

INHERITANCE OF FACTORS RELATED  
TO EARLINESS IN PEPPER  
CAPSICUM ANNUUM L.

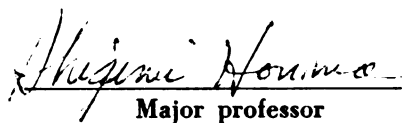
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## ABSTRACT

### INHERITANCE OF FACTORS RELATED TO EARLINESS IN PEPPER Capsicum annuum L.

by Nabeel S. Mansour

Studies on the inheritance of earliness factors: number of days to first anthesis, number of nodes to the first furcation and number of red ripe fruit were carried out.

A hybridization program using one plant selection from Earliest Red Sweet and Plant Introduction No. 251622 (early parents) and two individual plant selections of Resistant Florida Giant (late parent) was initiated during the summer of 1964. In the reciprocal crosses of Earliest Red Sweet x Resistant Florida Giant, the data suggest a high level of dominance for the shorter duration to first anthesis, fewer number of nodes to first furcation and greater number of red ripe fruit per plant by the first killing frost. One major gene was found to control the genetic variation observed. In the cross, PI 251622 x Resistant Florida Giant, the data supported the findings in the cross, Earliest Red Sweet x Resistant Florida Giant, except for number of nodes subtending the first furcation where a two gene model was proposed in which one gene was twice as effective as the other.

Correlation coefficients were obtained for relationships between leaf length, width and leaf area index (length x width) and the number of days to first anthesis, number of nodes to the first furcation and number of red ripe fruit by the first killing frost; also between fruit bearing habit and the earliness factors.

INHERITANCE OF FACTORS RELATED TO EARLINESS  
IN PEPPER Capsicum annuum L.

By

Nabeel S. Mansour

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DEDICATION

To My Family

Jean, Michael and Barry

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## INTRODUCTION

The pepper, Capsicum annuum, a perennial plant (4) is found in the mountains of northern Chile and Peru (19, 43). It is grown in the northern latitudes as an annual and is becoming increasingly important, especially in Michigan where it is now valued at nearly a million dollars (27).

The pepper is used in many different forms, dried, fresh and processed. In Michigan it is grown as a fresh market and processing crop. A small per cent is processed as a frozen product while the larger per cent is processed as a pickled product. With the mounting labor problem in the harvesting of cucumbers for pickling, processors are leaning toward the use of peppers to augment the shortage of cucumbers. Since the crop is grown as an annual, earliness as well as high productivity are attributes necessary to make this an economical crop.

Earliness has been defined by several investigators as the number of days to the anthesis of the first flower in the tomato and the squash, the number of days to silking or to pollen shed in corn, the number of days to heading in wheat,

or the days to the first fruit ripe in the tomato (1, 4, 6, 14, 16, 17, 20, 21, 25, 29, 31, 38, 41, 48). Some of these investigators have further subdivided each of the above components of earliness into the number of days from anthesis to first fruit set, and the number of days from first fruit set to first fruit ripe (16, 25, 38).

In this study, the following criteria were used to measure earliness:

1. Number of days to first anthesis...  
number of days from seeding to the  
opening of the first flower at the  
first furcation.
2. Number of nodes to the first furcation  
excluding cotyledonary node.
3. Number of red ripe fruit per plant by  
the first killing frost (October 5, 1965).

In order to learn the inherent behavior of these earliness factors in the pepper, widely divergent parental materials were selected from two seed sources, the Plant Introduction Station and commercial seed houses. Two parallel studies were conducted.



The variety, Earliest Red Sweet (ERS) with a maturity date of fifty-five days and Resistant Florida Giant (RFG) at eighty-five days were selected. The Plant Introduction (PI) accession No. 251622, classified as "early" in Plant Introduction catalogue was selected as the early parent for the second set of crosses.

All selected materials were screened for homozygosity prior to hybridization. For the first of two crosses, a single plant selection from the variety ERS was hybridized with a selection from RFG. For the second cross a single plant selection from PI No. 251622 was crossed to another single plant selection from the variety RFG.

Reciprocal crosses were made to obtain the  $F_1$ ,  $F_2$ , and backcross populations. All populations were field grown to obtain information for the inheritance study.

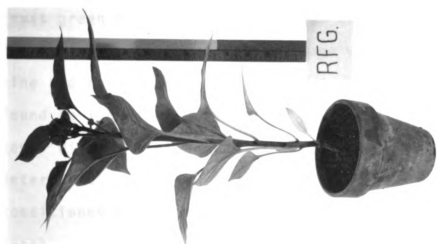
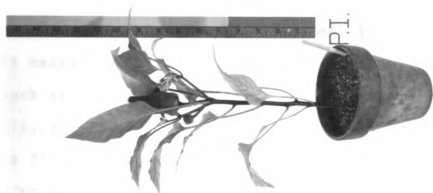
Other factors for which the parental selections differed were studied for their possible correlation with earliness. These factors are leaf shape and fruit bearing habit, Figure 1.

Figure 1. Plants of the three parent lines grown from seed under greenhouse conditions

Resistant Florida Giant (RFG) showing a greater number of nodes to first furcation. Lateness, larger leaf size and pendant fruit bearing habit may also be noted.

Earliest Red Sweet (ERS) showing less number of nodes to first furcation. Earliness and pendant fruit bearing habit may also be noted.

Plant Introduction No. 251622 (PI) showing similar growth characteristics as Earliest Red Sweet, except for upright fruit bearing habit.



## REVIEW OF LITERATURE

Several investigators studying earliness have found it necessary to partition earliness into several component such as the number of days from seeding to first anthesis (16, 21, 25, 31, 38); the number of days from first anthesis to first fruit set (16, 25, 38); and the number of days from first fruit set to first fruit ripe (16, 25, 38). In cereals earliness has been subdivided into the number of days from seeding to heading (1, 29, 49); the number of days from seeding to pollen shedding (29), and the number of days from seeding to the ripening of the grain (4, 49).

In the pepper, Odland (31) studied the inheritance of maturity in a cross between Harris Early Giant X Ornamental. Maturity was measured as the days to the appearance of the first blossom, days from seeding to the fruit green mature stage, and days from seeding to first fruit ripe. The green mature stage was difficult to determine and consequently was not used. The  $F_1$  generation was found to flower with the early parent. The number of genes differentiating the parents in the cross was not determined, but it was postulated that early maturity may be conditioned by several dominant or partially dominant maturity genes.

Early flowering in pepper hybrids has been reported by several other investigators. Hirose (19) reported that interspecific  $F_1$  hybrids involving five Capsicum species exhibited earliness in all species hybrids except those with C. annuum. Deshpande (14) reported that the  $F_1$  between an early and late pepper flowered one week earlier than the early parent.

Inheritance of earliness has been reported in the tomato and squash. In the tomato, overdominance for early flowering was reported by Burdick (6), Cram (11), Hays and Jones (18), Wellington (51), and Lyon (25). Dominance for early flowering was reported by Currence (12), Fogel and Currence (16), Honma, Wittwer and Phatak (21), and Powers, Locke and Garrett (38).

Burdick (6), studying the results of eight inbred tomato lines crossed in all combinations, found that  $F_1$ 's tend to be earlier than the earliest parent in days from germination to first fruit set. Burdick (6) also noted that earliness was not fully manifested until the time of first ripe fruit. The time of flowering in most of the  $F_1$ 's was approximately intermediate between the flowering dates of the two parents, however exceptions were found to this intermediate flowering date relationship between the  $F_1$  and the parents. Some of the  $F_1$ 's exhibited overdominance for earliness, while others

exhibited overdominance for lateness. Burdick (6) also noted that although two hybrids may show identical earliness, their developmental patterns may have been different. From a constant parent regression analysis of the data, Burdick (6) suggested that it appears that earliness in the tomato is due principally to dominance.

Honma, Wittwer and Phatak (21) studied the inheritance of earliness in a cross between Michigan State Forcing X Pennorange. Two characters, the number of days from seeding to first anthesis, and the number of nodes to the first flower cluster were studied. These investigators found that one major gene differentiated the two parents for both characters. A high correlation ( $r = +0.94$ ) was noted between the number of days to the first anthesis and the number of nodes to the first flower cluster. Based on this relationship and linkage studies, they suggested that the same gene may have conditioned both characters.

Lyon (25) studied the inheritance of earliness in a cross between two tomato species, and subdivided earliness into several components. The period from planting to first bloom was studied in two parts as pre-hail and post-hail response since shortly after first bloom, a severe hail left only the stubs of the plant stems above ground. The period from first fruit set to first complete color change,

and the summation of all these constituents as the period from seeding to first complete color change were also investigated. Lyon (25) observed that the range between early and late parents for the interval from seeding to first bloom before the hail was greater than after the hail. The  $F_3$  strains which showed earliness to first bloom before the hail, showed no indications of earliness after the hail. The  $F_1$ 's were found to be earlier than the earliest parent. No estimate of the number of genes differentiating the parents was made due to the complications caused by the hail.

Fogel and Currence (16) reported dominance for shorter duration to first bloom in tomato since the observed  $F_1$  mean was significantly lower than the arithmetic mean of the two parents. Geometric or logarithmic processes were not evident for this character. Earliness was subdivided into the period from seeding to first bloom, the period from first bloom to first fruit set, the period from fruit set to ripe fruit, and the sum of these components as the period from seeding to ripe fruit. The number of genes involved was estimated by two methods. Using Powers (38) partitioning method, five or more genes were suggested to condition the stage from seeding to flowering, four gene pairs for the period from flowering to fruit set, and three pairs for the stage from fruit set to fruit ripe. Association tests suggested

four or more gene pairs for the first stage, and three and two gene pairs for the second and third periods, respectively. Five to twelve genes were suggested to differentiate the two parents for earliness. Partial dominance was exhibited among alleles and an approximately additive nature was postulated between different earliness genes.

Powers, Locke and Garrett (38) reported dominance for early flowering in tomato. They divided earliness into the period from seeding to first bloom, the period from first bloom to first fruit set and the period from first fruit set to first fruit ripe. Using the partitioning method of genetic analysis they suggested that in the period from seeding to first bloom, the parents were differentiated by three major gene pairs, and the period from seeding to fruit ripe was conditioned by eight major gene pairs. Since this latter period and its components are interdependent, it was suggested that these two characters must have some genes in common.

Interactions of earliness genes with "unrelated" genes have been reported by Currence (12) and MacArthur (26). MacArthur (26) reported that the presence of the recessive allele of the gene lutescent (1) retards maturity



by two weeks. Currence (12) found that the gene for simple inflorescence (s) had an effect on seed germination percentage as well as the time required for seed germination. The presence of gene (s) delayed time to fruiting by 4 to 8 days. Differences in time of fruiting were noted to be associated with the (Dd) region and the (Pp) region, these being the genes for dwarf (d) recessive to normal habit (D); and pubescent fruit (p) recessive to smooth fruit (P).

In a study of the inheritance of earliness in squash, Singh (41) divided earliness into the number of days from seeding to the opening of the first male flower, the number of days from seeding to the opening of the first female flower and the difference between the opening of the first male flower and the first female flower. Using Powers (38) partitioning method, Singh (41) suggested that the two parents were differentiated by three major gene pairs for the number of days from seeding to the opening of the first male flower, and the number of days from seeding to the opening of the first female flower. Two major gene pairs were suggested for the interval between the opening of the first male and the first female flower.

In corn crosses between early and late inbred lines, dominance for earliness has been reported by Sprague (45).

Mohamed (29) studied the inheritance of maturity of Zea mays and reported complete phenotypic dominance for shorter duration from seeding to silking and from seeding to pollen shedding. There was also complete phenotypic dominance for longer interval between silking and pollen shedding. He suggested that for the number of days from seeding to silking, the parents were differentiated by three major genes; while for the number of days from seeding to pollen shedding, the parents were differentiated by two major genes. The number of days from silking to pollen shedding was conditioned by one major gene.

In wheat, dominance for early flowering and seed ripening (1, 5), as well as for late flowering and seed ripening (48) has been reported. Biffin (5) noted that in a cross between Polish (early) X Rivet (late) varieties, early ripening was a simple dominant over late ripening when the data were taken late in the season (August 3rd in his study). Data taken only four days before (July 30th) showed a ratio of 1:2:1 for ripe:half-ripe:unripe.

