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INHERITANCE OF AN UNIFLORA MUTANT IN TOMATO

By

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ABSTRACT

INHERITANCE OF AN UNIFLORA MUTANT IN TOMATO

By

Carl Eugene Mero

Inheritance of an uniflora (one flower per truss) mutant of Lycopersicon esculentum mill, was determined from crosses involving Uniflora and Michigan State Forcing (simple inflorescence), Pennorange (pseudo-simple inflorescence), and Apsory (compound inflorescence). Uniflora was also crossed with MSU 100 (single flower per truss) to learn the relationship between these mutants.

The data from these crosses suggest that uniflora inflorescence is conditioned by one major gene with modifiers. Frequency distributions of flower number per truss in the segregating populations from the cross Uniflora x Pennorange and Uniflora x Apsory suggest gene interactions. Genetic models in the inheritance of uniflora inflorescence from the data for these crosses are presented.

A non-allelic relationship between the genes conditioning uniflora (uf) and a single flower per truss (sft) is suggested by a F_1 phenotype of simple inflorescence for the corss Uniflora x MSU 100, and by the differences in inheritance observed when Uniflora and MSU 100 are crossed with Pennorange and Apsory.

DEDICATION

To Debbie and
My Parents

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INTRODUCTION

Variation exists in inflorescence (flower number per truss) within the cultivated tomato, Lycopersicon esculentum Mill. Limited research has been devoted to determining the inherent nature of this variation. Understanding the genetic factors underlying the phenotypic variation is useful for improving the tomato.

In this study an inflorescence is considered a branch or system of branches bearing flowers (Parkin, 1914). The inflorescence of the cultivated tomato is commonly a simple or little branched raceme with varying number of flowers (Lewis, 1953). This type has been called "simple" and is conditioned by a single gene (S) and is dominant to "compound" inflorescence (s) (Crane, 1915). The number of flowers on a simple inflorescence varies over a wide range and may have one to three branches (Lewis, 1953). The compound type is distinguished from the simple type by its intense branching and high flower number. Although the number of flowers and branches of an inflorescence varies between inflorescences on the same plant, the type of inflorescence, simple or compound, is constant.

Other forms of the tomato inflorescence have been identified and their relationship to simple inflorescence

determined. The cultivar Pennorange has a "pseudo-simple" inflorescence which has 1 to 4 flowers per truss. This type is conditioned by a single gene (ps) and is recessive to simple (Vriesenga and Honma, 1973). Another form of the tomato inflorescence is the single flower per truss type expressed by MSU 100. This inflorescence has only one flower per truss and is conditioned by a single gene (sft) and is some cases by a series of modifiers. Single flower per truss is recessive to simple inflorescence and the pseudo-simple inflorescence type is epistatic to single flower per truss (Vriesenga and Honma, 1973).

A mutant which affects the tomato inflorescence is the subject of this study. This mutant has been called "uniflora" (Fehleisen, 1967). The gene responsible for this character "suppresses the side branches of the inflorescence resulting in only one axis which ends in a single flower" (Fehleisen, 1967).

The purpose of this study is to determine the relationship between the factors conditioning uniflora and those responsible for the single flower per truss phenotype of MSU 100.

LITERATURE REVIEW

The earliest genetic investigation on the tomato inflorescence was conducted by M.B. Crane (1915). He dealt with two inflorescence types: simple, which consisted of about 9 flowers and compound, with a greater number of flowers and branches. The simple type of inflorescence behave as a complete dominant but the frequency of compound types was lower than expected in both F_2 and F_3 families. All F_2 progeny exhibiting the compound inflorescence phenotype bred true for this character. He concluded that these two types of inflorescence are conditioned by a single gene (Crane, 1915).

Since Crane's report, some controversy arose concerning the basic type of inflorescence in the tomato. Bailey (1924) noted that the tomato inflorescence has 3 to 7 flowers on jointed pedicels. Cooper (1927) suggested that the floral cluster of the tomato is a short, forked, racemose-cyme of 7 to 12 flowers. Although most researchers (Crane, 1915; Bailey, 1924; Haywood, 1948; Young and Mac Arthur, 1947; Butler, 1952; Lewis, 1953) agreed that the "simple" inflorescence form is more common, there was very little agreement over which inflorescences were to be classified as simple.

Bouquet (1932) developed a classification system for the tomato inflorescence. He proposed that the simple raceme-like type of inflorescence was the dominant form. Inflorescence with one peduncle and those with just slight branching at the distal end were classified as simple. Those with more branching were considered as compound. Bouquet (1932) noted that although a cultivar generally produced one type of cluster, some cultivars showed a tendency toward more branching in the upper portion of the plant.

Lewis (1953) investigated the variation between and within 14 homozygous simple (S) inflorescence cultivars. The results indicated a considerable difference in flower number between as well as within these simple inflorescence cultivars. The degree of branching also varied considerably. Lewis (1953) concluded that three factors were involved in inflorescence size in the tomato: a major gene, a system of polygenes, which cause the variation in flower number between simple inflorescence cultivars, and the environment. He also concluded that the branching of the inflorescence was the "result" and not the "cause" of increased flower number.

Based on Lewis' (1953) and Parkin's (1914) reports, Vriesenga (1972) classified the inflorescence in to three basic types: "the monochasial inflorescence in which all flowers originate from the primary axis of the inflorescence, the compound monochasial inflorescence which has at least

one branch originating from the primary axis, and the compound dichasial inflorescence which forks similar to dichotomous branching and each axis exhibits branching." The monochasial and compound monochasial types are called simple while the compound dichasial types are called compound. He further classified the compound dichasial types with a high degree of branching as compound while those with less than four branches on each axis were classified as high flower number types (Vriesenga, 1972).

Aside from the basic forms of the tomato inflorescence, simple and compound, several mutants affecting flower number and type of inflorescence have been reported. Young and MacArthur (1947) were the first to report mutant forms of the tomato inflorescence. They described the inflorescence of Early All Red and T519 as "compound flower trusses with a giant terminal flower which had a prominent brown joint." Burdick and Mertens (1955) later reported a similar mutant causing compound inflorescence. The degree of compounding is not as great as that related to the (s) gene and often a large fasciated flower is borne in the vortex between the two major parts of the inflorescence. They called this gene "bi" for bifurcate inflorescence.

