaced 15 cm apart. Two guard plants were placed at each end of a row and between blocks. Guard rows were placed at the ends of the plot. Standard cultural practices for celery production were used.

Data for basal shoot number, heart shoot number and leaf number were collected on an individual plant basis. Exceedingly small plants were discarded. Although the number of yellow petioled plants or selfs in Golden Spartan x green petioled crosses were recorded, only the information obtained from the green petioled plants were used in the analyses. The average rate of selfing in the Golden Spartan x green petioled crosses was 24.9%. Table 2 lists the number of plants of each genotype used in the analysis. The plants were pulled and the number of basal shoots (those lacking a subtending leaf) was recorded. The leaves were then

Table 2. Number of progeny examined for each genotype.

Number of Plants Examined				
	Female Genotype			
	Line			
Line	1	2	3	4
1	33	93	42	34
2	79	78	53	0
3	101	80	35	41
4	79	61	26	39

sequentially stripped from the plant and the number of heart shoots larger than 0.5 cm long and leaf number were recorded. The plants were stripped until the heart leaves were less than 5 cm long (Figure 2).

Data from individual plants were entered on a micro computer and uploaded to the MSU Control Data Corporation Cyber 750 for statistical analysis. The SPSS.9 (Statistical Package for the Social Sciences) program was used for the analysis. Additional analysis was performed using formulae and tables published by Steele and Torrie (1979) and Little and Hill (1982).

A combining ability analysis of the diallel data was performed using a modification of the fixed effects full diallel model (method 1, model I) of Griffing (1956). The fixed effects model limits statistical inferences to the population of the parents used in the diallel. The model was modified to partition out maternal and reciprocal effects (Cockerham, 1963) and adjusted to accomodate selfing after a model published by Dudley (1967).

The model was thus:

$$Y_{ijk} = u + (1-s)(g_i + g_j + s_{ij} + m_i - m_j + r_{ij}) + s(2g_{ii} + s_{ii}) + e_{ijk}$$

where:

Y_{ijk} = value of the k^{th} observation of the cross between the i^{th} and j^{th} parents

u = grand mean of the plot

s = proportion of selfs in a cross, $s = 0.249$ if the maternal parent was green petioled, $s = 0$ otherwise

g_i = general combining ability effect of the i^{th} parent,

$$\sum_i^p g_i = 0$$

s_{ij} = specific combining abliity effect associated with the cross between the i^{th} and j^{th} parents,

$$s_{ij} = s_{ji}, \quad \sum_i^p s_{ij} = s_{ij} = 0$$

m_i = maternal effect of the i^{th} parent,

$$\sum_i^p m_i = 0$$

r_{ij} = reciprocal effect associated with the cross between the i^{th} and j^{th} parents,

$$r_{ij} = -r_{ji}, \quad \sum_{i \neq j}^{p-1} r_{ij} = \sum_{i \neq j}^{p-1} r_{ij} = 0$$

e_{ijk} = random error, $e \approx NID(0, \sigma^2)$

The effects were estimated using the least squares method. The New Regression subprogram of SPSS.9 was used to provide the individual estimates and the variance/covariance matrix for each effect. The coefficients of each parameter are found in the design matrix for the analysis shown in Table 3. Since no progeny were obtained from the cross, Golden Spartan x 84-56, the reciprocal effect for this cross, r_{24}, was set to 0. The effects of unequal numbers of

Table 3. Parameter coefficients used in design matrix.

Genotype		g1	g2	g3	s11	s12	s13	s22	s23	s33	m1	m2	m3	r12	r13
1	1	2			1										
1	2	1.249	0.751		0.249	0.751					0.751	-0.751		0.751	
1	3	1.249		0.751	0.249		0.751				0.751		-0.751		0.751
1	4	0.498	-0.751	-0.751	-0.502	-0.751	-0.751				1.502	0.751	0.751	-0.751	-0.751
2	1	0.751	1.249			0.751		0.249			-0.751	0.751		-0.751	
2	2		2					1							
2	4		1.249	0.751				0.249	0.751			0.751	-0.751	0.751	
2	4	-0.751	0.498	-0.751		-0.751		-0.502	-0.751		0.751	1.502	0.751		
3	1	0.751		1.249			0.751			0.249	-0.751		0.751		-0.751
3	2		0.751	1.249					0.751	0.249		-0.751	0.751	-0.751	
3	3			2						1					
3	4	-0.751	-0.751	0.498			-0.751		-0.751	-0.502	0.751	0.751	1.502	0.751	0.751
4	1		-1	-1	-1	-1	-1				-2	-1	-1	1	1
4	3	-1	-1				-1		-1	-1	-1	-1	-2	-1	-1
4	1	-2	-2	-2	1	2	2	1	2	1	0	0	0		

observations and selfing resulted in a loss of orthogonality and balance. The equations for deriving the dependent individual effects are given in Table 4. The parental means for each character were estimated from the means of the selfed progeny of each parent.

The variances due to general combining ability, specific combining ability, maternal and reciprocal effects were estimated from the mean squares computed at each time a different group of individual effects was entered into the computations. Tests of significance were performed on each effect using the residual mean square as the error term. Differences between estimates of individual effects were tested for significance using Student's t test.