Allard (1) studying days to heading in wheat, attributed most of the variation observed to two genes, one being five times as effective as the other. In studying the same populations grown under five different sets of environmental circumstances, Allard (1) noted that in three of the

five experiments, one gene governed most of the genetic variability. Dominance varied from weak dominance for the shorter duration to heading, to over-dominance. In the other two of the five experiments with these same populations under different environmental conditions no more than one-half of the genetic variation could be attributed to any single gene.

In contrast to these two reports in wheat, Thompson (48) and Freeman (17) suggested that the number of days to flowering and ripening was a complex trait, and was quantitatively inherited. Furthermore Thompson (48) observed that the  $F_1$ 's resulting from crossing eight different wheat varieties headed and matured with the late parent. Thompson was reluctant to attribute this to dominance but preferred to attribute the lateness to vigor which may have postponed the heredity maturation period.

In other crops, over-dominance for lateness has been reported by Weber (50) in soy beans; Burton (7) in pearl millet; and by Suneson and Riddle (47) in barley. Quantitative inheritance was suggested in flowering of oats. In an inheritance study, St. Clair Capron (46) suggested that early heading in oats was found to be conditioned by three factors.

In rice, Ramiah (39) studied the inheritance of flowering in several crosses. In certain crosses, a single factor differentiated the early and late parents with earliness being generally dominant. In other crosses the inheritance of the number of days to first flower was rather complicated and was postulated to be conditioned by multiple factors. In these crosses, the  $F_1$ 's were intermediate and transgressive segregation was observed in the  $F_2$  generations. Van der Stok (49) reported dominance for early ripening in rice. However, in certain crosses, early ripening was completely dominant while in others reverse dominance was observed where late ripening was completely dominant.

Odland (31) studied the relationship between the number of days to first anthesis and the number of days to first ripe fruit. A correlation coefficient of ( $r = +0.70$ ) between these two characters suggested that either trait could be used as an indicator of earliness.

Miyazawa (28) and Carlson (8) reported that leaf shape in pepper was quantitatively inherited. Carlson (8), in a study of thirty-six  $F_1$  combinations, reported obtaining intermediate  $F_1$ 's in crosses between large and small leafed

varieties, and reported that leaf size was positively correlated with fruit size. Miyazawa (28), suggested at least 1.59 genes controlling leaf length and 7.69 genes controlling leaf width.

In the tomato Lopez (24) and Honma et al (21) reported a high correlation between number of nodes to first anthesis and number of days to first anthesis. Biffen (5) working with wheat found no relationship between plant habit and early or late ripening. Ramiah (40) studied the relationship between number of days to flowering and plant height and found an association between plant height and number of days to flowering.

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## MATERIALS AND METHODS

### Evaluation Of Parental Material

Eight late and six early accessions were obtained from the Plant Introduction Station at Experiment, Georgia. These accessions were selected from the Plant Introduction catalogue on the basis of fruit size, fruit bearing habit, fruit color, pungency, plant vigor and origin.

The Plant Introduction accessions together with five commercial varieties were planted at the Michigan Agricultural Experiment Station greenhouses on December 16, 1963 in flats filled with vermiculite. The seedlings were transplanted into soil-filled 2-1/4 x 2-1/4 inch peat pots on January 1, 1964, and later in 10-inch clay pots.

Four plants from each of the accessions and varieites were grown in the greenhouse using supplementary light and temperatures of 75 to 80 degrees F. to flowering. The temperature was lowered to 70 to 75 degrees F. for pollination and fruit set and then raised again to 75 to 80 degrees F. to hasten fruit ripening (9). A twelve hour photoperiod was imposed since it has been reported (3, 10) that flowering, fruit set and maturation were accelerated under this photoperiod.

At the time of flowering, the PI lines were classified according to the descriptions of the Capsicum sp. given by Smith and Heiser (42, 43) since the Plant Introduction catalogue does not distinguish between C. frutescens and C. annuum. Plants which appeared to be of C. annuum species were saved and selfed. Eight plants from each of these plants were evaluated in the field during the summer of 1964. The plants were observed for uniformity of characters to be investigated so that hybridization could be limited to one plant from an early and a late line for each of the two crosses. Two varieties were used as the early parents, Earliest Red Sweet (Stokes Seed Company) which had been in the Michigan Agricultural Experiment Station's collection for several years and a Plant Introduction accession No. 251622. For the late parent, the variety Resistant Florida Giant (Lot number 67140 from the Asgrow Seed Company) was used as a common parent for both crosses.

Reciprocal crosses were made between several plants of the late and early parents. Flowers were also allowed to self on the parental plants. Asexual propagation of parental material was made to insure against the loss that



may occur subsequent to lifting of the plants.

### Vegetative Propagation

Successful asexual propagation of the pepper plant was obtained by use of young vegetative shoots. Shoots six to eight inches long, with five to six leaves, cut at an angle through a node were found most desirable. The cut surface was moistened and dipped in Rootone #2, an indole butyric acid formulation, prior to placing in a sand-filled flat maintained at 75 degrees with bottom heat for rooting. In three weeks the cuttings were well rooted and were then potted.

### Hybridization

Although the pepper is considered to be a self-pollinated species (2), considerable outcrossing has been reported (30, 32). A modification of a pollination technique reported by Dempsey (13) was used to prevent foreign pollen contamination. Large (no. 0) gelatin capsule halves were placed over the unopened buds a day prior to anthesis to protect the flowers that were allowed to self. Capsules were also used to protect flowers used in hybridization. Emasculation and crossing of the flower was accomplished the day before the anthers dehisced since it has been reported that

the stigma is fully receptive at this time (35). The capsule was held in place by wrapping a small piece of cotton around the pedicel of the flower. The moistened opened end of the capsule was slipped over the flower bud till it came in contact with the cotton. All pollinations and selfs were labeled.

The cool late summer and early fall temperatures failed to ripen the cross-pollinated and self-pollinated fruits prior to the first frost. The parental plants were dug and potted in clay pots and were moved to the greenhouse where they were shaded until established. To prevent fruit drop, the pedicels of the fruits were treated with a naphthalene acetic acid lanolin formulation by applying a small amount of the paste to the pedicels of the developing fruits.

Selfed seeds from the parental plants were progeny tested during the winter of 1964-65 to check the uniformity of the parental plants. The  $F_1$ 's were also grown at this time. Records were obtained for the following characters: number of nodes to the first furcation, number of days to anthesis at the first furcation (first anthesis), and number

of days to anthesis at the second furcation (second anthesis).

Table 1 shows the means and standard deviations of the progeny test of the various selections of Resistant Florida Giant, Earliest Red Sweet and Plant Introduction Number 251622 used in hybridization during the summer of 1964. The progeny test was composed of 10 plants of each selection used in crossing. The plants were arranged in a 10 replicate randomized block design. Resistant Florida Giant selections number 1 and 16 were chosen since they showed the greatest uniformity together with greater number of days from seeding to flowering and high node number to the first furcation. Four  $F_1$  plants from each of the crosses ERS-6 x RFG-1, RFG-1 x ERS-6, PI-4 x RFG-16, and RFG-16 x PI-4 were selfed and backcrossed to the original parents. All other  $F_1$  plants and parental plants used in similar crosses were discarded.

### Field Trial

Since observations made during the course of study suggested that plants were set back in transplanting from the seedling flats to the peat pots, it was decided to seed

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Table 1. Progeny test of parents used in crosses during the summer of 1964

Selection	No. of days from seeding to first anthesis at the first furcation		No. of nodes to the first furcation		No. of days to first anthesis at the second furcation	
	Mean		Mean		Mean	
RFG-1*	98.80	± 2.78	15.4	± .52	104.22	± 3.94
2	91.89	± 2.98	15.8	± .42	100.90	± 5.13
3	96.25	± 6.84	15.5	± .85	105.40	± 6.98
4	87.67	± 3.19	15.1	± .60	95.83	± 1.48
9	89.00	± 4.36	14.3	± .83	101.89	± 4.07
10	99.33	± 6.86	16.3	± .68	105.60	± 6.22
16*	96.75	± 1.84	15.4	± .70	106.11	± 2.57
ERS-1	79.50	± 1.64	9.9	± .32	92.22	± 5.52
2	67.56	± 8.00	10.4	± .70	88.50	± 12.33
3	74.89	± 5.66	9.0	± .87	84.44	± 6.01
4	66.70	± 3.02	9.6	± .70	74.40	± 5.40
5	75.90	± 4.84	11.3	± .68	85.90	± 9.54
6*	69.40	± 2.45	11.3	± .68	76.50	± 3.07
PI-1	86.90	± 8.93	11.3	± 1.34	95.60	± 6.59
2	85.75	± 12.13	11.0	± 1.00	92.66	± 9.41
3	83.78	± 5.70	11.1	± .88	91.00	± 7.68
4*	87.33	± 2.24	10.7	± .48	95.20	± 3.33

\* Indicates selections used as parents

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on May 17, 1965 directly into the peat pots. The planting depth was controlled by partially filling the pot with soil, placing three seeds and then filling the remainder of the pot. To prevent crusting, the pots were watered once, then covered with plastic film until the seedlings emerged to the crook stage, at which time the film was removed. When the cotyledons were fully expanded and the first true leaf showing, the extra plants in each peat pot were pinched off so that only one plant remained.

The planting arrangement was a randomized block design with ten replications. The randomized block arrangement was begun at the time the seeds were sown in the peat pots. Each replicate consisted of eight plants from each of the parents and  $F_1$ 's, thirty-two plants of each  $F_2$ , and sixteen plants of each of the backcrosses. For the backcross  $(RFG \times PI) \times PI$ , there was seed sufficient for seven replicates. For the three remaining replicates, the  $(PI \times RFG) \times PI$  was used.

A complete stand consisted of 3200 plants of the following populations: 4 parents and 4  $F_1$ 's, 80 plants each; 4  $F_2$ 's, 320 plants each; 6 of the backcrosses with 160 plants each. In the two remaining backcrosses, there were 114 plants of  $(RFG \times PI) \times PI$  and 208 plants of  $(PI \times RFG) \times PI$ .

The final number did not always reflect the initial number due to losses during the growing season. Since four  $F_1$  plants from each of the crosses were used for the  $F_2$  and backcross populations, equal samples from each  $F_1$  plant were used for the respective populations.

The plants were placed in the cold frame for a period of four days when the third true leaf was fully expanded. Following this hardening period, the plants were moved to the field. The plants were transplanted by hand into a shallow trench and were spaced one and one-half feet apart in the row, with three feet between rows. Each plant received a pint of starter solution and was protected with a cedar shingle. The shingle was inserted at an angle on the southwest side of the plant and was removed three weeks later. Guard rows were placed around the experimental plot.

Flowering records were taken daily on an individual plant basis, beginning at the time the first flower opened and were continued until all entries were obtained. At the peak of the flowering, two days were required to go through the ten replications; therefore it was necessary to estimate the date of anthesis. The number of nodes to the first flower were also counted on the day the first flower on that plant opened.



The number of red ripe fruit per plant was recorded on October 5, 1965. The fruit number did not include the fruit at the first furcation since 90 per cent of the fruits at this furcation were lost due to blossom-end rot. Data on upright versus pendant fruit bearing habit were also obtained at this time.

Leaf length and width measurements were made on August 23, 1965 from the leaf immediately below the first furcation. At this time this leaf was fully expanded in all of the populations.

The individual plant data were assembled and entered on IBM cards. Means, variances, standard deviations and correlations were obtained from individual plant data and calculated by the use of the Control Data Corporation 3600 computer. An IBM card sorting machine was used to aid in the summarization of frequency distributions.

Population means were compared by use of the "t" test as outlined by Dixon and Massey (15) and summarized in the following formula:

$$t = \frac{\bar{x}_1 - \bar{x}_2}{S_p \sqrt{(1/N_1) + (1/N_2)}}$$

where  $S_p^2$  is the pooled mean-square estimate given by:

$$S_p^2 = \frac{(N_1-1) S_1^2 + (N_2-1) S_2^2}{N_1 + N_2 - 2}$$

and  $S_p$  is the square root of  $S_p^2$ .

Tests for normality of the frequency distributions of the non-segregating populations were conducted as outlined by Leonard, Mann and Powers (22) and Panse (33) utilizing the normal probability integral tables given by Pearson (34). The methods developed by Powers, Locke and Garrett (38) and outlined by Singh (41) and Leonard, Mann and Powers (22) were used to estimate the number of gene pairs differentiating the parents. These methods will be illustrated in conjunction with the analysis and the interpretation of the data. Chi-square tests were used to compare the observed and theoretical ratios. Segregating families were tested for heterogeneity prior to pooling the data for comparisons and interpretation.

