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INHERITANCE OF FACTORS AFFECTING INFLORESCENCE TYPE AND NUMBER OF FLOWERS ON THE INFLORESCENCE IN TOMATO
Lycopersicon esculentum Mill.

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ABSTRACT

INHERITANCE OF FACTORS AFFECTING INFLORESCENCE TYPE AND NUMBER OF FLOWERS ON THE INFLORESCENCE IN TOMATO *Lycopersicon esculentum* Mill.

By

Jerry Dale Vriesenga

Studies on the inheritance of a single flower per truss, compound inflorescence, simple inflorescence and low-flower-number inflorescence were carried out. The mode of inheritance for number of flowers and branching of the simple inflorescence was also investigated.

It was found that the character single flower per truss was determined by a recessive gene from crosses MSU 100 (single flower) x MSU 180 (simple inflorescence) and MSU 100 (single flower) x Pennorange (low-flower-number inflorescence). The Pennorange phenotype--low-flower-number inflorescence--was conditioned by a recessive gene and the gene was epistatic to the gene for single flower.

The mode in inheritance for the single flower character was more complex in crosses with compound inflorescence parents, Apsory and MSU 200. A model was proposed including the recessive single flower gene (a), an inhibitor gene (I) which inhibits the expression of single flower and a restorer gene (R) which negates the effect of the inhibitor.

The single flower gene (a) was suggested to be epistatic to the gene for compound inflorescence.

Compound inflorescence was suggested to be conditioned by two genes, intense branching and non-terminal flowering (ntf). The genes were linked with recombination values of 6% in the crosses MSU 100 x Apsory and Apsory x MSU 180, and 11% in the cross MSU 100 x MSU 200.

Simple florescence was found to be dominant in all crosses observed. Modifiers affecting the number of flowers on the unbranched inflorescence were studied. Two classes, 4-flower and 8-flower were observed in the cross MSU 100 x Pennorange. No dominance was noted between the 4-flower class and the 8-flower class. Two classes were observed in the cross MSU 100 x MSU 200. The classes, 10-flower and 7-flower, segregate to a digenic 9:7 ratio of 10-flower class to 7-flower class.

The inheritance of branched inflorescence was suggested to be related to the modifier conditioning the 4-flower and 8-flower classes in the cross MSU 100 x Pennorange. A single gene was suggested to affect branching in the cross MSU 100 x MSU 200 and the gene was independent from the number of flowers on the unbranched inflorescence.

It was suggested that intercalary inflorescence (ini)--indeterminant vegetative growth on the florescence--was conditioned by one gene.

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The gene for jointless pedicel (j) was suggested to be either closely linked or pleiotropic with the gene for intercalary inflorescence (ini).

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DEDICATION

To Marcy and
Our Children

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INTRODUCTION

An inflorescence in this study is considered as a branch or system of branches bearing flowers. Simple inflorescence (S̲) is observed in most cultivated tomato varieties and displays a wide range of expression. Variation in the number of flowers per unbranched monochasium (Figure 1b) and individuals with compound monochasial inflorescences (Figure 1c) were observed in the simple inflorescence class. This study is concerned with the inheritance of variations of unbranched and compound monochasial inflorescences as well as with the inheritance of mutants that affect specific inflorescence types (single flower per truss and compound inflorescence).

Compound inflorescence (s̲) exhibits the inflorescence structure of the compound dichasium (Figure 1a). This inflorescence type is associated with intense branching of the inflorescence and high flower number.

A study of low flower number per inflorescence is important because of its association with the jointless pedicel character (j̲). Jointless pedicel has potential value in that a variety possessing this character would have less fruit injury during mechanical harvest. Since fruits bearing

Figure 1. Representative types of inflorescence structure making up the compound and simple inflorescences in the tomato. Compound: a) compound dichasium. Simple: b) unbranched monochasium, c) compound monochasium. Classification after Parkin (20).