The mutant "cauliflower" which has increased branching and flower number was reported by Padock and Alexander (1952). They described this mutant as more extensively branched than compound (s) and as never having fully developed flowers. This mutant was reported as a single recessive gene (ca) and is non-allelic to (s).

Vanterpool (1957) also reported a mutant "powder-puff" that exhibits many bifurcations. This form of inflorescence shows extreme branching and aborted flower primordia where flowers are normally expected.

Vriesenga (1972) reported that the compound inflorescence phenotypes expressed by MSU 200 and the cultivar Apsory may not be the result of a single recessive gene. The F_2 segregation from (MSU 100 X MSU 200 and Apsory X MSU 180) suggest two distinct compound phenotypes. It was suggested that two closely linked genes, one for intense branching and one for non-terminal flowering, conditioned compound inflorescence.

Several forms of the tomato inflorescence with reduced flower numbers have also been reported. Young and MacArthur (1947) report that the stemless Pennred cultivar and two of their breeding lines (T1072 and T1073) have only one flower per truss. This single flower character appeared to be linked to the macrocalyx character.

Verkerk (1962) isolated a single flower per truss mutant from a radiated population of the cultivar Alisa Craig. Vriesenga (1972) obtained a single flower per truss mutant from this study which had a strong association with the macrocalyx character. It was suggested that the single flower per truss character expressed by this mutant was conditioned by a recessive gene (sft) and in some cases a series of modifiers (Vriesenga and Honma, 1973).

Vriesenga and Honma (1973) studied the inheritance of the pseudo-simple or low flower number inflorescence exhibited by the cultivar Pennorange. It was suggested that this mutant was conditioned by the recessive gene (ps) and that this gene is epistatic to (sft).

Another single flower per truss mutant, uniflora, has been described by Fehleisen (1967). The gene responsible for this character suppresses branching and elongation of the inflorescence producing one axis with one flower. This mutant is conditioned by a single recessive gene (uf), does not appear to be related to the macrocalyx character, and produces flowers and fruit which are fasciated.

A mutant which causes the abortion of the flower cluster in tomato has been reported (Azzam, 1962). This mutant is expressed as small inflorescence rudiments in the place of the normal flower cluster.

MATERIALS AND METHODS

PARENT MATERIAL

The uniflora mutant used in this study was discovered in a field of the cultivar Platense (Fehleisen, 1967). The single fasciated flower per truss character (Figure 1a) was stable through six generations of selfing. This mutant has robust growth and is fertile under both greenhouse and field conditions. The flower parts are larger than normal, the pistil is lobed, and the fruit is large and fasciated.

MSU 100 is a single flower per truss mutant which has the macrocalyx character (Figure 1b). This mutant has weak plant growth and pollen production is low in the greenhouse and was stable through at least seven generations of selfing (Vriesenga, 1972).

The cultivar Pennorange, pseudo-simple inflorescence, produces an inflorescence that bears between 1 and 4 flowers per truss (Figure 1 c). The number of flowers per truss varies between inflorescences on the same plant but never exceeds four flowers per truss.

Michigan State Forcing, a simple inflorescence cultivar, produces 3 to 14 flowers per truss (Figure 1 d). Although Vriesenga (1972) reported a range of 3 to 8 flowers per truss for this cultivar the increased range in flower number

FIGURE 1: Inflorescence types: (a) uniflora, (b) single flower per truss, (c) pseudo-simple inflorescence, (d) simple inflorescence, and (e) compound inflorescence.

can be attributed to the occasional production of compound monochasial inflorescences by this cultivar.

Apsory, a tomato cultivar developed in Bulgaria, was used as the compound inflorescnece parent. The inflorescence of this cultivar is intensely branched and is non-terminal flowering (Figure 1e). The non-terminal flowering habit makes it difficult to determine accurately the number of flowers per truss, however most inflorescences produced by this cultivar have 100 or more flowers. Aspory produces beaked, hairy, yellow, two-loculed fruit and has a dwarf growth habit.

HYBRIDIZATION

All parental material was grown in the greenhouse during the summer of 1977 and observed for homozygosity of inflorescence type. One plant of each cultivar or breeding line was selected for hybridization in the greenhouse during the winter of 1977. In the winter months supplemental lighting was provided to promote flowering; Uniflora required the use of G.E. 1000 watt multivapor lamps for flower production. All material was grown under sixteen hour days and was pruned to one or two main stems.

All backcrosses were made by using the F_1 hybrid as the female parent because of the limited number of flowers produced by the uniflora parent. Parents were maintained asexually by stem cuttings for use in backcrossing. The following reciprocal crosses were made:

Uniflora X MSU 100

Uniflora X Pennorange

Uniflora X Michigan State Forcing

Uniflora X Apsory

Field Trial 1978

Seed of parents, F_1, F_2, and backcross generations were sown in vermiculite and transplanted at the first true leaf stage. When the seedlings were six inches tall, they were transplanted into the field. The plants were placed 45 cm apart in rows and the rows were 1 meter apart. The experimental design was a randomized complete block design with four blocks. Each block contained 7 plants of each parent, 14 plants of each F_1 and backcross, and 70 F_2 plants. The number of plants from which data was recorded did not always reflect the number planted due to losses from insect and mechanical damage.