Scaling tests were used to determine if the data could be more accurately summarized for analysis by transformation to logarithm. Power's (36) formulas as shown below were used for the calculation of theoretical means of the segregating populations.

Arithmetic Scale (additive base)	Logarithmic anti log of:
$\bar{F}_2 = \frac{\bar{P}_1 + \bar{F}_1 + \bar{P}_2}{4}$	$\frac{\log \bar{P}_1 + 2 \log \bar{F}_1 + \log \bar{P}_2}{4}$
BC to $P_1$ (recessive parent) $= \frac{\bar{F}_1 + \bar{P}_1}{2}$	$\frac{\log \bar{F}_1 + \log \bar{P}_1}{2}$
BC to $P_2$ (dominant parent) $= \frac{\bar{F}_1 + \bar{P}_2}{2}$	$\frac{\log \bar{F}_1 + \log \bar{P}_2}{2}$

Where:  $\bar{P}_1$  is the mean of the recessive parent  
 $\bar{P}_2$  is the mean of the dominant parent  
 $\bar{F}_1$  is the theoretical mean of the  $F_1$   
generation calculated from  $\frac{\bar{P}_1 + \bar{P}_2}{2}$

## RESULTS AND INTERPRETATION

### Inheritance Of Number Of Days To First Anthesis:

#### Earliest Red Sweet x Resistant Florida Giant

The flowering period for this cross ranged from the 52nd day after seeding to the 81st day. Plants were classified as having bloomed on the day the corolla of the first flower at the first furcation opened.

The data showed that there was a reduction in number of plants blooming on the 58th, 63rd, and 65th days for all populations which was due to adverse temperature conditions. Therefore, the number of plants which opened on these days was added to the adjacent class to obtain distributions for each of the non-segregating populations which most nearly approached the calculated normal curve (38).

Table 2 shows that there was no difference between the theoretical arithmetic and geometric means, suggesting that the transformation to the logarithmic scale was unnecessary.

Data for days from seeding to first anthesis for the parents,  $F_1$ ,  $F_2$ , and backcross populations are shown in Table 3. The mean of the pooled  $F_1$ 's of  $57.46 \pm 1.17$  and the mean of ERS of  $57.12 \pm 1.77$ , and the lack of

Table 2. Observed and calculated means using the arithmetic (additive base) and logarithmic scales for days from seeding to first anthesis for the F<sub>2</sub> and back-cross populations from reciprocal crosses of Earliest Red Sweet x Resistant Florida Giant

Generation	No. of plants	Observed mean	Theoretical Means	
			Arithmetic	Logarithmic
F <sub>2</sub> pooled	625	58.50 $\pm$ 2.96	60.09	60.05
BC to RFG pooled	308	59.17 $\pm$ 2.39	61.65	61.55
BC to ERS pooled	316	57.30 $\pm$ 1.54	58.60	58.59

**Table 3. Frequency distribution for number of days from seeding to first anthesis for different generations of pepper plants from reciprocal crosses of Earliest Red Sweet X Resistant Florida Giant.**

[illegible]

difference between the means of the pooled backcrosses to ERS with that of ERS, suggest complete dominance for the shorter period of anthesis.

The skewness of the  $F_2$  and the bimodal characteristic of the backcross to RFG data suggest the possibility of monogenic inheritance for this character. The dividing point for the segregating populations is between the 59th and 60th day classes (Table 3), which approximates the arithmetic mean of the two parents of 60.09 days. This dividing point is also suggested by the lesser number of individuals falling in the 59th day class of the pooled backcross to the recessive (RFG) parent, and by the mean of the pooled backcross of 59.17.

The division of the two phenotypes as noted, suggested the necessity to determine the number of genes differentiating the two parents. Theoretical  $F_2$  means were calculated for a one factor-pair difference using the formula as suggested by Powers (38):

$$(\bar{P}_1) (3/4) + (\bar{P}_2) (1/4) = \bar{F}_2$$

Where:  $\bar{P}_1$  is the mean of the dominant parent,  
 $\bar{P}_2$  is the mean of the recessive parent,  
 $\bar{F}_2$  is the theoretical mean of the  $F_2$ .

Since the fractional parts of the formula vary according to the number of gene pairs involved, the formula for two and three gene pairs, assuming complete dominance, and the calculated theoretical means are presented in Table 4. The best calculated estimate for the number of genes controlling this factor appears to be that based on a one major gene hypothesis.

The calculated theoretical  $F_2$  means of  $58.61 \pm 2.04$  when compared with the observed  $F_2$  pooled mean of  $58.50 \pm 2.96$  showed no significant difference between the two means suggesting the one factor-pair hypothesis. This hypothesis is further supported by an estimate of the number of gene pairs using a technique developed by Powers (37) and illustrated by Leonard, Mann and Powers (22).

The following formula is applied:

$$\frac{F_2}{P_1} \times 100$$

Where:  $F_2$  is the frequency expressed in per cent  
for each  $F_2$  class,

$P_1$  is the frequency expressed in per cent  
for each corresponding class of the  
recessive parent (RFG).



Table 4. Theoretical F<sub>2</sub> means for one, two, and three gene pairs assuming complete dominance

No. gene pairs	Formula	Theoretical F <sub>2</sub> Mean	Observed F <sub>2</sub> Mean
1	$(3/4) \bar{P}_1 + (1/4) \bar{P}_2$	58.61	58.50
2	$(15/16) \bar{P}_1 + (1/16) \bar{P}_2$	57.49	58.50
3	$(63/64) \bar{P}_1 + (1/64) \bar{P}_2$	57.21	58.50

The observed number of individuals in each class in Table 3 is presented in per cent in Table 5. The values for each class were converted to per cent by dividing the observed number of the total number of plants (n) for that population and then multiplying by 100.

In using this formula the per cent of individuals in the 81st day class of the pooled  $F_2$  frequency distribution is first considered (Table 5). This percentage is added to the preceding classes until a class is reached that contains a percentage of  $P_1$  individuals in the same class. As an example, values for the  $F_2$  are  $0.32 + 0.64 = 0.96$  for the 81st and 68th day classes. The corresponding values for  $P_1$  (RFG) to the 68th day class are  $1.41 + 1.41 + 1.41 + 1.41 = 5.64$ . Then  $F_2/P_1 \times 100 = 0.96/5.64 \times 100 = 17.02$ . The next step is to proceed to the adjoining class and add to it to the previous values. For example in the pooled  $F_2$   $0.96 + 0.96 = 1.92$ . Then  $F_2/P_1 \times 100 = 1.92/5.64 \times 100 = 34.04$ . The subsequent classes are compared class by class. Table 6 shows the seven  $F_2$  estimates and the cumulative mean for each class from the 81st to 59th day. The seven estimates represent the RFG parental distribution classes. The mean of the seven  $F_2$  estimates was



Table 6. Calculated percentage values obtained, suggesting a one gene hypothesis, expressed in cumulative average and the percent obtained for each class considered

Class	Calculated percentage for each class	Cumulative average
68	17.02	---
67	34.04	25.50
65+66	30.66	27.24
64	22.22	25.98
62+63	15.07	23.80
61	15.79	22.47
60	26.44	23.03
59	41.92	---

23.03 per cent and when compared to the expected 25.00 per cent, gave a chi-square value of 1.29 and P value of .25-.30, suggesting a good fit.

The sudden rise in the ninth estimate to 41.92 per cent which occurs when calculating the estimate for the 59th day class, indicates that plants with genotypes other than the recessive occur in the class and also supports the point of division of the early and late classes.

Table 7 shows the results of the chi-square test for goodness of fit for the various populations for a single factor-pair hypothesis. Classes 52 to 59 have been grouped to compose the early class while classes 60 to 81 were grouped for the late class. The expected  $F_2$  ratio is 3 (early): 1 (late) and the expected BC to RFG ratio is 1 (early): 1 (late). The expected  $F_1$  and backcross to the dominant parent (ERS) ratios are 1 (early): 0 (late). The P values obtained from the various populations suggest good fit to a single gene-pair difference for this character.

The slight deviations from a 1:0 ratio of the  $F_1$  and backcross to the dominant parent (ERS) can be noted and are perhaps explainable since the dominant parent class also overlaps into the recessive parent class.

Table 7. Chi-square test for goodness of fit for individual and pooled populations based on one factor-pair hypothesis

Generation	Observed ratio	Expected Ratio	Chi-sq.	P
(RFG x ERS) F <sub>1</sub>	74:6	80:0 (1:0)	---	---
(ERS x RFG) F <sub>1</sub>	77:2	79:0 (1:0)	---	---
Pooled F <sub>1</sub>	151:8	159:0 (1:0)	---	---
(RFG x ERS) F <sub>2</sub>	245:70	236.25:78.25 (3:1)	1.29	.20-.30
(ERS x RFG) F <sub>2</sub>	217:93	232.50:77.50 (3:1)	4.13	.04-.05
Pooled F <sub>2</sub>	462:163	468.75:156.25 (3:1)	.39	.50-.60
(RFG x ERS) x RFG	83:72	77.50:77.50 (1:1)	.78	.35-.40
(ERS x RFG) x RFG	86:67	76.50:76.50 (1:1)	2.36	.10-.15
Pooled BC to RFG	169:139	154.00:154.00 (1:1)	2.92	.08-.10
(RFG x ERS) x ERS	149:9	158:0 (1:0)	---	---
(ERS x RFG) x ERS	145:13	158:0 (1:0)	---	---
Pooled BC to ERS	294:22	316:0 (1:0)	---	---

Inheritance Of Number Of Days From Seeding To First Anthesis:

Plant Introduction No. 251622 x Resistant Florida Giant

The flowering period for this cross ranged from the 54th day after seeding to the 74th day. Examination of the frequency distributions showed a reduction in flowering on the 58th, 63rd and 65th days which was caused by adverse temperature conditions as observed for the cross, Earliest Red Sweet x Florida Resistant Giant. Therefore, the number of plants which opened on these days was added to the adjacent class to obtain near normal distribution for each of the non-segregating populations.

Results from scaling tests (Table 8) suggest no difference between the theoretical arithmetic and logarithmic means and therefore, the data were not transformed to logarithm.

Data for days from seeding to first anthesis for parents,  $F_1$ ,  $F_2$  and backcross populations are summarized in Table 9. The parental overlap shown in Table 9 was taken into consideration in the analysis of these data. The individual  $F_1$ 's and pooled  $F_1$  mean did not differ significantly from the mean of the early parent (PI). The means of the backcrosses to PI are significantly different from that of PI, suggesting a high level of dominance for the shorter period of first anthesis.

Table 8. Observed and calculated theoretical means using the arithmetic (additive base) and logarithmic scales for days from seeding to first anthesis for the F<sub>2</sub> and backcross populations from reciprocal crosses of PI x Resistant Florida Giant

Generation	No. of plants	Observed mean	Theoretical Means	
			Arithmetic	Logarithmic
F <sub>2</sub> pooled	590	59.80 $\pm$ 2.38	60.16	60.15
BC to RFG pooled	280	60.03 $\pm$ 2.24	61.21	61.10
BC to PI pooled	303	59.45 $\pm$ 3.30	59.11	59.10



Table 9 Frequency distribution for number of days to 1st anthesis for different generations of pepper plants from reciprocal crosses of Plant Introduction No. 251622 X Resistant Florida Giant.