Since the means of each hybrid genotype with a green petioled maternal parent were assumed to be biased by selfs, the means were weighted, assuming the absence of maternal effects (Cockerham, 1963), based on the model:

$$Y_{ij} = (1-s)(Y'_{ij}) + s(Y_{ii})$$

where:

Y_{ij} = observed mean of the ij^{th} genotype

Y'_{ij} = mean of true hybrid progeny of i^{th} and j^{th} parents

Y_{ii} = observed mean of the maternal genotype

s = proportion of selfs detected = 0.249, $s = 0$ when the maternal parent = Golden Spartan

Table 4. Dependent effects and equations

Effect	Equation
g4	g4 = -(g1 + g2 + g3)
s14	s14 = -(s11 + s12 + s13)
s24	s24 = -(s12 + s24 + s23)
s34	s34 = -(s13 + s23 + s33)
s44	s44 = s11 + s22 + s33 + 2(s12 + s13 + s23)
m4	m4 = -(m1 + m2 + m3)
r14	r14 = -(r12 + r13)
r23	r23 = r12
r24	r24 = 0
r34	r34 = r12 + r13

Thus,

$$Y'ij = \frac{Yij - s(Yii)}{(1-s)}$$

The weighted genotypic means were used to compute potence ratios for each cross (Mather and Jinks, 1971). The equation used to compute the potence ratio (R) was:

$$R = \frac{2(F_1 - mp)}{|P_1 - P_2|}$$

where:

F_1 = the F_1 genotypic mean

mp = the mean to the parental genotypic means

P_1, P_2 = the parental genotypic means

Thus, for a single locus:

R = 0, only additive effects are present

$0 < |R| < 1$, partial dominance is present

$|R| = 1$, dominance is present

$|R| > 1$, overdominance is present

The potence ratio in a polygenic system is affected by the dispersion of the genes among the parents. Thus the complementation of genes of opposite effects could result in a potence ratio of zero, despite the presence of dominance. Similarly, partial dominance will result in a potence ratio of in crosses between parents of identical phenotype. The utility of the potence ratio in the this experiment is the ability to determine the the direction of dominance when detected.

The weighted genotypic means were then used to perform the graphical diallel analysis of each character in the manner described by Hayman (1954). The analysis uses the regression of the covariance of 1/2 sibs with their nonrecurring parent (Wr) on the variance of the group of 1/2 sibs for each parent (Vr). The selfed parents are included in each array of 1/2 sibs.

The regression of Wr on Vr provides a test for the presence of non-allelic interaction. If the slope of the regression line is significantly different from one then non-allelic interaction is present. The y - intercept provides an indication of the average degree of dominance; the lower the intercept the greater the dominance. The distribution of the parental points along the regression line provides a measure of the genetic diversity of the parents. The points closest to the origin are the parents with more dominant alleles, regardless of the increasing or decreasing effects of the alleles. If a parent lies on the regression line where the line intercepts the limiting parabola, then that parent posseses all of the dominant or recessive alleles at all loci that differ among plants in the population studied (Mather and Jinks, 1971, Allard, 1956)

Pearson product moment correlations between the characters basal shoot, heart shoot, and leaf production were computed using the Pearson Corr subprogram of SPSS.9. The phenotypic correlations were computed on an individual

plant basis. Genotypic correlations were computed on genotypic means, giving 13 degrees of freedom. Genetic correlations (Falconer, 1981) were computed using the individual general combining ability effects, giving two degrees of freedom.

RESULTS AND DISCUSSION

Combining ability analysis

The unweighted genotypic means for each character, basal shoots, heart shoots, leaf number, are shown in Table 5. Differences between reciprocal crosses were observed and were probably due to the presence of selfed plants. The amount of selfed plants in each cross was estimated at 24.9%, based on the selfs that occured when the recessive character, yellow petiole color was used.

Variance analysis for each character is presented in Table 6. Except for the reciprocal effects for the basal shoot data, all effects are significant at the 1% level. Since the magnitudes of the maternal and reciprocal effects vary with each character examined, and the maternal mean square of a character is smaller than its reciprocal mean square, it suggests that selfing may be present but the model does not account for the degrees of selfing among crosses.

The significance of the general combining ability (GCA) effects suggest that there are significant genetic differences between the parents and that the traits may be fixable by selection. The significance of the specific combining ability (SCA) effects suggest that some hybrid

Table 5. Unweighted genotypic means for all characters.

Male Genotype	Character	Female Genotype 1	2	3	4
1	B	1.0909*	2.0860	4.0000	2.3524
1	H	0.2424*	0.4409	1.6905	0.9412
1	L	13.9394*	15.3333	17.3333	16.0882
2	B	1.3924	1.0000*	3.6604	0
2	H	0.1392	0.4872*	1.2830	0
2	L	15.2532	16.4487*	16.7170	0
3	B	2.5743	3.0500	3.8000*	4.1707
3	H	0.3366	1.3875	2.3429*	5.0000
3	L	14.4554	16.4875	15.6000*	17.3659
4	B	1.6962	3.3279	3.6538	2.7949*
4	H	0.6076	1.3115	3.1154	4.6154*
4	L	16.2911	19.4590	17.3462	21.4103*

B = basal shoots

H = heart shoots

L = leaf number

* = used as estimate of parent values

Table 6. Analysis of variance of combining ability effects for each character

Character	Effect	Sum of Squares	Degrees Freedom	Mean Square
Basal Shoots	GCA	649.96577	3	216.65526**
	SCA	159.99472	6	26.66579**
	M	32.84325	3	10.94775**
	R	6.21816	2	3.10908
	error	1962.81906	859	2.28500
Heart Shoots	GCA	1260.82963	3	420.27654**
	SCA	197.86084	6	32.97681**
	M	23.37624	3	7.79208**
	R	35.76731	2	17.88366**
	error	2344.78383	859	2.72967
Leaf	GCA	2036.52796	3	679.84265**
	SCA	230.12416	6	38.35403**
	M	99.12354	3	33.04118**
	R	106.34004	2	53.17002**
	error	5303.32143	859	6.17383

** = significant at the 1% level

combinations can be expected to express a character more or less than the mean of the 1/2 sibs of the parent. This effect, if not allelic interaction, could be fixed. The high ratio of GCA to SCA sum of squares suggests a predominance of GCA effects. The reduced ratio for basal shoots may be due to a greater degree inconsistant deviations from the mean for this character.