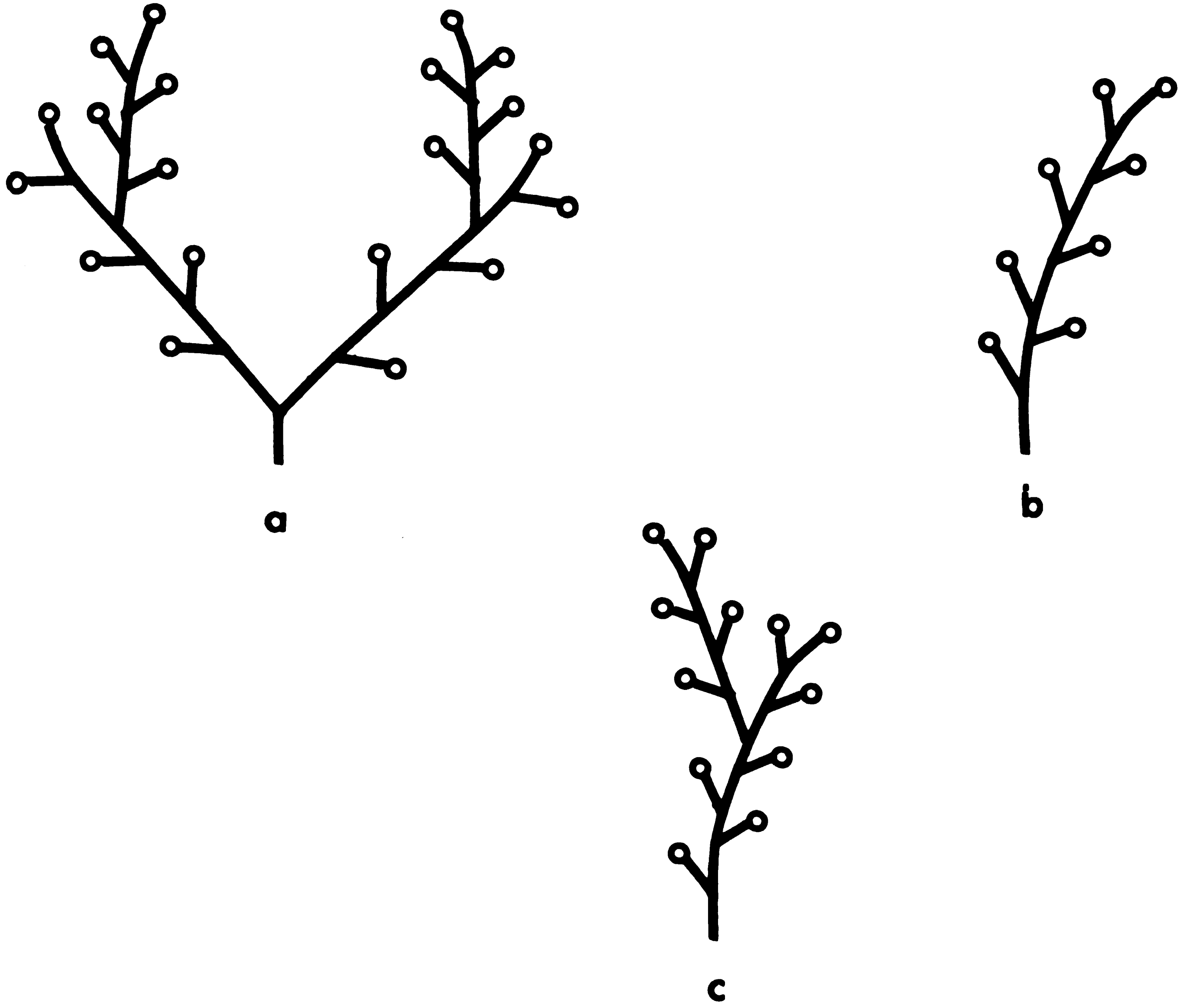


Figure 1

the jointless pedicel separate from the plant at the surface of the fruit, the possibility of puncture from another fruit's pedicel is eliminated.

It was earlier suggested that the jointless character is associated with low flower number per inflorescence and with leafy inflorescence (*lf*). A complete understanding of these associations is desirable in order to determine the value of the jointless pedicel in a breeding program.

Numerous investigations have been made on increasing the number of flowers on the first cluster of simple inflorescence bearing tomato varieties by manipulating the environment during early stages of plant growth. Knowledge on the inheritance of flower number and of environmental effects on flower number could increase the yield of future varieties.

The investigation of compound inflorescence and the single flower per truss character have little immediate horticultural significance. However, studies on the heritability of these characters aid in the understanding of the total genetic make-up of the tomato and may be of future use in breeding.

REVIEW OF LITERATURE

Inheritance studies on simple and compound inflorescence were first conducted by Crain (4) in 1915. Compound inflorescence was suggested to be controlled by a single recessive gene (s). F_3 segregates in subsequent years showed a deviation from the original single gene hypothesis. Segregations from simple and compound inflorescence conducted by Mac Arthur (12) showed a good fit to the single gene model.

According to Crain (4), the compound inflorescence character was made up of several distinct types. Butler (3) and Mac Arthur (13) described this character as having appoximately 80 flowers per inflorescence however; later reports by Young and Mac Arthur (26) and Lewis (11) describe the character as having up to 300 flowers.