DATA

Data on inflorescence type and flower number per truss were recorded when the first inflorescence was fully expanded. The validity of using the first inflorescence to determine the phenotype of each plant was investigated. Although Lewis (1953) and Bouquet (1932) reported that the inflorescence phenotype varied from inflorescence to inflorescence on the same plant, Vriesenga and Honma (1974) reported that the first

inflorescence gave a true estimate of the plants phenotype. They (Vriesenga and Honma, 1974) found no significant differences between the mean number of flowers and branches on the first inflorescence and the mean of the first ten inflorescences. Although Vriesenga and Honma's (1974) study involved some of the same plant material, an attempt was made to substantiate their sampling procedure. Mean flower number per truss was calculated for the first, second, and third inflorescence on all F_2 plants in the fourth replicate of this study, except those with compound inflorescence. The absence of significant difference between the mean of the first inflorescence and the mean of the second inflorescence, the mean of the first inflorescence and the mean of the third inflorescence, and the mean of the second inflorescence and the mean of the third inflorescence (Table 1) suggest that the phenotype of the first inflorescence represents the plant's phenotype.

The number of flowers per truss was recorded for all individuals exhibiting single flower per truss, pseudo-simple inflorescence, and simple inflorescence. Individuals with more than three branches and those with non-terminal flowering were classified as compound inflorescence types.

In the backcross and F_2 populations where Uniflora was used as the recurrent parent, various types of fasciations were observed. Fasciations are characterized by lack of organized regularity in growth and may affect all types

of plant structures (Zielenski, 1945). The type most often observed in this study was similar to that described by Mertens and Burdick (1954) as a modified inflorescence consisting of a single fasciated flower which terminates the main axis. Accurate estimates of the number of flowers per truss were difficult to make because the inflorescences were fused to the main axis. Therefore plants with this phenotype were recorded as being fasciated and were not used in the data analysis.

Data from individual plants were used to calculate means, variances, standard deviations, and standard errors for each population. The standard t-tests (Little and Hills, 1975) was used for comparison of population means. Analysis of variance was conducted on the data from each cross (Little and Hills,1975). The means of reciprocal populations were tested for differences prior to analysis of the data.

The flower number distributions for the segregating populations were continuous and therefore the data were analyzed biometrically when phenotypic classes could not be determined from parental and F_1 distributions, as was noted for the cross Uniflora x Pennorange. For this cross expected F_2 and backcross generation means were calculated from the formulae described by Mather and Jinks (1971): $\bar{F}_2 = .5\ \bar{B}_1 + .5\ \bar{B}_2$; $\bar{B}_1 = .5\ \bar{P}_1 + .5\ \bar{F}_1$; $\bar{B} = .5\bar{P}_2 + .5\ \bar{F}_1$ ($\bar{P}_1$ is the mean of Uniflora, $\bar{P}_2$ is the mean of Pennorange, $\bar{B}_1$ is the mean of the backcross to Uniflora, $\bar{B}_2$ is the mean of the backcross to Pennorange). These predicted relationships

between population means and the proposal that they depend on additive and dominance effects of the genes were tested by the scaling tests outlined by Mather and Jinks (1971).

Mather's ABC scaling test (Mather and Jinks, 1971) with $A = 2\overline{BC}_1 - \overline{F}_1 - \overline{P}_1$: $B = 2\overline{BC}_2 - \overline{F}_1 - \overline{P}_2$; and $C = 4\overline{F}_2 - 2\overline{F}_1 - \overline{P}_1 - \overline{P}_2$ was applied to the generation means. Cavalli's joint scaling test (Mather and Jinks, 1971) was also conducted. This test utilizes data from all generations to provide estimates of the mean (m), additive (a), and dominance (d) effects (symbols after Gamble, 1962). These estimates are provided by the weighted least squares method using as weights the reciprocals of the squared standard errors. Adequacy of this three parameter model was tested by predicting the six family means from the estimates of the three parameters. Goodness of fit was tested by squaring the deviations of the observed from the expected values for each of the families, multiplying by the corresponding weight and summing the products over all six families. This sum is a Chi-square with three degrees of freedom. Significance in either scaling test suggests the existence of non-additive gene effects other than dominance and thus the estimates of (a) and (d) are biased to an unknown extent by non-allelic interactions.

Generation means were also analyzed using the methods outlined by Gamble (1962) to fit a six parameter model. These parameters are the mean effect (m), the pooled additive effect (a), the pooled dominance effect (d), the

pooled additive x additive effect (aa), the pooled additive x dominance effect (ad), and the pooled dominance x dominance effects (dd). The equations giving the estimates of these parameters in terms of the generation means are:

$$m = \bar{F}_2$$

$$a = \overline{BC}_1 - \overline{BC}_2$$

$$d = 0.5\ \bar{P}_1 - 0.5\ \bar{P}_2 + \bar{F}_1 - 4\bar{F}_2 + 2\overline{BC}_1 + 2\overline{BC}_2$$

$$aa = 2\overline{BC}_1 + 2\overline{BC}_2 - 4\bar{F}_2$$

$$ad = -0.5\ \bar{P}_1 + 0.5\ \bar{P}_2 + \overline{BC}_1 - \overline{BC}_2$$

$$dd = \bar{P}_1 + \bar{P}_2 + 2\ \bar{F}_1 + 4\ \bar{F}_2 - 4\overline{BC}_1 - 4\overline{BC}_2$$

The standard errors of the corresponding population means were used to test the significance of the various gene effects.

The minimum number of major gene pairs differentiating the parents were calculated using the formulae proposed by Powers (1950 and 1955). These methods will be illustrated in conjunction with the analysis and the interpretation of the data. The geneic models proposed on the basis of the results from the above techniques, were tested for goodness of fit to the data by Chi-square tests.

TABLE 1: Comparison of mean flower number on the first three inflorescences for the F_2 population from Uniflora x MSU 100, Uniflora X Michigan State Forcing, Uniflora X Pennorange, and Uniflora X Apsory.