Basal shoots:

The estimates of individual effects for the character basal shoots are shown in Table 7. The GCA effects for each of the parents were significantly different, suggesting genetic diversity of all parents for this trait.

Parents 1 and 2 exhibit the lowest GCA effects for basal shoot production and would probably be the better parents for reduced basal shoot production. Parent 1 showed the least variance of its SCA effects (Table 8), and should be considered before parent 2 in a breeding program.

The significant negative SCA effects for the selfed progeny of parents 2, 3, and 4 suggest reduced basal shoot production in comparison to the hybrids. The presence of heterosis in the hybrids would result in greater shoot production. The combination of complementary genes for basal shoot production in the F_1 may also have influenced the the increase.

Heart shoots:

The individual estimates for the character heart shoots are shown in Table 9. All parents showed significant GCA

Table 7. Estimates of individual effects for basal shoots.

Effect	Estimate		Effect	Estimate	
Mean	2.95636**				
GCA 1	-0.76855**		M 1	-0.30125	
GCA 2	-0.27415**		M 2	0.13666	a
GCA 3	0.77517**		M 3	0.03991	a
GCA 4	0.26753**		M 4	0.12468	a
SCA 11	-0.32836	a			
SCA 12	0.05558	ab	R 12	-0.03895	
SCA 13	0.60320	c	R 13	-0.15896	
SCA 14	-0.33042*	a	R 14	0.19791	
SCA 22	-1.40805**				
SCA 23	0.21451	bc	R 23	-0.03895	
SCA 24	1.13796**		R 24	0	
SCA 33	-0.70671**	a			
SCA 34	-0.11100	ab	R 34	-0.19791	
SCA 44	-0.69654**	a			

GCA = general combining ability (parent)

SCA = specific combining ability (female,male)

M = maternal effect (parent)

R = reciprocal effect (female,male)

**,* = significant at the 1% and 5% levels respectively

a,b,c = not significantly different at the 5% level by Student's t

Table 8. Variance of individual SCA effects.

Character	Basis	Parent 1	2	3	4
Basal Shoots	1	0.1947	1.1089	0.3072	0.6339
	2	0.2381	0.6720	0.2111	0.7082
Heart Shoots	1	0.5456	0.1283	0.2827	0.6543
	2	0.5352	0.1703	0.3463	0.8296
Leaf	1	0.8157	0.8527	0.8367	1.1081
	2	0.1223	0.8312	1.1472	1.5052

1 = variance computed including selfed progeny

2 = variance computed exclusive of selfed progeny

Table 9. Estimates of individual effects for heart shoots.

Effect	Estimate		Effect	Estimate	
Mean	1.64200**				
GCA 1	-1.07609**		M 1	-0.20491*	a
GCA 2	-0.68261**		M 2	0.08647	b
GCA 3	0.54761**		M 3	-0.15957	ab
GCA 4	1.21109**		M 4	0.27801*	b
SCA 11	0.75261**	a			
SCA 12	0.38197*	a	R 12	0.13115	a
SCA 13	-0.19250	b	R 13	-0.50781**	b
SCA 14	-0.94208**	c	R 14	0.37666**	a
SCA 22	0.21040	a			
SCA 23	-0.19819	b	R 23	-0.50781**	b
SCA 24	-0.39418	bd	R 24	0	
SCA 33	-0.39437	b			
SCA 34	0.78506**	a	R 34	-0.37666**	b
SCA 44	0.55120*				

GCA = general combining ability (parent)

SCA = specific combining ability (female,male)

M = maternal effect (parent)

R = reciprocal effect (female male)

**,* = significant at the 1% and 5% levels respectively

a,b,c = not significantly different at the 5% level by Student's t

effects, suggesting parental genetic diversity. The selfed progeny of both parents 1 and 4 showed significant positive SCA effects. The positive SCA effects of the crosses 1x2 and 3x4 (similar phenotypes) and the negative SCA effect of the cross 1x4 suggest the possibile presence of complementary genes for increased heart shoot production. The significant positive SCA effects for the selfed progeny of the parents 1 and 4 suggest that complementary genes present in the parents may be the major cause of the negative SCA effects of the selfed parents.

Since parent 1 showed the lowest GCA effect and most of its progeny showed negative or no SCA effects, it may be the best parent for fixing a genotype with reduced heart shoot production.

The complementary genotypes of parents 3 and 4 for basal shoot and heart shoot production and the differences in the magnitude of GCA and SCA effects suggest that basal shoot production and heart shoot production are controlled, at least in part, by different genes.

For breeding purposes, parent 1 would be the best choice for decreased shoot production, since it exhibits the most negative GCA effects for each character. Additionally, most of its SCA effects are negative, and show low variance (Table 8) and transmits decreased shoot production to its progeny. Since parents 1 and 2 are genetically diverse, there is the possibility of the appearance of transgressive segregants for reduced lateral shoot production due to the recombination of complementary genes in the F_2 generation.

Leaf number:

The individual estimates for the character leaf number are listed in Table 10. While all of the GCA effects were significantly different from each other, only the effects for parents 1, 3 and 4 were significant. Thus the parents were probably genetically diverse for this character. Since the GCA effects of a parent are computed as the average deviation of its progeny from the grand mean, the nonsignificant GCA effect of parent 2 could be caused by the similarity of the mean leaf number of the parent and its progeny to the grand mean of the plot. The SCA and GCA effects of the parents allow them to separated into groups on the basis of positive interactions within groups and negative interactions between groups. These groups generally correspond with low or high leaf number, suggesting the probable presence of complementary genes.