The classification of inflorescence types suggested by Parkin (20) allows considerable latitude for the expression of both simple and compound inflorescences. The basic structure of the compound inflorescence is the compound dischasium (Figure 1a). Deviations in the intensity of branching or flower development can result in compound inflorescences with varying flower numbers.

The number of flowers per monochasium, and the number of branches on a compound monochasium allow for a wide range of flower number per inflorescence and structural variation within the simple inflorescence. Lewis (11) compared several tomato varieties and observed distinct classes of flower number within unbranched monochasial inflorescences. The presence of compound monochasial inflorescences were also noted.

Since the initial studies of simple inflorescence and the compound inflorescence (4,12), other mutants affecting the intensity of branching and inflorescence structure have been reported. Mertens (16) reported on the bifurcate inflorescence character (bi). This character was described as an extremely bifurcate inflorescence but not as greatly bifurcate as the compound inflorescence. The character was thought to be controlled by a single recessive gene. Phenotypic expression of this gene is similar to the branching of compound monochasium as reported by Lewis (11). Both characters are incompletely expressed, but the bi gene yields more bifurcations per inflorescence.

The gene cauliflower (ca) was reported by Paddock and Alexander (19) to give a multibifurcate inflorescence similar to the compound inflorescence. They differed in that the cauliflower gene failed to produce mature flowers.

An abortive flower cluster mutant was reported by Azzam (1). This mutant, although not fully investigated, was proposed to be controlled by a single recessive gene.

A mutant described by Young and Mac Arthur (26) gives a single flower per inflorescence. This character was suggested to be closely associated to the macrocalyx (mc) character. A similar phenotype was observed by Myers (18) in the jointless pedicel tomato variety Pennred.

A single flower character was observed in a radiated population of Alisa Craig. This mutant was described as a yellow topped plant with a single flower per truss and the flower appeared to be sterile (25). Similar single flower mutants were described by Young and Mac Arthur (26) and Myers (18), the single flower mutant obtained for this study (25) shows a strong association to the macrocalyx character.

Fehleisen (7) described a mutant that provided a single fasciated flower. This recessive character was designated as uniflora (uf).

The jointless pedicel (j) described by Butler (2) has been reported to be associated with 1-4 flowers per inflorescence. Studies by Rick and Sawant (23) and Emery and Munger (6) suggested that the phenotypes low flower number and jointless pedicel were closely associated.

The jointless pedicel was previously reported to be associated with other morphological characters in the tomato. The relationship of jointless pedicel to leafy inflorescence has been discussed by Mertens (16), Rick and Sewant (23) and Emery and Munger (6). All of the studies conclude that the jointless pedicel character is closely linked to the leafy inflorescence character or they are pleiotropic.

A strong relationship between the number of nodes to the first inflorescence and days to the first inflorescence was reported by Honma, Wittwer and Phatak (8). Elsayed and Foskett (5) reported on the association between jointless pedicel and the number of nodes between inflorescence and the masking of the <u>sp</u> locus by the action of the jointless pedicel character.

The close association of the jointless pedicel character to low flower number, leafy inflorescence, number of nodes between clusters and the masking of the <u>sp</u> locus are suggested by Emery and Munger (6) to be due to a morphogenic relationship of these characters to the jointless phenotype.

MATERIALS AND METHODS

PARENT MATERIAL

The tomato line MSU 100, a mutant expressing a single flower per truss (Figure 2) was received from Dr. K. VerKerk, Department of Horticulture of the Agricultural University of Wageningen, The Netherlands. This mutant shows similarity to the single flower character illustrated by Young and Mac Arthur (26). MSU 100 was selfed for seven generations prior to being used in this study.

The variety Pennorange was used as the low flower number parent. This variety exhibits 1-4 flowers per inflorescence and jointless pedicel.

Apsory, a tomato variety received from Dr. M. Jordanov, Maritsa Institute for Vegetable Crops, Plovdiv, Bulgaria, was used as a compound inflorescence parent (Figure 3a). This variety also displays the dwarf plant habit (d).