Cross	Mean	Means Compared	
Uniflora X MSU 100			
1st Inflorescence	6.43±.41	1st and 2nd	NS
2nd Inflorescence	6.20±.37	1st and 3rd	NS
3rd Inflorescence	6.08±.33	2nd and 3rd	NS
Uniflora X Michigan State Forcing			
1st Inflorescence	4.99±.26	1st and 2nd	NS
2nd Inflorescence	5.19±.24	1st and 3rd	NS
3rd Inflorescence	4.70±.23	2nd and 3rd	NS
Uniflora X Pennorange			
1st Inflorescence	4.14±.22	1st and 2nd	NS
2nd Inflorescence	4.02±.20	1st and 3rd	NS
3rd Inflorescence	4.14±.24	2nd and 3rd	NS
Uniflora X Apsory*			
1st Inflorescence	7.62±.52	1st and 2nd	NS
2nd Inflorescence	7.56±.49	1st and 3rd	NS
3rd Inflorescence	7.43±.48	2nd and 3rd	NS

*Means for this cross are based on phenotypes other than compound and high flower number types.

RESULTS AND DISCUSSION

Inheritance of Uniflora Inflorescence in tomato

Uniflora X MSU 100 (Single Flower Per Truss)

The cross Uniflora X MSU 100 (single flower per truss) was made to determine if these two forms of inflorescence were controlled by the same gene. Although both inflorescences have a shortened flower truss which terminates in a single flower, there are many morphological dissimilarities. Fehleisen (1967) suggested that uniflora inflorescence was conditioned by a single recessive gene, and Vriesenga and Honma (1973) suggested that single flower per truss was conditioned by a single recessive gene and in some cases a series of modifiers.

Uniflora and MSU 100 were used in reciprocal crosses to produce F_1, F_2, and backcross populations. Since no significant differences were observed between reciprocals, the data were pooled prior to analysis. The distribution of flower number per truss for each population is presented in Table 2.

The plants selected for parents in this study were self pollinated for six generations prior to use in this

TABLE 2: Frequency distribution for flower number per truss for the various generations from the cross between Uniflora and MSU 100

Generation	No of Plants	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Mean ± S.E.
Uniflora	26	26																														1.00
MSU 100	29	1				2	2	7	14	3		1																				7.62±.64
F_1	54				1	1	8	14	13	6	4	2	1	2	2																	8.09±.49
F_2	500	153	6	6	14	28	66	58	44	26	23	11	14	10	4	10	5	5	3	1	1	2		1		2	;		2	2	2	6.39±.24
BC to Uniflora	23	11		1			1	2	2	1	1		1	1	1	1																5.35±.96
BC to MSU 100	97	32		1	3	5	10	13	12	4	4	2	1	2	3	3	1		1													5.94±.44

study. At the time of hybridization the parental plants were also selfed to check on their homozygosity. In all cases the parental material bred true when grown under greenhouse conditions of sixteen hour days and a night temperature of 68° F. However, under the field conditions the phenotype of MSU 100 was quite variable, which was perhaps the result of modifiers as reported by Vriesenga and Honma (1973). A range of from 1 to 11 flowers per truss was observed for MSU 100 (Table 2) and only one individual had the single flower per truss phenotype characteristic of MSU 100. The uniflora phenotype was stable under these field conditions as no variation in flower number per truss was observed (Table 2).

The F_1 phenotype was simple inflorescence when grown in the greenhouse and in the field. The range in flower number per truss for the F_1 was 4 to 14 (Table 2). The simple inflorescnece in the F_1 suggest the absence of parental dominance and that both parents contributed genes to produce the simple inflorescence phenotype.

The F_2 population segregated for simple inflorescence, both unbranched and compound monochasial types, and one flower per truss types (Table 2). The 153 one flower per truss types observed included 95 uniflora types, 27 single flower per truss types and 31 single flowered types that could not be classified as uniflora or single flower per truss parental types. The frequency of uniflora types closely approximates that expected for a single recessive gene,

however, the frequency of single flower per truss types is considerably lower than expected and is possibly due to the instability of the single flower per truss gene under these field conditions. The range of 2 to 30 flowers per truss on the simple inflorescence types can partially be attributed to the presence of compound monochasial types and the presence of modifiers which effected the number of flowers and branches in simple inflorescences.

Both simple inflorescence and uniflora inflorescence were observed in the backcross to Uniflora (Table 2). The approximate 1:1 uniflora to simple (P =.90 - .80) ratio (Table 3) suggests that uniflora inflorescence is monogenically inherited.

Both simple inflorescence and single flower per truss were observed in the backcross to MSU 100 (Table 2). The frequency of single power per truss types was .330 while the frequency of simple inflorescence types was .670. This ratio is a deviation from the expected 1:1 (P .01).

Data from this cross suggest that uniflora inflorescence is conditioned by a single recessive gene and is non-allelic to MSU 100 (single flower per truss). The F_2 and backcross to MSU 100 segregations were confounded by the instability of the single flower per truss gene, therefore the interaction between the uniflora gene (uf) and the single flower per truss gene (sft) could not be ascertained. The variable behavior of the single flower per truss mutant was probably a result of an

TABLE 3: Chi-square test for goodness of fit to a digenic inheritance for uniflora and single flower per truss in the cross Uniflora X MSU 100

	Observed			Expected				
Generation	Uniflora	MSU 100	Simple	Uniflora	MSU 100	Simple	X^2	P
*F_2	95	27	347	125	94	281		
BC to Uniflora	11		12	11.5		11.5	.043	.90-.80
BC to MSU 100		32	65		48.5	48.5	11.227	.01

*No chi-square value was calculated for the F_2 population because of the presence of 31 one flower per truss types that could not be classified as uniflora or single flower per truss parental types.

accumulation of modifiers which was previously suggested by Vriesenga and Honma (1973) or due to genotype x environment interaction. The role of environmental factors such as light, temperature and nutrition in affecting the number of flowers on early inflorescneces in the tomato have been reported (Wittwer, 1960).

The unstable nature of the single flower per truss parent was further investigated. Shoot tip cuttings from the single flower per truss plant were grown in the greenhouse. These cuttings produced the single flower per truss inflorescence. Selfed progeny from these cuttings were grown in separate greenhouses. Although no attempt was made to monitor the environmental differences, such as light and temperature, differences in single flower expression were observed. In one of the greenhouses, all of the inflorescences were single flower per truss while 1 to 4 flowers per truss were observed in the other greenhouse. Thus it appears that the variable expression of this inflorescence type may be "normal" for this mutant under certain environmental conditions.