Selection for either increased or decreased leaf number should be possible, based on the the GCA effects. Parents 1 and 4 would be the best lines for decreased or increased leaf production respectively since the magnitude of their GCA effects is the largest.

Potence ratios

The weighted genotypic means for each character are shown in Table 11. Partial dominance and overdominance can be seen for each of the characters.

Table 10. Estimates for individual effects for leaf number

Effect	Estimate		Effect	Estimate	
Mean	17.08890**				
GCA 1	-1.56080**		M 1	-0.19670	a
GCA 2	0.15320		M 2	-0.14967	a
GCA 3	-0.51224**		M 3	0.55346**	
GCA 4	1.91984**		M 4	-0.20709	a
SCA 11	-0.02790	a			
SCA 12	-0.35516	ab	R 12	0.40965*	a
SCA 13	1.25144**	c	R 13	-0.89058**	
SCA 14	-0.86838**	a d	R 14	0.48093**	a
SCA 22	-0.94657**	b d			
SCA 23	0.06399	a	R 23	0.40965*	a
SCA 24	1.23774**	c	R 24	0	
SCA 33	-0.46441	a d			
SCA 34	-0.85102**	a d	R 34	-0.48093**	a
SCA 44	0.48166	a c			

GCA = general combining ability (parent)

SCA = specific combining ability (female,male)

M = maternal effect (parent)

R = reciprocal effect (female,male)

**,* = significant at the 1% and 5% levels respectively

a,b,c,d = not significantly different at the at the 5% level by Student's t

Table 11. Weighted genotypic means for all characters.

Male Genotype	Character	Female Genotype 1	2	3	4
1	B	1.0909	1.9692	3.5662	2.1249
1	H	0.2424	0.2653	0.9219	0.8349
1	L	13.9394	15.3261	16.2672	16.5795
2	B		1.0000	3.6719	4.0997
2	H		0.4872	1.3088	1.5848
2	L		16.4487	16.7939	20.4571
3	B			3.8000	3.8880
3	H			2.3429	4.1858
3	L			15.6000	17.6455
4	B				2.7949
4	H				4.6154
4	L				21.4103

B = basal shoots

H = heart shoots

L = leaf

Basal shoots:

The potence ratios for basal shoot production are shown in Table 12. Overdominance for increased shoot production was noted in the cross 1x2, 2x4 and 3x4. Partial dominance for increased basal shoot production was noted for crosses 1x3, 1x4 and 2x3. It appears that increased basal shoot production is dominant to decreased basal shoot production. The high potence ratio for the cross 1x2 may be due to the minimum difference between the parental values (Table 5).

Heart shoots:

The potence ratios for the character heart shoots are shown in Table 13. Partial dominance for increased heart shoot production is shown in the cross 3x4. Overdominance for decreased heart shoot production was shown in the cross 1x4. Partial dominance for decreased heart shoot production was noted for the remainder of the crosses. It appears that, in general, decreased heart shoot production is dominant to increased heart shoot production. The increase noted in the cross 3x4 may be due to complementary genes.

Leaf number:

The potence ratios for the character leaf number are shown in Table 14. Partial dominance for increased leaf number was observed in crosses 1x2 and 2x4. Overdominance for increased leaf number was noted in crosses 1x3 and 2x3 while partial dominance for decreased leaf number was noted in crosses 1x4 and 3x4. The overdominance observed in crosses 1x3 and 2x3 may be due to the mean of parent 3 appearing between the means of parents 1 and 2 (Table 5).

Table 12. Potence ratios for basal shoots.

Male Genotype	Female Genotype 2	3	4
1	20.3250	0.8274	0.2136
2		0.9085	2.4540
3			1.1752

Table 13. Potence ratios for heart shoots.

Male Genotype	Female Genotype 2	3	4
1	-0.8132	-0.3538	-0.1108
2		-0.1146	-0.4682
3			0.6219

Table 14. Potence ratios for leaf number.

Male Genotype	Female Genotype 2	3	4
1	0.1052	1.8036	-0.2932
2		1.8134	0.6158
3			-0.1479

Parent 4 appears to posseses genes that allow partial dominance for reduced petiole number.

Covariance-variance analysis

Basal shoots:

The graph on the regression of Wr on Vr for the character basal shoots is presented in Figure 3. The correlation coefficient was 0.9114. The slope was 0.7986. The slope was significantly different from 0 ($p = 0.0885$) but not significantly different from 1. The y-axis intercept was 0.005147, which was not different from 0. Since the slope of the regression line is close to one, no non-allelic interaction was detected. The insignificant intercept suggests full dominance. The dominance order of the parents, in order of increasing dominance, is 2,1,4,3 and corresponds with the amount of basal shoots produced by each parent. Parent 3 also appears to possess all of the dominant alleles for basal shoot production. Thus increased basal shoot production appears to be controlled by dominant genes.

Heart shoots:

The graph on the regression of Wr on Vr for the character heart shoots is presented in Figure 4. The correlation coefficient was 0.97496. The slope of the regression was 0.84420, which was significantly different from 0 at the ($p = 0.025$) and not different from 1. This suggests the absence of non-allelic interaction for this character. The y-axis intercept was 0.76779, significantly

Figure 3. Graph of the regression of Wr on Vr for basal shoot production.