Generation	No. of Plants	Days to anthesis																			Mean
		54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	73	74	
Resistant Florida Giant (P <sub>1</sub> )	73	..	..	..	..	..	5	12	16	22	9	5	3	..	..	1	..	..	..	62.26 ± 2.19	
Plant Introduction No. 251622 (P <sub>2</sub> )	77	1	2	15	25	16	11	4	2	1	..	..	..	..	..	..	..	..	..	58.06 ± 1.98	
(P <sub>1</sub> X P <sub>2</sub> ) F <sub>1</sub>	60	..	1	4	37	18	17	2	1	..	..	..	..	..	..	..	..	..	..	58.43 ± 1.41	
(P <sub>2</sub> X P <sub>1</sub> ) F <sub>1</sub>	74	..	1	9	33	18	11	1	1	..	..	..	..	..	..	..	..	..	..	58.04 ± 1.46	
Pooled F <sub>1</sub>	154	..	2	13	70	36	28	3	2	..	..	..	..	..	..	..	..	..	..	58.24 ± 1.44	
(P <sub>1</sub> X P <sub>2</sub> ) F <sub>2</sub>	291	..	1	10	55	66	89	25	16	12	10	3	2	1	1	..	..	..	..	59.93 ± 2.45	
(P <sub>2</sub> X P <sub>1</sub> ) F <sub>2</sub>	299	..	2	13	61	77	80	19	27	12	3	1	2	2	..	..	..	..	..	59.68 ± 2.30	
Pooled F <sub>2</sub>	590	..	3	23	116	143	169	44	43	24	13	4	4	3	1	..	..	..	..	59.80 ± 2.38	
(P <sub>1</sub> X P <sub>2</sub> ) X P <sub>1</sub>	138	..	..	..	21	41	48	8	12	2	1	..	4	..	..	1	..	..	..	60.02 ± 2.24	
(P <sub>2</sub> X P <sub>1</sub> ) X P <sub>1</sub>	142	..	1	3	23	33	42	13	13	10	2	1	1	..	..	..	..	..	..	60.04 ± 2.25	
Pooled Backcross to P <sub>1</sub>	280	..	1	3	44	74	90	21	25	12	3	1	5	..	..	1	..	..	..	60.03 ± 2.24	
(P <sub>1</sub> X P <sub>2</sub> ) X P <sub>2</sub>	102	1	3	11	25	23	9	7	1	7	7	4	1	1	2	..	..	..	..	59.89 ± 3.69	
(P <sub>2</sub> X P <sub>1</sub> ) X P <sub>2</sub>	201	1	2	20	71	40	29	3	18	3	5	4	3	..	1	..	1	..	..	59.21 ± 3.06	
Pooled Backcross to P <sub>2</sub>	303	2	5	31	96	63	38	10	19	10	12	8	4	1	3	..	1	..	..	59.45 ± 3.30	

The bimodal character of the backcrosses to the recessive parent (RFG), as well as the mean for the pooled backcross to RFG of 60.03 and the arithmetic mean of the two parents of 60.16, suggest the dividing point in this cross to be the 60th day class. Based on the tendency toward bimodality of the backcross to the recessive parent (RFG) and the skewness of the  $F_2$  frequency distribution, a monogenic difference between PI and RFG is theorized.

The theoretical  $F_2$  means were calculated using the formulas for one, two and three gene pairs. The results are shown in Table 10. The calculated  $F_2$  mean of 59.11 for a one factor-pair difference was the best approximation of the observed  $F_2$  mean of 59.80, suggesting a one factor-pair hypothesis.

For the estimation of the number of genes controlling this character, Power's (37, 38) formula  $vix. F_2/P_1 \times 100$  was also investigated. Table 11 shows the frequency distributions for the various populations expressed in percentages which were used in calculating the estimates of the number of genes. The first six estimates ranged around 29 per cent and are presented in Table 12. These

Table 10. Theoretical  $F_2$  means for one, two and three gene pairs assuming complete dominance

No. gene pairs	Formula	Theoretical $F_2$ Mean	Observed $F_2$ Mean
1	$(3/4) \bar{P}_1 + (1/4) \bar{P}_2$	59.11	59.80
2	$(15/16) \bar{P}_1 + (1/16) \bar{P}_2$	58.32	59.80
3	$(63/64) \bar{P}_1 + (1/64) \bar{P}_2$	58.22	59.80

Table 11 Frequency distribution for number of days to anthesis (in percent) for different generations of pepper plants from reciprocal crosses of Plant Introduction No. 251622 X Resistant Florida Giant.

Generation	No. of Plants	Days to anthesis																Mean
		54	55	56	57 & 58	59	60	61	62 & 63	64	65 & 66	67	68	69	70	73	74	
Resistant Florida Giant (P <sub>1</sub> )	73	..	..	..	..	6.85	16.44	21.92	30.14	12.33	6.85	4.11	..	..	1.37	..	..	62.26±2.19
Plant Introduction No. 251622 (P <sub>2</sub> )	77	1.30	2.60	19.49	32.48	20.78	14.29	5.20	2.60	1.30	..	..	..	..	..	..	..	58.06±1.98
(P <sub>1</sub> X P <sub>2</sub> ) F <sub>1</sub>	80	..	1.25	5.00	46.25	22.50	21.25	2.50	1.25	..	..	..	..	..	..	..	..	58.43±1.41
(P <sub>2</sub> X P <sub>1</sub> ) F <sub>1</sub>	74	..	1.35	12.16	44.58	24.32	14.86	1.35	1.35	..	..	..	..	..	..	..	..	58.04±1.46
Pooled F <sub>1</sub>	154	..	1.30	8.44	45.45	23.38	18.18	1.95	1.30	..	..	..	..	..	..	..	..	58.24±1.44
(P <sub>1</sub> X P <sub>2</sub> ) F <sub>2</sub>	291	..	.34	3.44	18.92	22.70	30.62	8.60	5.50	4.13	3.44	1.03	.68	.34	.34	..	..	59.93±2.45
(P <sub>2</sub> X P <sub>1</sub> ) F <sub>2</sub>	299	..	.67	4.36	20.44	25.80	26.80	6.37	9.05	4.02	1.01	.34	.67	.67	..	..	..	59.68±2.30
Pooled F <sub>2</sub>	590	..	.51	3.90	19.66	24.24	28.64	7.46	7.29	4.07	2.20	.68	.68	.51	.17	..	..	59.80±2.38
(P <sub>1</sub> X P <sub>2</sub> ) X P <sub>1</sub>	138	..	..	..	15.23	29.73	34.80	5.80	8.70	1.45	.73	..	2.90	..	..	.73	..	60.02±2.24
(P <sub>2</sub> X P <sub>1</sub> ) X P <sub>1</sub>	142	..	.70	2.11	16.20	24.24	29.58	9.15	9.15	7.04	1.41	.70	.70	..	..	..	..	60.04±2.25
Pooled Backcross to P <sub>1</sub>	280	..	.36	1.07	15.71	26.43	32.14	7.50	8.93	4.29	1.07	.36	1.79	..	..	..	..	60.03±2.24
(P <sub>1</sub> X P <sub>2</sub> ) X P <sub>2</sub>	102	.98	2.94	10.78	24.50	22.54	8.82	6.86	.98	6.86	6.86	3.92	.98	.98	1.96	..	..	59.89±3.69
(P <sub>2</sub> X P <sub>1</sub> ) X P <sub>2</sub>	201	.49	.99	9.95	35.32	19.90	14.43	1.49	8.96	1.49	2.49	1.99	1.49	..	.49	..	.49	59.21±3.06
Pooled Backcross to P <sub>2</sub>	303	.66	1.65	10.23	31.68	20.79	12.54	3.30	6.27	3.30	3.96	2.64	1.32	.33	.99	..	..	59.45±3.30

Table 12. Calculated percentage values obtained suggesting a one gene hypothesis expressed in cumulative averages and the percent obtained for each class considered

Class	Calculated percentage for each class	Cumulative average
70	12.69	---
67	37.23	24.95
65+66	34.39	28.09
64	33.70	29.50
62+63	28.47	29.29
61	30.06	29.42
60	55.50	---

six estimates with an average of 29.42 per cent represent the single recessive genotype and approximates the expected 25.00 per cent. The rise to 55.50 per cent which occurred when the estimate for the 60th day class was calculated indicates that plants with genotypes of other than that of the single recessive occurred in that class. This further suggests division of the early and late phenotypic classes to be between the 60th and 61st day classes.

Table 13 shows the chi-square test for goodness of fit for the various segregating populations calculated on the basis of the net overlap of the parents and  $F_1$ . The theoretical ratios were calculated as follows: Since the dividing point between the two phenotypes falls between the 60th and 61st day classes, the recessive parent (RFG) overlapped into the 59th and 60th day classes by 23.29 per cent, while the dominant parent (PI) overlapped into the 61st and 62nd day classes by 9.10 per cent. The pooled  $F_1$  also overlapped into the 61st and 62nd day classes by 3.25 per cent. Assuming the genotypic ratio to be  $1(\underline{aa}):2(\underline{Aa}) + 1(\underline{AA})$ , the net overlap of the genotype ( $\underline{aa}$ ) into the ( $\underline{Aa}$ ) - ( $\underline{AA}$ ) class is as follows:  $23.29 - (9.10 + (2)(3.25)) = 7.69$  per cent.

Table 13. Chi-square test for goodness of fit for individual and pooled populations based on calculated theoretical ratios for a one factor-pair difference

Generation	Observed ratio	Theoretical ratio	Chi-sq.	P
(RFG x PI) $F_1$	77:3	72.72:7.28	---	---
(PI x RFG) $F_1$	72:2	67.27:6.73	---	---
Pooled $F_1$	149:5	139.99:14.01	---	---
(RFG x PI) $F_2$	221:70	215.44:65.56	.61	.40-.50
(PI x RFG) $F_2$	233:66	230.83:68.17	.09	.75-.80
Pooled $F_2$	454:136	453.83:136.17	.00	.99-1.0
(RFG x PI) x RFG	110:28	82.48:55.52	22.82	.01
(PI x RFG) x RFG	102:40	85.63:56.37	7.88	.01
Pooled BC to RFG	212:68	168.05:111.94	28.75	.01
(RFG x PI) x PI	72:30	88.89:13.11	24.97	.01
(PI x RFG) x PI	163:38	177.28:23.72	9.68	.01
Pooled BC to PI	235:68	265.58:37.43	28.50	.01

The theoretical ratio in the  $F_2$  for a one factor-pair hypothesis with dominance is 75.00 per cent (AA) + (Aa):25.00 per cent (aa). However, due to the net overlap of 7.69 per cent in favor of the dominant phenotype, the observed recessive class represents 92.31 per cent of the expected 25 per cent or 23.08 per cent. The adjusted theoretical ratio in the  $F_2$  is therefore, 76.92 per cent early to 23.08 per cent late. The chi-square and P-values shown suggest a good fit to the hypothesis of a one factor-pair difference between parents. The theoretical ratios for the individual  $F_2$  ratios were calculated in a similar manner.

The theoretical backcross ratios were also calculated based on the net overlap. In the backcross to RFG (the recessive parent) the  $F_1$  (Aa) and RFG (aa) genotypes occur in a 1:1 ratio. The net overlap was calculated by subtracting the pooled  $F_1$  overlap from that of RFG. The total per cent overlap of the recessive parent (RFG) into 59th and 60th day classes is 23.29 per cent (Table 11). The pooled  $F_1$  shows an overlap of 3.25 per cent into the 61st and 62nd day classes. The net overlap of RFG is then 20.04 per cent. Due to the net overlap of 20.04 per cent in favor of the dominant phenotype, the observed recessive class represents



79.96 per cent of the expected 50.00 per cent or 39.98 per cent. The calculated theoretical ratio for the pooled backcross is 60.02:39.98. The theoretical ratios for the individual reciprocal backcrosses to RFG were calculated in similar manner.

The backcrosses to PI (dominant parent) and the  $F_1$ 's are expected to have the same distribution as that of the dominant parent, which overlapped by 9.10 per cent. The  $F_1$ 's would therefore, be expected to overlap by the same percentage and would have a theoretical ratio of 90.90:9.10 per cent instead of a 100:0 or 1:0 ratio. The backcrosses to PI involve both the  $F_1$  and PI parent, and their phenotype is theoretically represented by (Aa) and (AA) genotypes. The expected overlap would then be the sum of the overlap of  $F_1$  (Aa), and PI (AA) and the theoretical ratios would be 87.5:12.85 per cent for (RFG x PI) x PI; 88.20:11.80 per cent for (PI x RFG) x PI; and 87.65:12.35 per cent for the pooled backcross.

The high chi-square values for the backcrosses to RFG and PI are partially explained by the fact that penetrance level is determined by the genotypic background of the plant (2). For the backcross to RFG, theoretically seventy-five per cent of the genes of the individuals were from the

RFG parent. Although no distinct cytoplasmic effect was noted in the reciprocal  $F_1$  plants, the mean of the  $F_1$  in which RFG was used as the female parent is slightly higher than the reciprocal. This relationship is also apparent in the  $F_2$  and backcross to PI.

The backcross to PI shows an excess of individuals falling into the recessive class, resulting in a poor fit. The presence of these individuals in the recessive class can probably be explained by the parental overlap and the incompleteness of dominance.