Uniflora X Michigan State Forcing (Simple Inflorescence)

In the only report on Uniflora, Fehleisen (1967) suggested that uniflora inflorescence was recessive to "normal" and appeared to be monogenically inherited. Details of this study were not available therefore uniflora and simple inflorescence were hybridized to learn the nature of the uniflora

character. The results were also used for comparison with those from single flower per truss x simple inflorescence (Vriesenga and Honma, 1973).

There were no significant differences between populations resulting from reciprocal crosses between Uniflora and Michigan State Forcing (MSF) and therefore the data were pooled prior to analysis.

Distribution of the data for flower number per truss for the parents, F_1, F_2, and backcross populations are presented in Table 4. Dominance of the simple inflorescence type was suggested since there was no significant difference between the mean of the F_1 (5.73 ± .07) and the mean of MSF (5.92 ± .41), and no significant difference (1% level) between the mean of the backcross to MSF (5.96 ± .17) and the mean of MSF (Table 4).

The skewed distribution for flower number in the F_2 and the bimodal characteristic of the backcross to Uniflora (Table 4) suggest monogenic inheritance. The segregating populations were classified based on the parental phenotypes into those with one flower per truss with the remainder being classified as simple inflorescence types. The slightly wider range in flower number per truss for the segregating populations were attributed to environmental effects and segregation of modifier genes (Lewis, 1953 and Vriesenga and Honma, 1973).

Division of the two phenotypes into classes according to the above criteria suggest a single major gene is responsible for the difference between uniflora and simple inflorescence

of MSF. Dominance of the MSF phenotype is based on the absence of significant differences between both the BC to MSF and the F_1 means with that of the simple inflorescence parent, MSF. The data were examined further to determine if they fit this theory.

A theoretical F_2 mean was calculated, based on the number of factors assumed to be differentiating the parents, after the formulae proposed by Powers, et al. (1950). In this formula the symbol $\overline{P}_1$ is the mean of the dominant parent; $\overline{P}_2$ is the mean of the recessive parent; and $\overline{F}_2$ is the theoretical F_2 mean. Table 5 shows calculations for the theoretical F_2 means based on one, two or three factor-pair hypotheses. The calculated F_2 mean for the one factor-pair hypothesis is 4.60 ± .21 which was not significantly different from the observed F_2 mean (5.00 ± .41) and gave the best estimate of the number of major genes controlling this character.

The one factor-pair hypothesis for this cross can be further supported by the method developed by Powers (1955) which estimates the number of genes involved. In this method the following formula is applied:

$$F_2 / P_1 \times 100$$

where F_2 is the frequency expressed in percent for each F_2 class, and P_1 is the frequency expressed in percent for each corresponding class of the recessive parent (Uniflora). A $F_2 / P_1 \times 100$ value is calculated for each class of the F_2 which has a corresponding class of P_1 types. A mean F_2/P_1

TABLE 4. Frequency distribution for flower number per truss for the various generations from the cross between Uniflora and Michigan State Forcing (MSF).

Generation	No. of Plants	Number of Flowers 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	Mean ± S.E.
Uniflora	26	26																					1.00
MSF	26			1	3	8	9	2	1	1					1								5.92 ± .41
F_1	105		2	6	10	25	36	19	4		2				1								5.73 ± .07
F_2	485	117	10	14	37	89	94	43	25	22	15	7	5	3	3							1	5.00 ± .14
BC to Uniflora	106	49	1	2	4	11	12	8	4	5	5	3	1						1				4.21 ± .35
BC to MSF	87		1	5	7	16	31	14	9	3		1											5.96 ± .17

TABLE 5 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= 4.69 ± .55	5.00 ± .14
2	(15/16) P_1 + (1/16) P_2 = 5.61 ± .62	5.00 ± .14
3	(63/64) P_1 + (1/64) P_2 = 5.84 ± .64	5.00 ± .14

X 100 value is calculated to give an estimate of the percentage of the F_2 population that corresponds to the recessive parent's phenotype. In this case the recessive phenotype is only found in one class of the F_2, that being the one flower per truss class. The estimate of the percent of the recessive parent types in the F_2 is 24% which when compared to the expected (25%) based on a one factor-pair hypothesis gave a good fit (P = .90 -.50).

The following genetic model is proposed for the inheritance of inflorescence type in this cross: One major locus (Uf) is responsible for the difference in inflorescence type between Uniflora and MSF. The homozygous recessive condition at this locus (ufuf) gives uniflora inflorescence while the presence of at least one dominant alllele (Uf-) gives simple inflorescence (Table 6). Based on this single gene model the expected ratios are 3 (simple): 1 (uniflora) in the F_2, 1 (simple): 1 (uniflora) in the backcross to Uniflora, and 1

TABLE 6: Proposed inheritance of the uniflora inflorescence from the cross Uniflora X Michigan State Forcing

UNIFLORA (P_1) (ufuf)	X	MICHIGAN STATE FORCING (P_2) (UfUf)

F_1 SIMPLE (Ufuf)

F_2 3/4 SIMPLE (Uf-)

1/4 UNIFLORA (ufuf)

BACKCROSS TO P_1	BACKCROSS TO P_2
1/2 SIMPLE (Ufuf)	1 SIMPLE (Uf-)
1/2 UNIFLORA (ufuf)	0 UNIFLORA

(simple): 0 (uniflora) in the backcross to MSF. The P-values for the F_2 (P = .95 - .90) and backcross to Uniflora (P = .50 -.30) showed a good fit to this model (Table 7). The backcross to MSF population is not testable by Chi-square, since 0 is the expected frequency of one of the classes. However, based on the assumptions of this model, the observed ratio of 87 simple to 0 uniflora suggest agreement with the model.

TABLE 7: Chi-square test for goodness of fit to a monogenic inheritance for uniflora and simple inflorescence in the cross Uniflora X Michigan State Forcing (MSF).