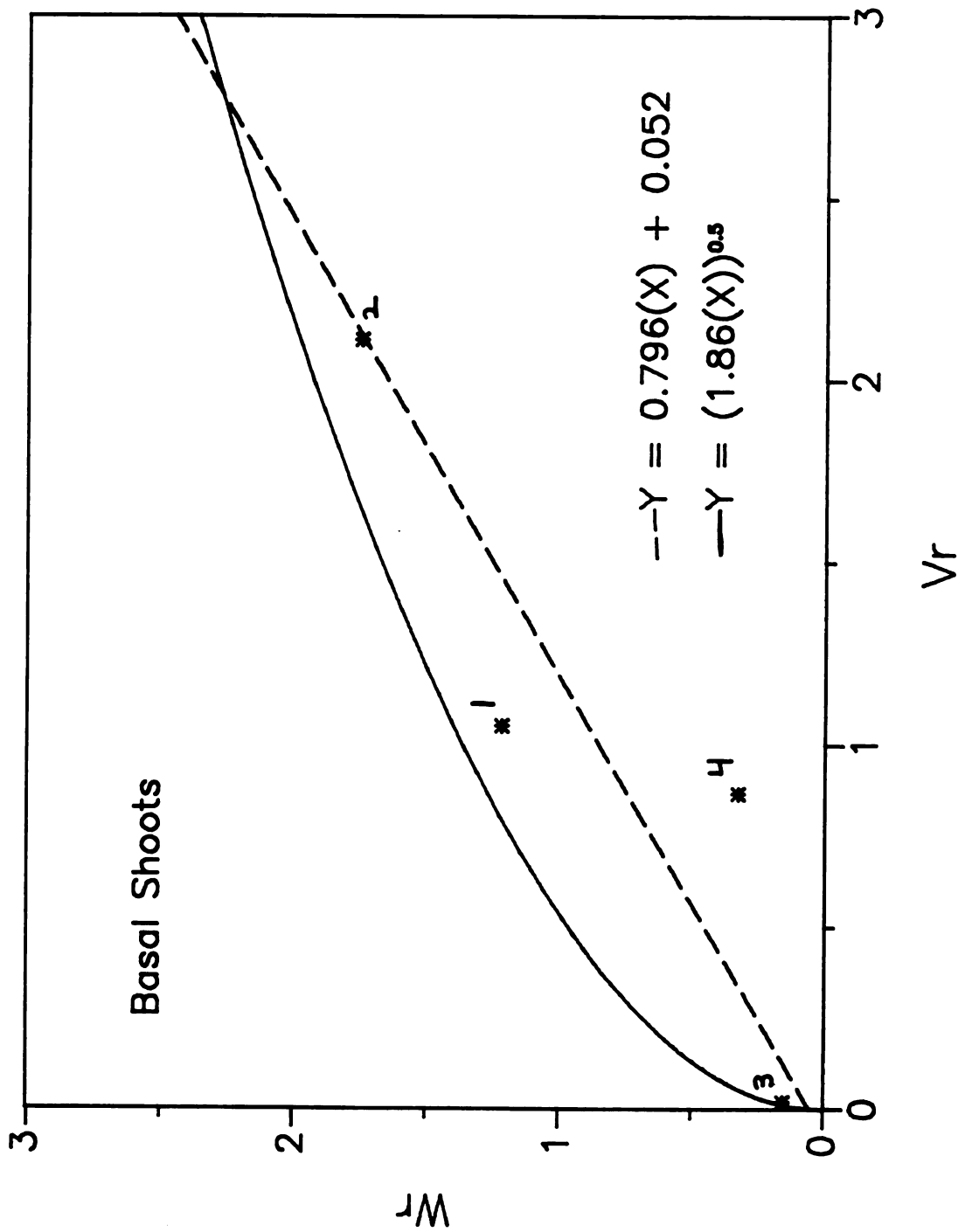

Figure 3.