#### Inheritance Of Number Of Nodes To The First Furcation:

##### Earliest Red Sweet x Resistant Florida Giant

Table 14 shows the results of scaling tests applied to the data for number of nodes to the first furcation of the  $F_2$  and backcross populations. The arithmetic means more closely approximate the observed means and suggest that no advantage would be derived from transforming the data to logaithms.

Table 15 shows the frequency distribution of numbers of plants in each node class. The parental overlap shown was taken into consideration in the analysis. The mean of

Table 14. Observed and calculated means using the arithmetic (additive base) and logarithmic scales for number of nodes subtending the first furcation for the F<sub>2</sub> and backcross populations from reciprocal crosses of Earliest Red Sweet x Resistant Florida Giant

Generation	No. of plants	Observed mean	Theoretical Means	
			Arithmetic	Logarithmic
F <sub>2</sub> pooled	637	8.78 ± 1.41	8.97	8.53
BC to RFG pooled	319	9.14 ± 1.25	9.49	9.90
BC to ERS pooled	320	8.34 ± .865	8.46	9.67

Table 15. Frequency distribution of number of nodes subtending the first furcation for different generations of pepper plants from reciprocal crosses of Earliest Red Sweet X Resistant Florida Giant.

Generation	No. of Plants	5	6	7	8	9	10	11	12	13	14	15	16	Mean
Resistant Florida Giant ( $P_1$ )	79	..	..	..	3	19	33	23	1	..	..	..	..	$10.00 \pm 0.862$
Earliest Red Sweet ( $P_2$ )	79	..	2	18	43	15	1	..	..	..	..	..	..	$7.94 \pm 0.762$
( $P_1$ X $P_2$ ) $F_1$	80	..	..	8	38	26	8	..	..	..	..	..	..	$8.43 \pm 0.808$
( $P_2$ X $P_1$ ) $F_1$	80	..	1	11	44	22	2	..	..	..	..	..	..	$8.16 \pm 0.737$
Pooled $F_1$	160	..	1	19	82	48	10	..	..	..	..	..	..	$8.29 \pm 0.780$
( $P_1$ X $P_2$ ) $F_2$	320	2	9	29	108	93	54	18	4	1	1	1	..	$8.74 \pm 1.318$
( $P_2$ X $P_1$ ) $F_2$	317	..	7	36	97	93	53	20	4	4	1	1	1	$8.82 \pm 1.503$
Pooled $F_2$	637	2	16	65	205	186	107	38	8	5	2	2	1	$8.78 \pm 1.410$
( $P_1$ X $P_2$ ) X $P_1$	159	1	..	8	46	40	46	13	5	..	..	..	..	$9.13 \pm 1.218$
( $P_2$ X $P_1$ ) X $P_1$	160	..	1	8	53	32	37	25	4	..	..	..	..	$9.15 \pm 1.285$
Pooled Backcross to $P_1$	319	1	1	16	99	72	83	38	9	..	..	..	..	$9.14 \pm 1.250$
( $P_1$ X $P_2$ ) X $P_2$	160	1	2	22	78	45	10	2	..	..	..	..	..	$8.26 \pm 0.908$
( $P_2$ X $P_1$ ) X $P_2$	160	..	1	19	68	60	12	..	..	..	..	..	..	$8.39 \pm 0.817$
Pooled Backcross to $P_2$	320	1	3	41	146	105	22	2	..	..	..	..	..	$8.34 \pm 0.865$

the  $F_1$ 's and backcrosses to ERS (Table 15) show dominance for the lower node number. The mean of (ERS x RFG)  $F_1$  of  $8.16 \pm .737$  and that of ERS of  $7.94 \pm .762$  did not differ significantly. Although the mean of the reciprocal  $F_1$  of  $8.43 \pm .808$  was significantly different from that of ERS, the means of the two  $F_1$ 's were not significantly different.

The means of the individual and pooled backcrosses to ERS although significantly different from that of ERS were closer to ERS than would be expected when calculated on an additive base (Table 14). This information also suggests dominance for the lower node number.

The skewed  $F_2$  and bimodal character of the backcross to RFG (recessive parent) suggest the possibility that the inheritance for this character was not complex. The dividing point for the segregating populations is between the 9th and 10th node as is suggested by the mean of the pooled backcross to RFG of 9.14 and by the lesser number of individuals at the 9th node class of the pooled backcross frequency distribution (Table 15). This dividing point at the 9th node also corresponds with the arithmetic mean of the two parents of 8.97.

Based on dominance and this point of division, an estimate of the number of genes differentiating the two parents was calculated using the formulas for one, two and three genes (38). The calculated  $F_2$  mean of 8.45 for a one factor-pair difference most nearly approximates the observed  $F_2$  mean of 8.78 (Table 16).

An examination on possible number of genes controlling this character, by use of Power's (37, 38) formula viz.  $F_2/P_1 \times 100$ , was investigated. The frequency distributions for the various populations expressed per cent used in calculating the estimates and are shown in Table 17. The estimate of the pooled  $F_2$  for the 11th node class was 28.95 per cent, while the estimate for the 10th node class was 35.47 per cent. The higher value of the latter estimate may be a reflection of the partial dominance already mentioned. The rise to 56.69 per cent in the estimate for the 9th node class further suggests dividing the  $F_2$  between the 9th and 19th node classes.

Another test developed by Powers (38) and described by Singh (41) was also used to estimate the possible number of genes involved. The formula is:

Table 16. Theoretical  $F_2$  means for one, two and three gene pairs assuming complete dominance

No. genes	Formula	Observed
1	$(3/4) P_1 + (1/4) P_2 = 8.45$	8.78
2	$(15/16) P_1 + (1/16) P_2 = 8.07$	8.78
3	$(63/64) P_1 + (1/64) P_2 = 7.98$	8.78

Table 17. Frequency distribution (in percent) for number of nodes subtending the first furcation for different generations of pepper plants from reciprocal crosses of Earliest Red Sweet X Resistnat Florida Giants.

Generation	No. of Plants	5	6	7	8	9	No. of Nodes			12	13	14	15	16	Mean
Resistant Florida Giant (P <sub>1</sub> )	79	..	..	..	3.80	24.05	41.77	29.11	1.27	..	..	..	..	10.00 ±0.862	
Earliest Red Sweet (P <sub>2</sub> )	79	..	2.54	22.78	54.43	18.99	1.27	..	..	..	..	..	..	7.94 ±0.762	
(P <sub>1</sub> X P <sub>2</sub> ) F <sub>1</sub>	80	..	..	10.00	47.50	32.50	10.00	..	..	..	..	..	..	8.43 ±0.808	
(P <sub>2</sub> X P <sub>1</sub> ) F <sub>1</sub>	80	..	1.25	13.75	55.00	27.50	2.50	..	..	..	..	..	..	8.16 ±0.737	
Pooled F <sub>1</sub>	160	..	.63	11.88	51.25	30.00	6.25	..	..	..	..	..	..	8.29 ±0.780	
(P <sub>1</sub> X P <sub>2</sub> ) F <sub>2</sub>	320	.63	2.80	9.06	33.75	29.06	16.88	5.63	1.25	.31	.31	.31	..	8.74 ±1.318	
(P <sub>2</sub> X P <sub>1</sub> ) F <sub>2</sub>	317	..	2.21	11.35	30.59	29.33	16.72	6.31	1.26	1.26	.32	.32	.32	8.82 ±1.503	
Pooled F <sub>2</sub>	637	.31	2.51	10.20	32.18	29.20	16.80	5.97	1.26	.78	.31	.31	.16	8.78 ±1.410	
(P <sub>1</sub> X P <sub>2</sub> ) P <sub>1</sub>	159	.63	..	5.03	28.93	25.16	28.93	8.18	3.14	..	..	..	..	9.13 ±1.218	
(P <sub>2</sub> X P <sub>1</sub> ) P <sub>1</sub>	160	..	.63	5.00	33.13	20.00	23.13	15.63	2.50	..	..	..	..	9.15 ±1.285	
Pooled Backcross to P <sub>1</sub>	319	.31	.31	5.02	31.03	22.57	26.02	11.91	2.82	..	..	..	..	9.14 ±1.250	
(P <sub>1</sub> X P <sub>2</sub> ) P <sub>2</sub>	160	.63	1.25	13.75	48.75	28.13	6.25	1.25	..	..	..	..	..	8.26 ±0.908	
(P <sub>2</sub> X P <sub>1</sub> ) P <sub>2</sub>	160	..	.63	11.86	42.50	37.50	7.50	..	..	..	..	..	..	8.39 ±0.817	
Pooled Backcross to P <sub>2</sub>	320	.31	.94	12.81	45.63	32.81	6.88	.63	..	..	..	..	..	8.34 ±0.865	



$$\frac{BC_1}{F_1} \times 100$$

Where:  $BC_1$  is the frequency expressed in per cent for each class of the distribution of the pooled backcross to the recessive parent.

$F_1$  is the frequency expressed in per cent of each corresponding class of the pooled  $F_1$ .

Calculations for this test are similar to those used in the formula  $F_2/P_1 \times 100$  previously illustrated. The percentages are, however, accumulated beginning with the 5th node class (Table 17). The first estimate is made for the 7th node class, this being  $5.64/12.51 \times 100 = 45.10$  per cent. The estimate for the 8th node class is 57.51 per cent. These two estimates fluctuate about the expected 50.00 per cent (Table 18) and therefore, suggest a hypothesis of a one major factor-pair difference between parents. The estimate for the 9th node class was 63.18 per cent. This estimate reflects some of the overlap shown by the recessive parent (RFG) into the 9th node class (Table 17).

Table 18. Calculated percentage values obtained suggesting a one gene hypothesis expressed in cumulative averages and the percent obtained for each class considered

Class	Calculated percentage for each class	Cumulative average
7	45.10	---
8	57.51	51.31
9	63.18	55.26
10	85.26	---

The jump to 85.26 per cent which occurs in the estimate for the 19th node class further suggests dividing the classes between the 9th and 10th node classes.

Table 19 shows the chi-square test for goodness of fit based on expected ratios for the  $F_1$ ,  $F_2$  and backcross populations calculated on the basis of the overlap of the parents and  $F_1$ 's as described in the preceding section (number of days to first anthesis in the cross PI x RFG). The chi-square and P-values shown show an acceptable fit to the proposed hypothesis of a one major factor-pair difference between parents.

The high number of individuals observed in the recessive class of the (RFG x ERS)  $F_1$  and the (ERS x RFG)  $F_2$  reflect incomplete dominance. This deviation from the expected may also be due to the small population number of the  $F_1$ . It is also possible that the effect of the major gene was modified in the presence of the RFG cytoplasm.

#### Inheritance Of Number of Nodes To The First Furcation:

##### Plant Introduction No. 251622 x Resistant Florida Giant

Table 20 shows the results of scaling tests applied to the data for number of nodes to the first furcation of the  $F_2$  and backcross populations. Since arithmetic means closely

Table 19. Chi-square test for goodness of fit for individual and pooled populations based on a one factor-pair hypothesis with dominance

Generation	Observed ratio	Theoretical ratio	Chi-sq.	P
(RFG x ERS) F <sub>1</sub>	72:8	78.98:1.02	---	---
(ERS x RFG) F <sub>1</sub>	78:2	78.98:1.02	---	---
Pooled F <sub>1</sub>	150:10	157.97:2.03	---	---
(RFG x ERS) F <sub>2</sub>	241:79	245.25:74.75	.31	.55-.60
(ERS x RFG) F <sub>2</sub>	233:84	254.84:62.37	9.52	.01
Pooled F <sub>2</sub>	474:163	500.17:136.83	6.38	.01-.05
(RFG x ERS) x RFG	95:64	93.70:65.30	.05	.85-.90
(ERS x RFG) x RFG	94:66	100.29:59.71	1.05	.30-.50
Pooled BC to RFG	189:130	193.95:125.05	.33	.50-.60
(RFG x ERS) x ERS	148:12	141.97:18.03	2.28	.10-.20
(ERS x RFG) x ERS	148:12	153.97:6.03	6.12	.01-.05
Pooled BC to ERS	296:24	295.94:24.06	0.00	.99-1.0

Table 20. Observed and calculated means using the arithmetic (additive base) and logarithmic scales for number of nodes subtending the first furcation for the F<sub>2</sub> and backcross populations from reciprocal crosses of Plant Introduction No. 251622 x Resistant Florida Giant

Generation	No. of Plants	Observed mean	Theoretical Means	
			Arithmetic	Logarithmic
F <sub>2</sub> pooled	635	8.83 ± 1.130	8.36	8.32
BC to RFG pooled	320	9.25 ± .989	8.93	8.91
BC to PI pooled	317	7.85 ± .966	7.80	7.78

approximated the observed means the data were not transformed to logarithm.