Generation	Observed		Expected		X^2	P
	Uniflora	Simple	Uniflora	Simple		
F_2	117	368	121.25	363.75	.199	.95-.90
BC to Uniflora	49	57	53	53	.604	.50-.30
BC to MSF	0	87	0	87		

Uniflora X Pennorange (Pseudo-simple Inflorescence)

The cross Uniflora X Pennorange was studied to further substantiate that the gene or genes controlling the inflorescence forms of Uniflora and MSU 100 are non-allelic and therefore should differ in their inheritance in crosses to Pennorange.

Uniflora and Pennorange were crossed reciprocally to produce F_1, F_2, and backcross populations. The frequency distributions for the pooled data are shown in Table 6. The Pennorange parent had a range of 1 to 4 flowers per truss and a mean flower number per truss of 2.50 ± .14, while the uniflora parent produced only one flower per truss.

The F_1 population was simple inflorescence and the number of flowers per truss ranged from 3 to 7 flowers. The simple inflorescence in the F_1 suggest the absence of parental dominance and that both parents contributed to the simple inflorescence phenotype.

The F_2 population ranged from 1 to 14 flowers per truss and had three inflorescence types: uniflora, pseudo-simple, and simple. The presence of simple inflorescence in the F_2 was probably due to recombination of parental genes and modifiers.

The overlap of the Uniflora and Pennorange phenotypes as well as the overlap of the Pennorange and the F_1 phenotypes makes it difficult to classify the F_2 population into discrete phenotypic groups. The arithmetic mean of the two parents is 1.78 and the arithmetic mean of the Pennorange parent and the F_1 is 4.67 which suggest separation of the flower number distribution between the 1 and 2 flowers per truss classes and between the 4 and 5 flowers per truss classes corresponding to the uniflora, pseudo-simple and simple inflorescence types, respectively. Based on the parental and F_1 distributions (Table 8), 10.70% of the

TABLE 8: Frequency distribution for flower number per truss for the various generations from the cross between Uniflora and Pennorange

Generation	No. of Plants	Number of Flowers															Mean ± S.E.
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Uniflora	26	26															1.00
Pennorange	28	3	9	15	1												2.50 ± .14
F_1	110			8	13	44	36	9									5.23 ± .10
F_2	519	134	29	60	57	89	79	26	20	7		6	5	3	2	2	4.10 ± .11
BC to Uniflora	108	46	2	4	4	18	12	4	4	6		5	1		1	1	4.09 ± .32
BC to Pennorange	108	14	19	27	14	20	10	2	1					1			3.55 ± .18

pseudo-simple inflorescence types had one flower per truss while 19.09% of the simple inflorescence types had less than five flowers per truss.

The frequency of inflorescence types in the F_2 were .258 uniflora, .281 pseudo-simple, and .460 simple. The expected F_2 segregation was determined from the adjusted frequencies calculated with the overlap values and a theoretical F_2 segregation of .562 simple, .250 uniflora, and .188 pseudo-simple inflorescence. The calculation of the adjusted F_2 frequencies was as follows:

uniflora inflorescence = .250 + (.107 x .188) = .270

simple inflorescence = .562 - (.191 x .562) = .455

pseudo-simple inflorescence = .188 + (.191 x .562) - (.107 x .188) = .275

The backcross to Uniflora population had a range of 1 to 14 flowers per truss. The frequency of uniflora types was .423 while the frequency of simple inflorescence types was .481. The presence of .091 individuals of the 2 to 4 flower class is perhaps due to modifier genes or to genotype x environment interactions. The observed segregation suggest that uniflora inflorescence is monogenically inherited.

The backcross to Pennorange population had a range of 1 to 12 flowers per truss. The one flower per truss class belongs to the pseudo-simple types since observation of succeeding inflorescences on the same plant were of the Pennorange phenotype of 1 to 4 flowers per truss. The frequency

of the pseudo-simple class is .685 while the frequency of simple inflorescence types is .315. The expected frequency based on a single recessive gene conditioning pseudo-simple inflorescence, adjusted for the overlap of the Pennorange and and F_1 phenotypes (19%) is .595 pseudo-simple to .405 simple inflorescence and the data fits this single gene model (P = .10 - .05) (Table 9).

TABLE 9: Chi-square test for goodness of fit to a digenic inheritance for inflorescnece type in the cross Uniflora X Pennorange

	Observed			Expected				
Generation	Uniflora	Pseudo-simple	Simple	Uniflora	Pseudo simple	Simple	X^2	P
F_2	134	146	239	140	143	236	.386	.90-.80
BC to Uniflora	46		62	54		54	2.365	.20-.10
BC to Pennorange		74	34		64	44	3.610	.10-.05

Due to the continuous distribution and probable genetic interactions, the data were analyzed biometrically. Expected F_2 and backcross generation means were calculated after the formulae described by Mather and Jinks (1971). The observed and calculated means are 4.10 and 3.82 for the F_2, 4.09 and 3.12 for the backcross to Uniflora (BC_1), and 3.55 and 3.86

for the BC_2. These relationships between population means and the proposal that they depend on additive and dominance effects of the genes was tested by Mather's A,B,C scaling test and Cavalli's joint scaling test (Mather and Jinks, 1971). The results of these scaling tests are shown in Table 10. Both factors A and C were significant in the A, B, C scaling test (1% level) and the joint scaling test was significant (1% level). Significance in either test suggest the possibility of epistasis in the expression of inflorescence type.

The inadequacy of the three parameter model made it necessary to use a six parameter model outlined by Gamble (1962) in order to determine the nature of the epistatic effects. The six parameter estimates (Table 11) show that a dominant gene effect made the major contribution to variation in inflorescence type in the cross Uniflora X Pennorange. Also, the additive x dominance epistatic effects are significant (1% level) suggesting that genetic models which assume minimal epistasis may be biased. The relative importance of the three types of epistatic effects were expected since the F_1 mean suggest considerable heterosis.