Figure 4. Graph of the regression of Wr on Vr for heart shoot production

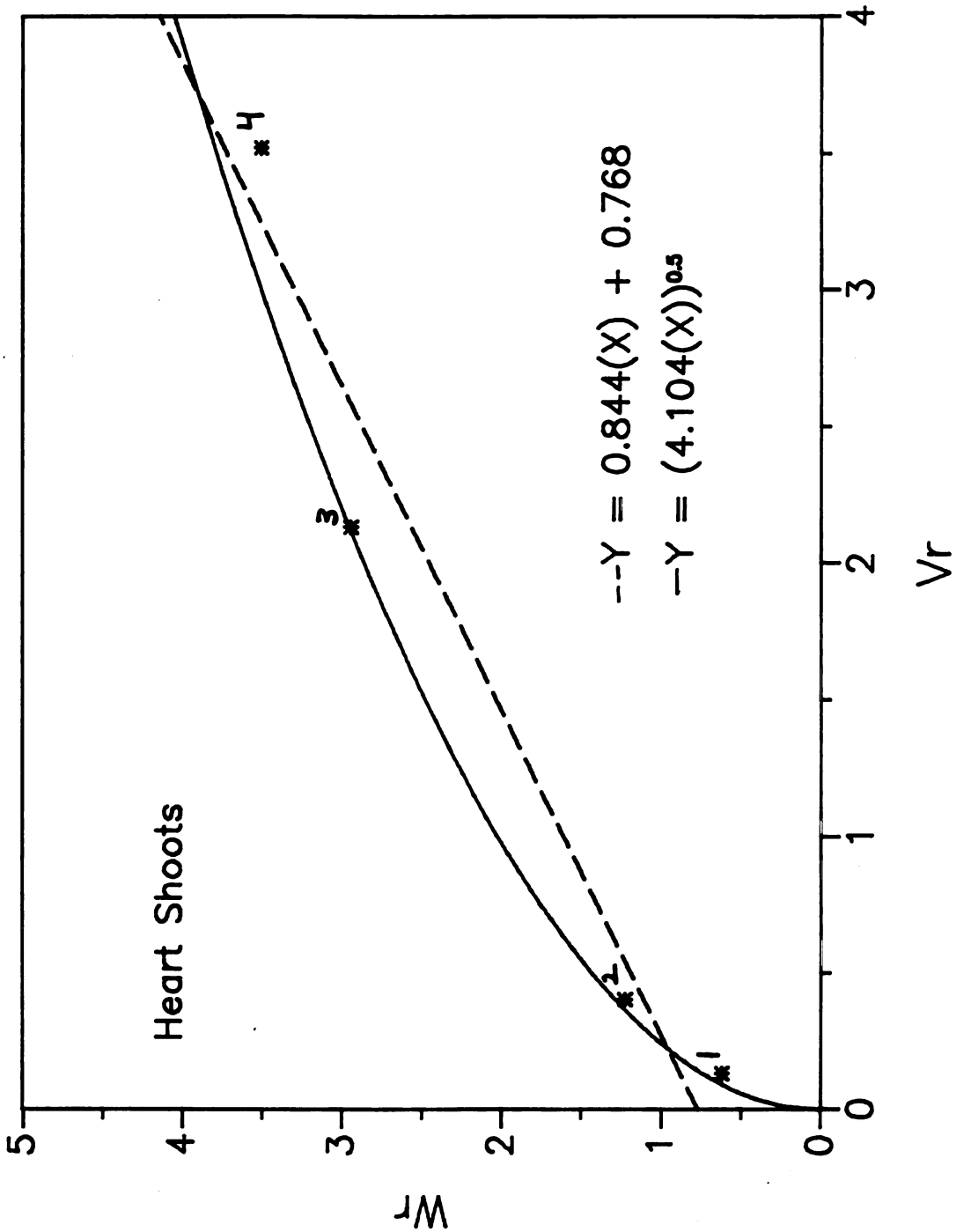

Figure 4.

different from 0 at the (p = 0.1122), suggesting the possibilty of partial dominance. The increasing dominance order of the parents is 4,3,2,1 which also corresponds with the degree of heart shoot production of each of the parents. Parents 1 and 4 are at the limits of genetic variation for this character for this study and it appears that reduced heart shoot production is conditioned by partially dominant genes.

Leaf number:

The graph on the regression of Wr on Vr for the character leaf number is presented in Figure 5. The correlation coeffecient was 0.9574. The slope of the regression line was 1.0221, significantly different from 0 at the (p = 0.0126) and not different from 1. This suggests the absence of non-allelic interaction. The y-axis intercept of 1.5011, significant at (p = 0.0721), suggests the possibility of partial dominance.

The clustering of the parents suggests that parents 1 and 3 are similar genetically, as are parents 2 and 4. Parents 1 and 3 appear to differ from parents 2 and 4 by a dominant major gene for reduced leaf number and modifiers. Parents 3 and 2, while not extreme phenotypes, may be near the limits of genetic variability in this population.

Correlations

The phenotypic and genetic correlations between the characters basal shoots, heart shoots, and leaf are shown in Table 15. The phenotypic correlations computed on the individual plant basis are statistically significant for