Table 21 gives the frequency distribution of numbers of plants in each class. The parental overlap shown in Table 21 was considered in the interpretation of the data. The  $F_1$  means of this table show an absence of dominance for the lower node number. The mean of (RFG x PI)  $F_1$  of  $8.54 \pm .75$  and that of (PI x RFG)  $F_1$  of  $8.31 \pm .72$  are significantly different, suggesting partial cytoplasmic influence. The significant difference between the means of the individual  $F_2$  populations further suggests some cytoplasmic influence. The fact that the individual  $F_1$  means fluctuate around the arithmetic mean of the two parents of 8.36, suggests an additive gene model. The close agreement of the mean of the pooled backcrosses to PI of  $7.85 \pm .966$  (Table 20), with the theoretical arithmetic mean (on an additive base) of 7.80, also suggests additivity.

The absence of bimodality in the backcrosses as well as the presence of an overlap between the parents and the type of  $F_1$  distributions do not suggest any definite dividing point, or distinguishable phenotypic classes. The narrow range between the two parents and the discrete classes makes it impossible to partition the  $F_2$  distribution into fractions of nodes.

Table 21. Frequency distribution of number of nodes subtending first furcation for different generations of pepper plants from reciprocal crosses of Plant Introduction No. 251622 X Resistant Florida Giant.

Generation	No. of Plants	4	5	6	7	8	9	10	11	12	13	14	Mean
Resistant Florida Giant (P <sub>1</sub> )	80	..	..	..	..	10	26	39	5	..	..	..	9.49 ± 0.795
Plant Introduction No. 251622 (P <sub>2</sub> )	80	..	..	4	54	22	..	..	..	..	..	..	7.23 ± 0.527
(P <sub>1</sub> X P <sub>2</sub> ) F <sub>1</sub>	80	..	..	..	5	34	34	7	..	..	..	..	8.54 ± 0.745
(P <sub>2</sub> X P <sub>1</sub> ) F <sub>1</sub>	80	..	..	1	6	43	27	3	..	..	..	..	8.31 ± 0.722
Pooled F <sub>1</sub>	160	..	..	1	11	77	61	10	..	..	..	..	8.43 ± 0.740
(P <sub>1</sub> X P <sub>2</sub> ) F <sub>2</sub>	316	1	..	3	14	80	127	62	24	3	2	..	9.02 ± 1.134
(P <sub>2</sub> X P <sub>1</sub> ) F <sub>2</sub>	319	..	..	2	42	110	91	62	10	1	1	..	8.65 ± 1.099
Pooled F <sub>2</sub>	635	1	..	5	56	190	218	124	34	4	3	..	8.83 ± 1.130
(P <sub>1</sub> X P <sub>2</sub> ) X P <sub>1</sub>	160	..	..	..	1	29	68	48	13	1	..	..	9.29 ± 0.900
(P <sub>2</sub> X P <sub>1</sub> ) X P <sub>1</sub>	160	..	..	3	4	31	53	59	8	1	1	..	9.21 ± 1.072
Pooled Backcross to P <sub>1</sub>	320	..	..	3	5	60	121	107	21	2	1	..	9.25 ± 0.989
(P <sub>1</sub> X P <sub>2</sub> ) X P <sub>2</sub>	110	..	..	8	37	43	14	6	1	..	..	1	7.84 ± 1.169
(P <sub>2</sub> X P <sub>1</sub> ) X P <sub>2</sub>	207	..	..	4	65	102	32	3	..	..	1	..	7.86 ± 0.841
Pooled Backcross to P <sub>2</sub>	317	..	..	12	102	145	46	9	1	..	1	1	7.85 ± 0.966

The possible mode of inheritance of this character was investigated by comparing the observed means with the theoretical means calculated on the basis of several genetic models. The suggested gene model is one based on two genes whose action is additive, but in which one gene is twice as effective as the other.

The proposed genotype (AAbb) was assigned to the PI parent (the parent with lesser nodes to the first furcation) and (aaBB) to RFG. This model assumes that the double recessive genotype (aabb) in the  $F_2$  will produce a mean of 4 nodes to the first furcation. Gene (A) is assigned a mean value of 1.5 nodes and gene (B) a mean value of 3 nodes.

Based on these assumptions, the PI parent with the genotype (AAbb) will have a mean of  $4 + 2 (1.5)$  or 7 nodes. This closely approximates the observed PI mean of  $7.23 \pm 0.527$ . The RFG parent (aaBB) will have  $4 + 2 (3)$  or 10 nodes which approximates the observed mean of  $9.49 \pm 0.795$ . The  $F_1$  (AaBb) with a mean of  $4 + 1.5 + 3.0$  or 8.5 nodes is also in agreement with the observed pooled  $F_1$  mean of  $8.45 \pm 0.740$  nodes.

Using the proposed model, the theoretical  $F_2$  and back-cross means were calculated for each of the genotypes



theoretically present in these populations. The theoretical means for the  $F_2$ , backcross to RFG, and backcross to PI are presented in Tables 22 and 23. These tables show the possible  $F_2$  and backcross tenotypes, the mean node value for each genotype, the possible number of plants with each of these genotypes, and the calculation of the theoretical means for each of the populations. The total node value was calculated by multiplying the mean node value by the number of plants appearing in each genotype. The  $F_2$  phenotypes possible by the use of this model encompass the range from the 4 to 13 node classes as shown in Table 21. This model does not include 1.25 per cent of the pooled backcross to RFG, and 0.96 per cent of the backcross to PI (Table 24). The close agreement between the observed and calculated theoretical means for the segregating populations supports the proposed two gene additive model.

Inheritance Of Number of Red Ripe Fruit By The First Killing Frost:

Earliest Red Sweet x Resistant Florida Giant

Table 25 shows the results of scaling tests applied to the data for number of red or ripe fruit produced per plant

Table 22. Calculated theoretical  $F_2$  mean based on the number of plants of each possible genotype from a dihybrid segregation

Genotypes	Mean node value*	No. of plants	Total node value
aabb	4.0	1	4.0
Aabb	5.5	2	11.0
AAbb	7.0	1	7.0
aabB	7.0	2	14.0
aaBB	10.0	1	10.0
AaBb	8.5	4	34.0
AaBB	11.5	2	23.0
AABb	10.0	2	20.0
AABB	13.0	1	13.0
		Totals: 16	136.0

Theoretical  $F_2$  mean:  $136/16 = 8.5$

Observed pooled  $F_2$  mean: 8.83

\* Mean node value was calculated on the basis that the genotype (aabb) will have a mean of 4 nodes; gene (A) = 1.5 nodes; gene (B) = 3.0 nodes

Table 23. Calculated theoretical backcross means based on the number of plants of each possible genotype from a dihybrid segregation

Population	Genotype	Mean node value*	No. of plants	Total node value
BC to RFG:	AaBB	11.5	1	11.5
	AaBb	8.5	1	8.5
	aaBB	10.0	1	10.0
	aaBb	7.0	1	7.0
	Totals:		4	37.0
BC to PI:	AABb	10.0	1	10.0
	AAbb	7.0	1	7.0
	AaBb	8.5	1	8.5
	Aabb	5.5	1	5.5
	Totals:		4	31.0
Theoretical mean of backcross to RFG:				$37.0/4 = 9.25$
Observed mean of pooled backcross to RFG:				9.25
Theoretical mean of backcross to PI:				$31.0/4 = 7.75$
Observed mean of pooled backcross to PI:				7.85

\*Mean node value was calculated on the basis that the genotype (aabb) will have a mean of 4 nodes; gene (A) = 1.5 nodes; gene (B) = 3.0 nodes

Table 24. Frequency distribution (in percent) of number of nodes, subtending first furcation for different generations of pepper plants from reciprocal crosses of Plant Introduction No. 251622 X Resistant Florida Giant.

Generation	No. of Plants	4	5	6	7	8	9	10	11	12	13	14	Mean
Resistant Florida Giant (P <sub>1</sub> )	80	..	..	..	..	12.50	32.50	48.75	6.25	..	..	..	9.49±0.795
Plant Introduction No. 251622 P <sub>2</sub>	80	..	..	5.00	67.50	27.50	..	..	..	..	..	..	7.23±0.527
(P <sub>1</sub> X P <sub>2</sub> ) F <sub>1</sub>	80	..	..	..	6.25	42.50	8.75	..	..	..	..	..	8.54±0.745
(P <sub>2</sub> X P <sub>1</sub> ) F <sub>1</sub>	80	..	..	1.25	7.50	53.75	33.75	3.75	..	..	..	..	8.31±0.722
Pooled F <sub>1</sub>	160	..	..	..	.63	6.88	48.13	38.13	6.25	..	..	..	8.43±0.740
(P <sub>1</sub> X P <sub>2</sub> ) F <sub>2</sub>	316	.32	..	..	.96	4.43	25.31	40.18	19.62	7.59	.95	.63	9.02±1.134
(P <sub>2</sub> X P <sub>1</sub> ) F <sub>2</sub>	319	..	..	..	.63	13.16	34.47	28.52	19.43	3.13	.31	.31	8.65±1.099
Pooled F <sub>2</sub>	635	.16	..	..	.79	8.82	29.92	34.33	19.52	5.35	.63	.47	8.83±1.130
(P <sub>1</sub> X P <sub>2</sub> ) X P <sub>1</sub>	160	..	..	..	..	.63	18.13	42.50	30.00	8.13	.63	..	9.29±0.900
(P <sub>2</sub> X P <sub>1</sub> ) X P <sub>1</sub>	160	..	..	..	1.88	2.50	19.38	33.13	36.88	5.00	.63	.63	9.21±1.072
Pooled Backcross to P <sub>1</sub>	320	..	..	..	.94	1.56	18.75	37.81	33.44	6.56	.63	.31	9.25±0.989
(P <sub>1</sub> X P <sub>2</sub> ) X P <sub>2</sub>	110	..	..	..	7.27	33.63	39.09	12.73	5.45	.91	..	.91	7.84±1.169
(P <sub>2</sub> X P <sub>1</sub> ) X P <sub>2</sub>	207	..	..	..	1.93	31.40	49.27	15.46	1.45	..	.48	..	7.85±0.841
Pooled Backcross to P <sub>2</sub>	317	..	..	..	3.79	32.18	45.74	14.51	2.84	.32	.32	.32	7.85±0.966

Table 25. Observed and calculated means using the arithmetic (additive base) and logarithmic scales for number of red ripe fruit by the first killing frost for the F<sub>2</sub> and backcross population from reciprocal crosses of Earliest Red Sweet x Florida Resistant Giant

Generation	No. of Plants	Observed mean	Theoretical Means	
			Arithmetic	Logarithmic
F <sub>2</sub> pooled	637	3.00 ± 1.36	2.49	2.78
BC to RFG pooled	316	2.04 ± 1.33	1.43	1.69
BC to ERS pooled	320	2.09 ± 1.35	3.55	3.39

by the killing frost for the  $F_2$  and backcross populations. Neither the arithmetic scale (on an additive base) nor the logarithmic scale agreed with the observed means and therefore transformation of the data was not necessary.

Table 26 shows the frequency distribution of the numbers of individuals in each class. The means of the pooled and individual  $F_1$ 's (Table 26), when compared to the ERS parent, did not differ significantly suggesting some dominance for the lower number of ripe fruit.

The means of the individual and pooled backcrosses to ERS, although significantly different from that of ERS, were closer to ERS than would be expected when calculated on an additive base (Table 25).

These means were not significantly different from the  $F_1$  means.

The skewed  $F_2$  and the bimodal character of the backcross to RFG (recessive parent) suggest the possibility that the genetic situation was not complex. The mean of the pooled backcross to RFG of  $2.04 \pm 1.33$ , and the lesser number of individuals appearing in the 2 fruit class of the pooled backcross frequency distribution suggest the dividing point for the segregating populations to be between the 2 and

Table 26. Frequency distribution of number of red ripe fruit per plant by the first killing frost for different generations of pepper plants from reciprocal crosses of Earliest Red Sweet X Resistant Florida Giant.