Mather and Jinks (1971) report that the type of epistatic interaction (complementary or duplicate) can be inferred from the relative signs of $\underline{d}$ and $\underline{dd}$. Like signs indicate complementary epistasis while opposite signs indicates duplicate epistasis. In this cross, the estimate of $\underline{d}$ is significantly positive but the estimate of $\underline{dd}$ is not significantly different

TABLE 10: Significance of the A,B,C and joint scaling tests for inflorescence type in the cross Uniflora X Pennorange

Test			
A	B	C	Joint
**	ns	**	**

**Significant at the 1% level
ns, non-significant at the 5% level

TABLE 11: Gene effects estimated using a six-parameter model on the generation means for the cross Uniflora X Pennorange

Model and Effect	Estimates
Six-parameter	
m	4.10 ± .012**
a	0.54 ± .134
d	3.36 ± .074**
aa	-1.12 ± .728
ad	0.75 ± .005**
dd	-.020 ± .788

**significantly different from zero.

from zero and therefore the type of epistatic interaction cannot be determined.

The F_2 and backcross populations were partitioned into uniflora, pseudo-simple and simple inflorescence types and the following genetic model is proposed: Two major loci are responsible for the difference in inflorescence type between Uniflora and Pennorange. The proposed genotype of Uniflora is ufufPsPs while the genotype of Pennorange is UfUfpsps. The F_1, with a genotype of UfufPsps, is simple inflorescence. The observed F_2 and backcross segregations suggest a 9 (simple): 4 (uniflora): 3 (pseudo-simple) recessive epistasis gene model. Uf-Ps-conditions simple inflorescence, recessive homozygosity at the uf locus conditions uniflora inflorescence regardless of the genotype of the Ps locus, and recessive homozygosity at the ps locus in combination with at least one dominant allele at the Uf locus conditions pseudo-simple inflorescence. That is, the gene for uniflora inflorescence (uf) exhibits recessive epistasis to the gene for pseudo-simple inflorescence (ps) (Table 12).

The data from this cross were tested for goodness of fit to this digenic model in which the uniflora gene is epistatic to the gene for pseudo-simple inflorescence. Based on this model the expected ratios are 9 (simple): 4 (uniflora): 3 (pseudo-simple) in the F_2, 1 (simple): 1 (uniflora) in the backcross to Uniflora and 1 (simple): 1 (pseudo-simple) in the backcross to Pennorange. The P values for the F_2 (P = .90-.80), the backcross to Uniflora (P = .20 -.10), and the

TABLE 12: Proposed inheritance of the uniflora inflorescence from the cross Uniflora X Pennorange

UNIFLORA (P_1)	X	PENNORANGE (P_2)
(ufufPsPS)		(UfUfpsps)

F_1 SIMPLE
(UfufPsps)

F_2 9/16 SIMPLE
(Uf-Ps-)

3/16 PSEUDO-SIMPLE
(Uf-psps)

4/16 UNIFLORA
(ufufPs- or ufufpsps)

BACKCROSS TO P_1	BACKCROSS TO P_2
1/2 SIMPLE (UfufPs-)	1/2 SIMPLE (Uf-Psps)
1/2 UNIFLORA (uf_{uf}Ps-)	1/2 PSEUDO-SIMPLE (Uf-psps)

backcross to Pennorange (P = .10 - .05) all suggest a good fit to the proposed model (Table 9).

Uniflora X Apsory (compound Inflorescence)

The cross Uniflora x Apxory (compound Inflorescence) was made to provide further evidence supporting the proposed non-allelic relationship between the genes controlling uniflora and single flower per truss.

Uniflora and Apsory were used in reciprocal crosses to produce F_1, F_2, and backcross populations. Since no significant differences were observed between reciprocals, the data were pooled. The distribution of flower number per truss for each population is shown in Table 13.

The inflorescence type of Apsory is a compound dichasium. This inflorescence form is characterized by intense branching and indeterminate production of new flowers. The continual production of new flowers at the terminal ends of the inflorescence makes accurate estimates of flower number difficult and therefore individuals with dichotomous-like branching and indeterminate flowering were classified as compound inflorescence. In this study, all individuals with more than 30 flowers per truss had the characters of compound inflorescence, and therefore 30 flowers was chosen as the division point between simple and compound inflorescence.

The F_1 population ranged from 5 to 16 flowers per truss and were simple inflorescence (Table 13). The presence of simple inflorescnece in the F_1 suggest an absence of parental

TABLE 13: Frequency distribution for flower number per truss for the various generations from the cross Uniflora X Apsory

Generation	No. of Plants	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	*
Uniflora	26	26																														
Apsory	16																															16
F_1	104					3	11	32	32	11	6	1	2	4	1		1															
F_2	498	97	8	12	2	17	65	93	54	18	11	17	11	14	5	7	5	3	5	1	1	5	1	1	2	2	1	1	1	1	13	24
BC to Uniflora	104	46		1	2	5	12	11	7	1	3	2	1	3	1	3	1		1			1				1					2	
BC to Apsory	107					1	6	27	24	8	2	3	2	2	2	3					1			1		1					6	30

* = Compound Inflorescence

dominance and that genes from both parents contributed to the simple inflorescence phenotype in the F_1.

The F_2 population included inflorescences with 1 to 30 flowers per truss and compound inflorescence (Table 13). The simple inflorescence type was most frequent (.745) and included trusses with 2 to 30 flowers with both branched and compound monochasial types. The frequency of uniflora types was .195 which is lower than that expected for a single recessive gene and suggest the presecne of modifiers and/or genic interactions. The frequency of compound inflorescence types was .048 and suggest a digenic inheritance for compound inflorescence.

The backcross to Uniflora population ranged from 1 to 30 flowers per truss and segregated for both uniflora and simple inflorescence (Table 10). The frequency of uniflora types was .442 while the frequency of simple inflorescence types was .558. This segregation ratio suggests that uniflora inflorescence is conditioned by a single recessive gene (P = .30 -.20) (Table 14).

The backcross to Apsory population segregated for simple inflorescence (5 to 30 flowers per truss) and compound inflorescence (Table 13). The frequency of simple inflorescence types was .795 while the frequency of compound inflorescence types was .205. This low frequency of compound inflorescence serves as further support for the proposal that compound inflorescence may be conditioned by two genes in this cross.