Figure 5. Graph of the regression of Wr on Vr for leaf number

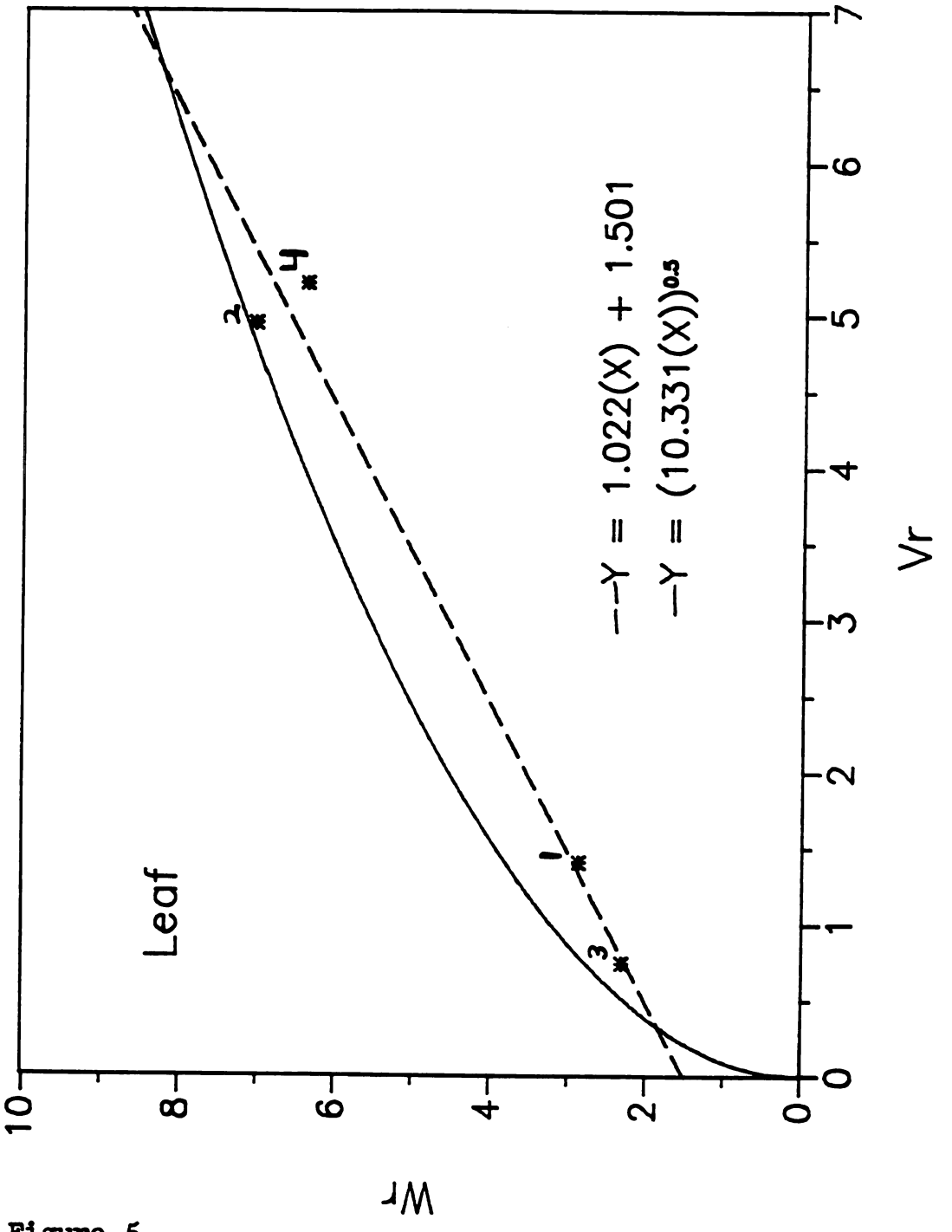

Figure 5.

Table 15. Correlations between characters.

Character	Type	character: Heart Shoots	character: Leaf
Basal Shoots	1	0.3332**	0.3898**
	2	0.5207	0.4505
	3	0.8275	0.4351
Heart Shoots	1		0.3934**
	2		0.6716*
	3		0.7766

*, * significant at the 5% and 10% levels respectively

1. phenotypic, computed on individual plant basis, df = 857

2. phenotypic, computed on genotypic means, df = 10

3 genetic, computed on GCA effects, df = 2

all characters. The low correlations between the variables basal shoot production,heart shoot production and leaf number suggest minimum relationship between these characters.

The phenotypic correlations computed from the genotypic means showed reduced significance due to the lesser degrees of freedom. The nonsignificant correlations between basal shoots and heart shoots and basal shoots and leaf number suggest no relationship between these traits. The significant correlation between heart shoots and leaf number suggests a relationship between these traits. This is probably due to the upper limit on the number of axillary shoots imposed by the number of leaves.

There was no genetic relationship among the characters.

CONCLUSIONS

Several analyses were performed on the data from the diallel crosses. The fixed effect models used limit the interpretations to the parents studied. The combining ability analysis revealed highly significant GCA effects, suggesting that selection would be effective on any of the traits, basal shoot number, heart shoot number, or leaf number. The high ratio of GCA to SCA sum of squares for all effects suggests that large portion of the genetic variation was probably due to general combining ability effects. The SCA effects, while statistically significant may be of less practical importance.

The positive SCA effects and overdominance observed in the hybrids may be due to inbreeding depression of the selfed parents (Orton, 1984) or the combination of complementary genes in the hybrids. The variation of sign of the significant SCA effects of the selfed progeny suggests that the combination of complementary genes contributed by the parents may be the predominant cause of increased character expression in the hybrids.

The genetic and phenotypic differences between basal and heart shoot production suggested by the combining ability analysis and potence ratios were also noted for the Wr-Vr

regressions. Increased basal shoot production was conditioned by dominant genes. The results showed that decreased heart shoot production was conditioned by partially dominant genes. Since increased basal shoot production is conditioned by dominant genes, selection and fixation of lines with reduced basal suckering would be possible. This is important since removal of basal suckers requires a major portion of the grower's trimming time.

Based on the combining ability and Wr-Vr regression analyses for leaf number it appears that parents 1 and 3 and parents 2 and 4 may be of similar genotypes. The two groups of parents probably differ by a dominant major gene and modifiers for reduced leaf number. Interaction of the minor genes may have affected the sign and magnitude of the potence ratios.

The phenotypic correlation between heart shoot and petiole production is probably due to the dependence on the presence of leaf axils. The phenotypic correlations between basal shoot and heart shoot production were low, suggesting near independence of these characters.

CHAPTER 2: INHERITANCE OF A DWARF MUTANT IN CELERY

INTRODUCTION

Since celery has few genes for morphological markers, recovery of hybrid plants can be difficult due to uncontrolled selfing (Orton, 1984). A dwarf celery mutant identified by Orton (1982) was considered for use as a marker. The plants were described as spindley with a elongated infloresence and reduced seed production, reducing the utility of the mutant as a marker (Orton, 1982). The dwarf studied in this investigation differs from the previously described dwarf in that it is compact and stocky, with a normal inflorescence. The amount of seed produced by these dwarf plants is normal.

Since this gene has distinctive phenotype and adequate seed yield, it could be a useful addition to the markers already in use.

The objective of this study was to determine the mode of inheritance of the dwarf phenotype.

LITERATURE REVIEW

A literature review by Pelton (1964) of the single gene dwarfs in the angiosperms cites 112 dwarf mutants in 17 families. Most of the dwarfs were found to be recessive, the exceptions being D8 in maize and sterile dwarf (D) in barley. Dwarf plants exhibit a reduction in size of all organs or exhibit reduced internode length only as in the dwarf (d) and brachytic (br) mutants of tomato (Butler, 1962).

Pelton (1964) cites several physiological traits associated with dwarfism;

(1) abnormal gibberellin biosynthesis or utilization

(2) decreased auxin levels in dwarf plants

(3) Abnormally high peroxidase activity and abnormal peroxidase types observed in maize dwarfs (McCune, 1961).

Reduced mitotic activity, cell number and cell size have been reported in several histological studies of dwarf plants (Liu and Loy, 1972; Sandhu et al., 1972; Pelton 1964). Precocious secondary thickening of the cell wall has been observed in several dwarfs (Pelton, 1964).