Generation	No. of Plants	0	1	2	3	4	5	6	7	8	9	Mean
Resistant Florida Giant ( $P_1$ )	79	53	23	3	..	..	..	..	..	..	..	$0.37 \pm 0.54$
Earliest Red Sweet ( $P_2$ )	78	..	7	..	14	20	14	12	4	3	4	$4.60 \pm 1.96$
( $P_1 \times P_2$ ) $F_1$	80	..	2	3	20	29	14	9	3	..	..	$4.11 \pm 1.26$
( $P_2 \times P_1$ ) $F_1$	80	..	2	3	23	27	17	6	2	..	..	$4.00 \pm 1.19$
Pooled $F_1$	160	..	4	6	43	56	31	15	5	..	..	$4.06 \pm 1.23$
( $P_1 \times P_2$ ) $F_2$	320	18	36	20	139	70	31	5	..	1	..	$3.02 \pm 1.36$
( $P_2 \times P_1$ ) $F_2$	317	16	37	28	141	67	17	7	3	1	..	$2.97 \pm 1.37$
Pooled $F_2$	637	34	73	48	280	137	48	12	3	2	..	$2.99 \pm 1.36$
( $P_1 \times P_2$ ) $\times P_1$	159	18	53	11	59	17	1	..	..	..	..	$2.04 \pm 1.28$
( $P_2 \times P_1$ ) $\times P_1$	157	25	42	16	52	19	3	..	..	..	..	$2.04 \pm 1.38$
Pooled Backcross to $P_1$	316	43	95	27	111	36	4	..	..	..	..	$2.04 \pm 1.33$
( $P_1 \times P_2$ ) $\times P_2$	160	2	4	..	56	51	27	15	1	2	2	$4.01 \pm 1.38$
( $P_2 \times P_1$ ) $\times P_2$	160	..	3	8	61	40	26	15	6	1	..	$3.96 \pm 1.32$
Pooled Backcross to $P_2$	320	2	7	8	117	91	53	30	7	3	2	$3.98 \pm 1.35$

3 fruit classes. This dividing point at the 2 ripe fruit class corresponds with the arithmetic mean of the two parents of 2.49.

Based on dominance and the established point of division, an estimate of the number of genes differentiating the two parents was calculated using the formulas for one, two and three genes (38). The calculated  $F_2$  mean of 3.54 for a single factor-pair difference most nearly approximates the observed  $F_2$  mean (Table 27) of 3.00.

The possible number of genes controlling this character was further investigated by use of the formula,  $F_2/P_1 \times 100$  (37, 38). The frequency distributions for the various populations expressed in per cent (Table 28) were used in calculating the estimates. Calculations for these estimates have been previously illustrated.

Due to the termination of growth caused by the frost, a large number of plants of the RFG parent fell into the "no ripe fruit" class. The resulting frequency distribution therefore, represents only a portion of the parental curve. Therefore, one estimate was made representing the entire recessive class (classes 0, 1 and 2). This estimate for  $F_2/P_1 \times 100$  is  $24.34/100 \times 100$  or 24.34 per cent. The rise



Table 27. Theoretical  $F_2$  means for one, two and three gene pairs assuming complete dominance

No. genes	Formula	Observed
1	$(3/4) P_1 + (1/4) P_{I_2} = 3.54$	3.00
2	$(15/16) P_1 + (1/16) P_2 = 4.53$	3.00
3	$(63/64) P_1 + (1/64) P_2 = 4.53$	3.00

Table 28. Frequency distribution (in percent) of number of red ripe fruit per plant by the first killing frost for different generations of pepper plants from reciprocal crosses of Earliest Red Sweet X Resistant Florida Giant.

Generation	No. of Plants	0	1	2	3	4	5	6	7	8	9	Mean
Resistant Florida Giant (P <sub>1</sub> )	79	67.10	29.12	3.80	..	..	..	..	..	..	..	0.37 ± 0.54
Earliest Red Sweet (P <sub>2</sub> )	78	..	8.97	..	17.95	25.64	17.95	15.38	5.13	3.85	5.13	4.60 ± 1.96
(P <sub>1</sub> X P <sub>2</sub> ) F <sub>1</sub>	80	..	2.50	3.75	25.00	36.25	17.50	11.25	3.75	..	..	4.11 ± 1.26
(P <sub>2</sub> X P <sub>1</sub> ) F <sub>1</sub>	80	..	2.50	3.75	28.75	33.75	21.25	7.50	2.50	..	..	4.00 ± 1.19
Pooled F <sub>1</sub>	160	..	2.50	3.75	26.88	35.00	19.38	9.38	3.13	..	..	4.06 ± 1.23
(P <sub>1</sub> X P <sub>2</sub> ) F <sub>2</sub>	320	5.63	11.27	6.26	43.51	21.91	9.70	1.57	..	.30	..	3.02 ± 1.36
(P <sub>2</sub> X P <sub>1</sub> ) F <sub>2</sub>	317	5.04	11.66	8.82	44.42	21.11	5.36	2.21	.95	.32	..	2.97 ± 1.37
Pooled F <sub>2</sub>	637	5.34	11.46	7.54	43.96	21.51	7.54	1.88	.47	.31	..	3.00 ± 1.36
(P <sub>1</sub> X P <sub>2</sub> ) X P <sub>1</sub>	159	11.32	33.34	6.92	37.11	10.69	.63	..	..	..	..	2.04 ± 1.28
(P <sub>2</sub> X P <sub>1</sub> ) X P <sub>1</sub>	157	15.93	26.75	10.19	33.12	12.10	1.91	..	..	..	..	2.04 ± 1.38
Pooled Backcross to P <sub>1</sub>	316	13.61	30.06	8.54	35.13	11.39	1.27	..	..	..	..	2.04 ± 1.33
(P <sub>1</sub> X P <sub>2</sub> ) X P <sub>2</sub>	160	1.25	2.50	..	35.00	31.88	16.88	9.38	.63	1.25	1.25	4.01 ± 1.38
(P <sub>2</sub> X P <sub>1</sub> ) X P <sub>2</sub>	160	..	1.88	5.00	38.13	25.00	16.25	9.38	3.75	.63	..	3.96 ± 1.32
Pooled Backcross to P <sub>2</sub>	320	.63	2.19	2.50	36.56	28.44	16.56	9.38	2.19	.94	.63	3.99 ± 1.35

in the estimate for the 3 ripe fruit class to 68.30 per cent indicates the presence of genotypes other than that of the recessive and suggests that the point of division of the two phenotypes is between 2 and 3 fruit classes.

When the formula  $BC/F_1 \times 100$  is applied by accumulating the entire  $F_1$  distribution to the dividing point between the 2 and 3 fruit class and the corresponding pooled back-cross (to RFG) classes, the values,  $47.79/93.77 \times 100.00 = 50.09$ , are obtained. This approximates a 1:1 ratio and suggests the hypothesis that a single major gene conditions this character.

Table 29 shows the chi-square test for goodness of fit for a single gene hypothesis for the segregating populations. The excess number of individuals seen in the recessive class (Table 29) for the  $F_1$  and backcross to ERS, can be explained by the fact that dominance was not complete. The chi-square and P-values show an acceptable fit to the proposed hypothesis for a one major gene difference between parents.

Table 29. Chi-square test for goodness of fit for individual and pooled populations based on a one factor-pair hypothesis with dominance

Generation	Observed ratio	Theoretical ratio	Chi- sq.	P
(RFG x ERS) F <sub>1</sub>	75:5	80:0	(1:0) ---	---
(ERS x RFG) F <sub>1</sub>	75:5	80:0	(1:0) ---	---
Pooled F <sub>1</sub>	150:10	160:0	(1:0) ---	---
(RFG x ERS) F <sub>2</sub>	246:74	240.00:80.0	(3:1) .60	.4-.5
(ERS x RFG) F <sub>2</sub>	236:81	237.75:79.25	(3:1) .05	.9-.95
Pooled F <sub>2</sub>	482:155	477.75:159.25	(3:1) .15	.6-.7
(RFG x ERS) x RFG	77:82	79.50:79.50	(1:1) .16	.6-.7
(ERS x RFG) x RFG	74:85	78.50:78.50	(1:1) .52	.4-.5
Pooled BC to RFG	151:165	158.00:158.00	(1:1) .62	.4-.5
(RFG x ERS) x ERS	154:6	160:0	(1:0) ---	---
(ERS x RFG) x ERS	149:11	160:0	(1:0) ---	---
Pooled BC to ERS	303:17	320:0	(1:0) ---	---

Inheritance Of Number Of Red Ripe Fruits By The First  
Killing Frost:

Plant Introduction No. 251622 x Resistant Florida Giant

Table 30 shows the results of scaling tests applied to the data for number of red ripe fruits by the first killing frost of the  $F_2$  and backcross populations. Neither the arithmetic scale (on an additive base) or the logarithmic scale agreed with the observed means, therefore, the data were not transformed to logarithm.

Table 31 gives the frequency distribution of numbers of plants in each "number of ripe fruit" class. The parental overlap shown was taken into consideration in the analysis. The means of the  $F_1$  and backcross to PI (Table 31) show incomplete dominance for the greater number of ripe fruit. The mean of (RFG x PI)  $F_1$  of  $3.06 \pm 1.02$  and that of PI of  $3.41 \pm 1.55$  did not differ significantly. Although the mean of the reciprocal  $F_1$  of  $2.71 \pm 1.27$  was significantly different from the of PI, the means of the two  $F_1$ 's were not significantly different from one another. Although the means of the pooled backcross of PI and that of PI were significantly different, the mean was closer

Table 30. Observed and calculated means using the arithmetic (additive base) and logarithmic scales for number of red ripe fruit by the first killing frost for the F<sub>2</sub> and backcross populations from reciprocal crosses of Plant Introduction No. 251622 x Resistant Florida Giant

Generation	No. of Plants	Observed mean	Theoretical Means	
			Arithmetic	Logarithmic
F <sub>1</sub> pooled	635	2.15 ± 1.50	1.96	2.28
BC to RFG pooled	320	1.50 ± 1.26	1.24	1.52
BC to PI pooled	317	2.93 ± 1.48	2.69	2.59

Table 31 Frequency distribution of number of red ripe fruit per plant by the first killing frost for different generations of pepper plants from reciprocal crosses of Plant Introduction No. 251622 X Resistant Florida Giant.

Generation	No. of Plants	0	1	2	3	4	5	6	7	8	9	Mean
Resistant Florida Giant (P <sub>1</sub> )	80	41	37	2	..	..	..	..	..	..	..	0.51 ± 0.55
Plant Introduction No. 251622 (P <sub>2</sub> )	80	2	4	11	33	15	9	1	3	2	..	3.41 ± 1.55
(P <sub>1</sub> X P <sub>2</sub> ) F <sub>1</sub>	80	..	8	9	39	18	6	..	..	..	..	3.06 ± 1.02
(P <sub>2</sub> X P <sub>1</sub> ) F <sub>1</sub>	80	5	10	12	35	13	4	1	..	..	..	2.71 ± 1.27
Pooled F <sub>1</sub>	160	5	18	21	74	31	10	1	..	..	..	2.89 ± 1.17
(P <sub>1</sub> X P <sub>2</sub> ) F <sub>2</sub>	316	65	60	40	100	35	12	4	..	..	..	2.10 ± 1.52
(P <sub>2</sub> X P <sub>1</sub> ) F <sub>2</sub>	319	55	63	39	106	44	9	2	..	1	..	2.19 ± 1.49
Pooled F <sub>2</sub>	635	120	123	79	206	79	21	6	..	1	..	2.15 ± 1.50
(P <sub>1</sub> X P <sub>2</sub> ) X P <sub>1</sub>	160	40	52	18	46	4	..	..	..	..	..	1.51 ± 1.22
(P <sub>2</sub> X P <sub>1</sub> ) X P <sub>1</sub>	160	47	48	14	42	9	..	..	..	..	..	1.49 ± 1.31
Pooled Backcross to P <sub>1</sub>	320	87	100	32	88	13	..	..	..	..	..	1.50 ± 1.26
(P <sub>1</sub> X P <sub>2</sub> ) X P <sub>2</sub>	110	15	13	16	32	22	8	2	2	..	..	2.68 ± 1.65
(P <sub>2</sub> X P <sub>1</sub> ) X P <sub>2</sub>	207	8	25	21	80	44	23	5	1	..	..	3.07 ± 1.37
Pooled Backcross to P <sub>2</sub>	317	23	38	37	112	66	31	7	3	..	..	2.93 ± 1.48

than would be expected on an additive scale (Table 30), suggesting incomplete dominance for the greater number of ripe fruit.