TABLE 14: Chi-square test for goodness of fit to a three gene model for the inheritance of inflorescence type in the cross Uniflora x Apsory

	Observed			Expected				
Generation	Uniflora	Simple	Compound	Uniflora	Simple	Compound	X^2	P
F_2	97	371	30	101	374	23	2.086	.50-.30
BC to Uniflora	46	58		52	52		1.384	.30-.20
BC to Apsory		85	22		80	27	1.125	.30-.20

The expected frequency of compound inflorescence types based on a digenic inheritance is .250 and the data shows a good fit to this hypothesis (P = .30-.20) (Table 14).

The proposed model involves three major genes (designated Uf, B, and C) which make up the parents, Uniflora and Apsory. The proposed genotype of Uniflora is ufufBBCC (uniflora inflorescence) and that of Apsory is UfUfbbcc (compound inflorescence). The F_1, with a genotype of UfufBbCc, is simple inflorescence. The observed F_2 and backcross ratios suggest a (13:3) (3:1) factorial gene model. At least one dominant allele at the Uf locus conditions simple inflorescence in all cases except when both locus b and locus c are homozygous recessive. This is the genotype of Apsory and is

compound inflorescence. The homozygous recessive condition at the uf locus conditions uniflora inflorescence in all cases except when locus b is homozygous recessive and locus C has at least one dominant allele. That is, the three loci exhibit recessive and dominant epistasis which result in the expression of simple inflorescence for this genotype (ufufbbC-). When all three loci are homozygous recessive, ufufbbcc, the uniflora gene (uf) exhibits recessive epistasis over the genes for compound inflorescence resulting in the uniflora phenotype. This model is presented in Table 15. Chi-square analysis suggests a good fit to this three gene epistatic gene model (Table 14).

Vriesenga (1972) also reported genic interactions and a deficiency of single flower per truss and compound inflorescence in the cross MSU 100 x Apsory. In that study Vriesenga used F_3 data to support his proposal that the gene for single flower per truss (sft) was epistatic to the gene for compound inflorescence. The present study suggest that uniflora inflorescence is also conditioned by a single recessive gene (uf) which is epistatic over the genes for compound inflorescence. However, this data differs from that reported by Vriesenga (1972) for the cross MSU 100 x Apsory in that it suggest a digenic inheritance for compound inflorescence. This difference can probably be attributed to the presence of the gene designated C which was carried by the Uniflora parent in the homozygous dominant condition. These

TABLE 15: Proposed inheritance of the uniflora inflorescence from the cross Uniflora X Apsory

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UNIFLORA (P_1) X APSORY (P_2) COMPOUND

(ufufBBCC) (UfUfccbb)

F_1 SIMPLE
(UfufBbCc)

F_2 48/64 SIMPLE
(UF-B-C-)
(Uf-B-cc)
(Uf-bbC-)
(ufufbbC-)

13/64 UNIFLORA
(ufufB-C-)
(ufufB-cc)
(ufufbbcc)

3/64 COMPOUND
(Uf-bbcc)

BACKCROSS TO P_1

1/2 SIMPLE
(UfufB-C-)

1/2 UNIFLORA
(ufufB-C-)

BACKCROSS TO P_2

3/4 SIMPLE
(Uf-BbCc)
(Uf-Bbcc)
(Uf-bbCc)

1/4 COMPOUND
(Uf-bbcc)

observations support the proposed model, however, and F_3 population would be desirable before final conclusions can be made.

SUMMARY AND CONCLUSIONS

The inheritance of the uniflora inflorescence type and its relationship to the single flower per truss type was investigated by hybridizing Uniflora and MSU 100 (single flower per truss), Uniflora and Michigan State Forcing (simple inflorescence), Uniflora and Pennorange (pseudo-simple inflorescence), and Uniflora and Apsory (compound inflorescence). The results from these crosses were compared with those reported by Vriesenga and Honma (1973) in order to learn the relationship between these two inflorescence forms.

Uniflora inflorescence was suggested to be conditioned by a single major gene (uf) from these crosses. The presence of simple inflorescence in the F_1 population of all of the crosses suggest that uniflora inflorescence is recessive and supports the proposal that simple inflorescence is the wild type for the cultivated tomato (Vriesenga and Honma, 1973). The continuous distribution for the flower number per truss in the segregating populations suggest that the Uniflora parent has modifier genes which play a role in inflorescence type. The uniflora gene (uf) exhibits recessive epistasis over the gene for pseudo-simple inflorescence (ps) and both dominant and recessive epistasis exists between the genes for uniflora inflorescence and those for compound inflorescence.

The compound inflorescence parent, Apsory, also contributed modifiers which effected the expression of uniflora inflorescence.

A non-allelic relationship between the genes conditioning uniflora (uf) and single flower per truss (sft) is suggested by the following: (1) the apparent complementation of the genes to produce simple inflorescence in the F_1 population, (2) the observation that the uniflora gene (uf) is epistatic to the gene for pseudo-simple inflorescence (ps) while the opposite epistatic relationship between the gene for single flower per truss (sft) and the ps gene was reported by Vriesenga and Honma (1973), and (3) these two mutants differ in their inheritance when crossed with the compound inflorescence cultivar, Apsory.

The inflorescence in the tomato exhibits a sympodial growth habit similar to that of the main stem. Since determinate, semi-determinate, and indeterminate tomato cultivars exist, it is possible that similar types of inflorescence are produced by the tomato. The uniflora and single flower per truss inflorescnece forms could be considered as determinate inflorescence types, the pseudo-simple inflorescence type could be considered as semi- determinate and the simple inflorescence type could be considered as indeterminate. The compound inflorescence type which is both indeterminate and highly branched could be the result of a combination of the gene for indeterminate inflorescence and a gene for intensive branching as was suggested by Vriesenga (1972). In addition to the

major genes controlling inflorescence type, both modifiers and environment played a role in the ultimate inflorescence phenotype.

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