The altered seedling appearance mutant (as) of celery, is a single gene recessive and probable hormone mutant

(Orton, 1982). The dwarf condition is characterized by: very slow growth, spindly stems, narrow deformed leaves, an elongated "vine-like" inflorescence and reduced seed set (Orton, 1982; Orton, 1985; Quiros, 1985). The trait was discovered in PI 229526 and is linked to the ms8 locus (Orton, 1982).

The genetics of the recessive semi-dwarf in wheat is more complex, since it may be controlled by alternate alleles Gai/Rht 1 and Gai/Rht 3, located on chromosome 4A, and the gene Gai/Rht 2, located on chromosome 4D (Gale and Law, 1977). The genes Gai/Rht 1 and Gai/Rht 2 are additive in nature (Gale and Law, 1977; Allan et al., 1968). Additional modifier genes appear to affect culm length, contributing to the quantitative nature of the Norin 10 based semi-dwarfism (Gale and Law, 1977; Allan et al., 1968).

Recessive single gene dwarfs, d1, d2, and recessive polygenic dwarfs d3 and d4 in Pennisetum typhoides were reported by Burton and Fortson (1966). Estimates of 1.8 to 6.1 effective factors controlling the action of d3 and d4 were obtained. Further studies by Gupta et al. (1985) indicated that the brachytic dwarf (db) gene of pearl millet exhibited recessive epistasis to the d2 gene.

The dwarf modifier gene (dm) of tomato has been reported to be epistatic to the dwarf (d) gene (Butler, 1952). The homozygous dwarf and the homozygous dwarf modifier condition must be present to produce the "extreme dwarf" phenotype.

MATERIALS AND METHODS

Parents for this study were obtained as follows: segregation of a dwarf phenotype was identified in a population of a massed seed increase of the MSU experimental line 81-648 in the 1983 and 1984 growing seasons. The dwarf plants showed a nearly 50% reduction in height, reduced leaf size and gnarled petioles, (Figure 6). Since the genetic make-up of the massed population was unknown and the inheritance of the character could be determined from the segregation of the progeny of heterozygous plants, several plants of each phenotype were selected for selfing.

In the fall, normal and dwarf plants were lifted from the field, pruned, and potted in 25 cm pots filled with muck soil. The plants were placed in the lath house for two weeks for establisment and were then moved into a lighted 5 C vernalization chamber for eight weeks. The vernalized plants were then moved to a 19 C greenhouse with supplemental lighting with a 14 hour day. After two weeks, the temperature was raised to 22 C to hasten flower stalk development. The plants began to flower in February of 1985.

Eight normal and 15 dwarf plants were each enclosed with a polyethylene cheese cloth bag to prevent outcrossing.

Figure 6. Plants exhibiting normal and dwarf phenotypes

Left: dwarf phenotype

Right: normal phenotype

Figure 6.

The bags were retained until seed harvest. The seed was sown in vermiculite and the flats were placed on a timed heating pad, providing a minimum day temperature of 22 C and a night temperature of about 15 C (ambient).

The seedlings were transplanted into flats filled with a commercial peat-perlite mix when they had developed at least on true leaf. A maximum of 90 seedlings of each line were transplanted. The eight week old plants were set in the field in June. The experimental plot was arranged as a completely randomized block design with three replications. The plants of a line were divided equally between replications. Guard plants were placed at the ends of the rows and in any spaces within rows and plots.

The height of each plant was defined as the distance from the crown at soil level to the tip of the longest leaf and was determined to the nearest 1.3 cm (0.5 inch) and recorded. Individual plant data were entered on a micro computer and uploaded to the MSU Control Data Corporation Cyber 750 computer for statistical analysis using the SPSS.9 program. Chi-square analysis of the data was performed according to the formulae and tables published by Steele and Torrie (1979) and Little and Hill (1982).

RESULTS AND DISCUSSION

The selfing of 13 of the 15 dwarf plants showed homozygosity for the dwarf plant habit while two plants were discarded due to possible contamination. The mean height of the dwarf plants was 41 cm. The progeny of two of the eight tall plants showed no segregation and were thus considered homozygous. The mean height of the tall plants was 63 cm. The mean of the two classes was 52 cm. Since 52 cm approximated the minimum height of the tall lines and the mean maximum height of the dwarf lines, 52 cm was used as the dividing point of the two classes.

The expected values for each class were computed for each of the six segregating lines. The observed and expected numbers of each class, the Chi-square value and the probability are shown in Table 16. Two of the progenies showed a poor fit to the monogenic recessive hypothesis. A test of heterogeneity was nonsignificant (Table 16) and a Chi-square on the pooled data showed a good fit to a 3 tall to 1 dwarf ratio. Thus it is assumed that the dwarf phenotype is conditioned by a single recessive gene.

Tests for allelism with the dwarf gene, _as_, described by Orton (1982) were not performed since plants of the _as_ _as_ genotype were not available and the two dwarf types showed

marked phenotypic differences.

Table 16. Observed and expected values, Chi-square values and probalities for dwarf and tall classes and ratios.

Line	Observed Ratio	Expected Ratio	Chi-square	Probability
2	18 : 55	18.25 : 54.75	0.0046	0.95 > p > 0.90
4	21 : 65	21.5 : 64.5	0.0000	p > 0.99
5	14 : 56	17.5 : 52.5	0.6857	0.50 > p > 0.25
7	26 : 48	18.5 : 55.5	3.5315	0.10 > p > 0.05
8	12 : 70	20.5 : 61.5	4.1626	0.05 > p > 0.02
17	21 : 57	19.5 : 58.8	0.0684	0.90 > p > 0.75
Total			9.8604	0.25 > p > 0.10
Pooled	112 : 351	115.75 : 347.25	0.1619	0.75 > p > 0.50
Heterogeneity			9.6985	0.10 > p > 0.05

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