The skewed  $F_2$  and the bimodal character of the backcross to RFG (recessive parent) suggest the possibility that the inheritance of this character was not complex. The mean of the pooled backcross to RFG of  $1.50 \pm 1.26$  and the lesser number of individuals in the 2 ripe fruit class suggest the dividing point for the segregating populations to be between 1 and 2 fruit classes.

The similarity of the frequency distributions of this cross (Table 31) to those of ERS x RFG (Table 26), suggest that the inheritance of the character may be similar. Based on a one major gene difference between the parents, and a point of division between the 1 and 2 red ripe fruit classes, an excessive number of individuals in the  $F_2$  and backcross to PI distributions is observed in the lower number of ripe fruit class than would be expected on the basis of 1:3 and 1:1 ratios, respectively. It is apparent therefore, that due to incomplete dominance, a portion of the plants in the 1 ripe fruit class are of a genotype other than that of the single recessive (aa). The narrow range



between the two parents and the discrete classes assigned make it impossible to further partition the 1 ripe fruit class, and to test the hypothesis by chi-square analysis.

In consideration of the above, the proposed mode of inheritance of this character was tested by comparing the observed means with theoretical means calculated on the basis of one gene difference between the two parents (number of nodes to the first furcation in the cross PI x RFG).

The proposed genotype of RFG (the parent with least number of ripe fruit per plant) is (aa) and that of PI is (AA). The gene (a) is assigned a mean "number of ripe fruit value" of 0.255 and the gene (A), the mean value of 1.45. The recessive genotype (aa) will then have a mean value of  $0.255 + 0.255 = 0.51$  which corresponds to the observed mean of the recessive parent (RFG). The dominant genotype (AA) will have a mean of  $0.51 + (2)(1.45) = 3.41$ , which corresponds to the mean of the dominant parent (PI). The  $F_1$  with the resulting genotype (Aa), is assigned a mean value of 2.5 ripe fruit. This mean value was assigned to the  $F_1$  since this represents a level of dominance between 1.95, which is the arithmetic mean of the two parents, and 3.41 which would be expected if dominance were complete.

To test the proposed model, theoretical  $F_2$  and backcross means were calculated for all the genotypes theoretically present in each of these populations. The theoretical means for the  $F_2$ , backcross to RFG, and backcross to PI are presented in Table 32. The table shows the possible  $F_2$  and backcross genotypes, the mean "number of ripe fruit" value for each genotype, the possible number of plants with each of these genotypes, and the calculation of the theoretical means for each of the populations.

The entire range of the  $F_2$  can be accounted for by the combined ranges of the two parents. The agreement between the observed and calculated theoretical means for each of the populations supports the proposed one major gene model.

#### Correlation Studies:

##### Relationship Between Earliness Factors and Various Leaf Dimensions In The Cross of Earliest Red Sweet x Resistant Florida Giant

Figure 2 shows the differences in leaf size between Earliest Red Sweet and Resistant Florida Giant. Correlation

Table 3.2 Calculated theoretical F<sub>2</sub> and backcross means based on the number of plants of each possible genotype from a monohybrid segregation

Population	Genotype	Mean "number of ripe fruit" value*	No. of plants	Total "number of ripe fruit" value
F <sub>2</sub> :	aa	.51	1	.51
	Aa	2.50	2	5.00
	AA	3.41	1	3.41
	Totals:		4	8.92
BC to RFG:	aa	.51	1	.51
	Aa	2.50	1	2.50
	Totals:		2	3.01
BC to PI:	Aa	2.50	1	2.50
	AA	3.41	1	3.41
	Totals:		2	5.91
Theoretical F <sub>2</sub> mean:			8.92/4 = 2.23	
Observed pooled F <sub>2</sub> mean:			2.15	
Theoretical mean of backcross to RFG:			3.01/2 = 1.51	
Observed mean of backcross to RFG:			1.50	
Theoretical mean of backcross to PI:			5.91/2 = 2.96	
Observed mean of backcross to PI:			2.93	

\* Mean "number of ripe fruit" value was calculated on the basis that gene (a) = .255 ripe fruit; gene (A) = 1.45 ripe fruit and the heterozygote (Aa) will have a mean of 2.50 ripe fruit

Figure 2. Plants of Resistant Florida Giant (front row) showing  
larger leaf dimensions and Earliest Red Sweet (back row)  
showing leaves with the smaller dimensions



coefficients between leaf length, leaf width, and leaf area index (as determined by length X width measurements), and the number of days to the first anthesis, number of nodes to the first furcation, and number of red ripe fruit per plant by the first killing frost were obtained from the individual  $F_2$  plants.

The correlation coefficients are presented in Table 33. The number of days to first anthesis and number of nodes to the first furcation, show a relationship with greater leaf length, leaf width, and the leaf area index. This association between these leaf dimensions and lateness is not sufficiently large enough to suggest linkage.

There was no relationship between the various leaf measurements and number of red ripe fruit.

Relationship Between Earliness Factors Studied and Fruit Bearing Habit (upright vs. pendent) in the Cross of Plant Introduction No. 251622 x Resistant Florida Giant

Since Plant Introduction No. 251622 manifests the mutant character upright fruit bearing habit, the relationship between this character and the number of days to the first anthesis, number of nodes to the first furcation and number of ripe fruit per plant were studied. No correlations were found between these characters.

Table 33. Correlation coefficients showing relationship between earliness factors and leaf measurements

Earliness Factor	Calculated r		
	Leaf Length	Leaf Width	Leaf Area Index
Number of days to first anthesis	+ .289	+ .207	+ .287
Number of nodes to first furcation	+ .369	+ .265	+ .338
Number of red ripe fruit	- .080	+ .017	- .060

## DISCUSSION

Single plant selections used in the two independent sets of crosses were selected on the basis of uniformity studies made in the greenhouse and the field. The overlapping of the frequency distributions of the parents as observed in this study was greater than expected as based on the commercial seed and Plant Introduction catalogue descriptions, and the progeny test. The progeny test was conducted during the winter of 1965. The response of the plants grown in the greenhouse differed from those grown in the field. This was especially evident in the Resistant Florida Giant selections. The differences between the early and late parents were also greater than when observed in the field.

Since the preliminary observations showed that the first fruit on the variety Resistant Florida Giant tended to abort more often than those of Plant Introduction No. 251622 or Earliest Red Sweet when the seedlings were transplanted, seeds of the various populations were sown directly into the peat pots. This procedure may have reduced the parental differences observed earlier when



seedlings were transplanted to peat pots. The difference between the early and the late parents may have been further reduced through direct seeding since ERS and PI may have been able to recover at a faster rate from transplant shock, than the late parent (RFG).

Prior to the analysis of the data, it was necessary to condense and normalize the non-segregating populations as suggested by Powers (38). The reduction in the number of plants blooming on the 58th, 63rd, and 65th days which was observed for the character, number of days to first anthesis, occurred in all the populations of both crosses. These three periods of reduced anthesis could not be attributed to genetic differences. Normalizing the frequency distributions of the non-segregating populations in these two crosses by grouping classes 57 + 58, 62 + 63 and 65 + 66, made it possible to remove some of the environmental effects. Once these groupings were made, they were applied to all populations.

The nature of the distributions and discrete classes, limited the partitioning of the distributions into more than the two parental phenotypes for chi-square analysis. Chi-square tests were applied to those characters for which a high level of dominance was observed. In the ERS and RFG

cross, dominance was observed for all three characters. Dominance was expressed to a greater extent in this cross than in the PI x RFG cross. Perhaps, as pointed out by Powers (38), it is possible that in the grouping of the data small differences were obscured, and therefore what appeared to be complete dominance in reality could have been partial dominance.

The varying levels of dominance in the PI x RFG cross from those observed in the ERS x RFG cross further complicated the analysis of the data. Allard (1) has reported variable expressions of dominance in a wheat cross in which the same populations were studied under five different environments. This is not unexpected in view of the statement by Snyder and David (44) that dominance is a relative phenomenon.

For most of the characters studied it is apparent that one major gene affected the genetic control of the majority of the variability observed. Although Odland (31) did not arrive at any specific conclusions as to the inheritance of maturity in the pepper, 77 per cent of the  $F_2$  in the cross between Harris Early Giant x Ornamental flowered by a point midway between the parental means. When this material

was carried out to the  $F_3$ , true breeding early strains were readily recovered and distinct segregation in the  $F_3$  for early and late lines was noted. Odland's  $F_2$  observations were similar to those reported here for the inheritance of the number of days to the first anthesis.

Reports of simple inheritance for various earliness components have been reported; in the tomato by Honma et al (21), in wheat by Biffin (5), in rice by Ramiah (39) and Van der Stok (49), and in cotton by Lewis and Richmond (23). Although Allard (1) suggested that two genes were involved in the inheritance of number of days to heading in wheat, he pointed out that the majority of the variability observed could be attributed to one gene. In this study, the presence of some modifiers is evident since discrete phenotypic classes were not obtained. Allard (2) has pointed out that most major genes are believed to have a complement of modifiers.

Although the data from both crosses for most of the characters studied suggest a simple genetical control, the data of the ERS x RFG cross conformed better to the expected 3:1 and 1:1 ratios than the data from the PI x RFG cross. One reason may be that the differences between parental means

for all factors studied was smaller in the PI x RFG parents than in the ERS x RFG parents, and that the PI x RFG parental distributions were not as kurtotic as those of the parents in the ERS x RFG cross. This resulted in greater overlap, which had to be considered for the calculation of the theoretical ratios. The calculations were made assuming that dominance was complete and that gene action would be the same in the  $F_2$  and backcross population genotypic backgrounds as in the parents. Another reason may be that one or both of the parents of the PI x RFG cross may have been less homeostatically stable and thus more responsive to environmental influences.

Allard (1) states that chances of successful analysis are increased when inheritance studies are conducted using parental material differing only for the gene or genes being considered. Since these hybrids would be expected to segregate for other genes than those being studied, the segregation of these other genes could have complicated the analysis in the PI x RFG cross to a greater extent than would have occurred in the ERS x RFG cross.

In the inheritance of the number of nodes to the first furcation for the PI x RFG cross a two gene model was postulated.

Although a one major gene difference was suggested for the parents of the ERS x RFG cross, the inheritance of the number of nodes to the first furcation in the pepper appeared to be conditioned by at least two genes. The genotypes in the ERS x RFG corss would then be (AAbb x AABB) and in the PI x RFG cross (AAbb x aaBB).

The presence of partial cytoplasmic influence in the PI x RFG cross for the inheritance of number of days to first anthesis and for both crosses in the inheritance of number of nodes to the first furcation is suggested from the data. Cram (11) reported similar behavior from reciprocal crosses made between the Redskin tomato and four other varieties.

## SUMMARY AND CONCLUSIONS

(1) The progenies of reciprocal crosses between Earliest Red Sweet (early) x Resistant Florida Giant (late) together with those of Plant Introduction No. 251622 (early) x Resistant Florida Giant were evaluated to learn the mode of inheritance of several earliness factors. The earliness factors concerned were the number of days from seeding to first anthesis, the number of nodes to the first furcation, the number of red fruit per plant by the first killing frost.

(2) In the cross, Earliest Red Sweet x Resistant Florida Giant, a single major gene apparently governed the genetic differences in each of the earliness factors. Dominance was observed for lesser number of days to first anthesis, lesser number of nodes to the first furcation and greater number of red ripe fruit by the first killing frost.

(3) In the cross, PI 251622 x Resistant Florida Giant, a single major gene was also found to account for the genetic variability of the earliness factors; number of days to first anthesis, and number of ripe fruit. A two gene additive model,

with one gene being twice as effective as the other, was postulated to account for the difference between parents for the number of nodes to the first furcation. Incomplete dominance was expressed for shorter duration to first anthesis and greater number of ripe fruit.

(4) In the cross, ERS x RFG, the data suggested some relationship between large leaf dimensions of length, width and leaf area index (calculated on the basis of length x width) and greater duration to first anthesis, and greater number of nodes to the first furcation. These correlation however were not high enough to suggest linkage. No significant correlation was found between leaf dimensions and number of ripe fruit per plant.

(5) In the cross, PI x RFG, no significant correlations were found between upright or pendent fruit bearing habit and the number of days to first anthesis, the number of nodes to the first furcation or the number of ripe fruit.

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