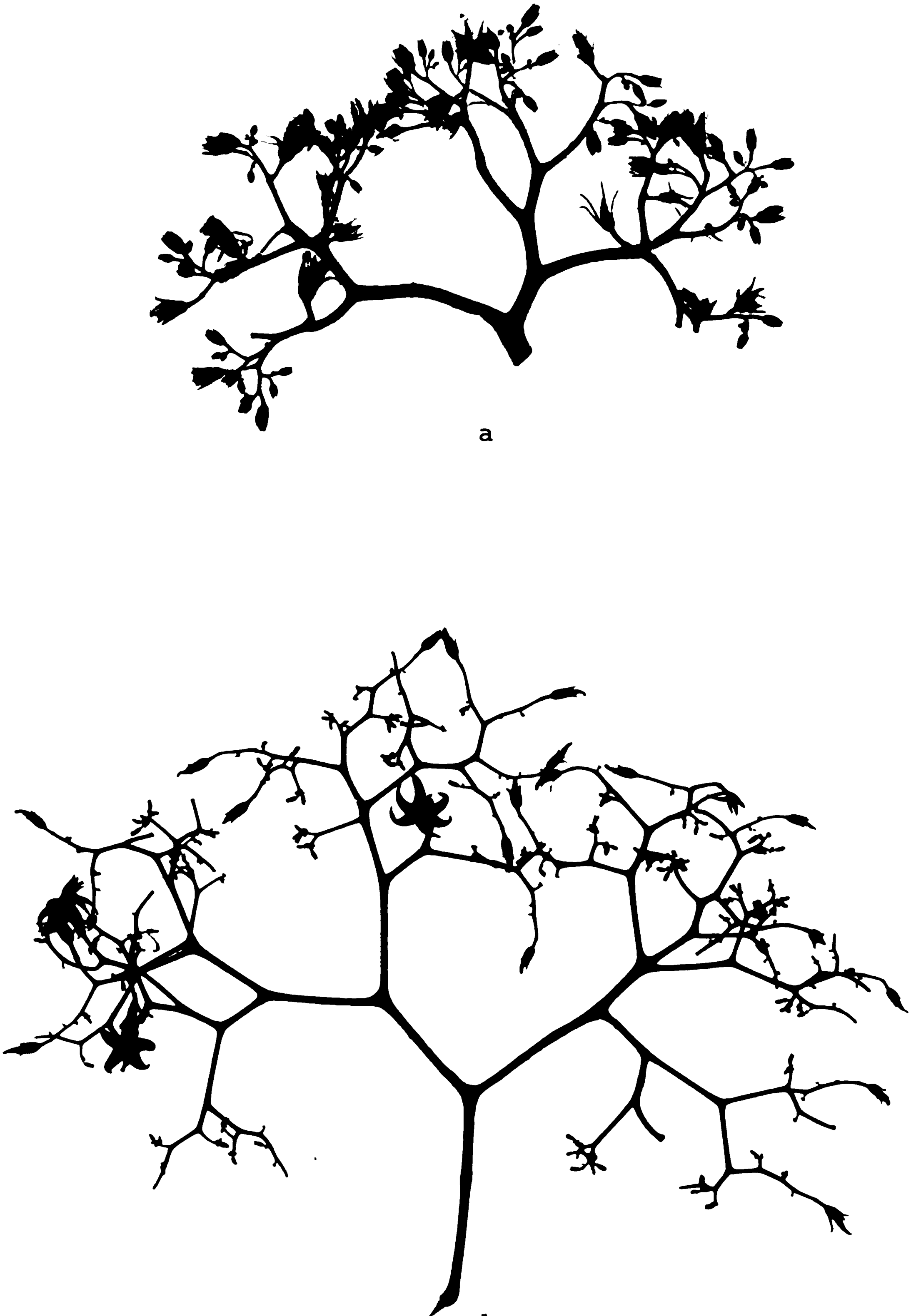
A breeding line of Lycopersicon pimpinellifolium Mill. (MSU 200) was also used as a compound inflorescence parent (Figure 3b).

Two cultivars were used as simple inflorescence parents, MSU 180 with 6-18 flowers per inflorescence and Michigan State Forcing with 3-8 flowers per inflorescence. The range 6-18

Figure 2. The character single flower per truss as it appears on MSU 100.

Figure 2

Figure 3. The compound inflorescence phenotype exhibited by a) Apsory and b) MSU 200.



a

b

Figure 3

flowers observed on MSU 180 was due to a high frequency of compound monochasial inflorescences. Michigan State Forcing shows a low frequency of compound monochasial inflorescences.

HYBRIDIZATION

All parental material was grown in the greenhouse and evaluated for homozygosity, prior to hybridization. Individual plants were used in making each cross. All crosses and selfs were made in the greenhouse. The parents used for hybridization were also selfed for use in this study. Parental plants were maintained by cuttings for making backcrosses.

Seed of the parental and segregating populations for the cross Pennorange x Michigan State Forcing were acquired from a previous study by Honma, Wittwer and Phatak (8). The following reciprocal crosses were made for this study:

MSU 100 x Pennorange
MSU 100 x Apsory
Pennorange x Michigan State Forcing

The following crosses did not include reciprocal crosses:

MSU 100 x MSU 200
MSU 100 x MSU 180
Apsory x MSU 180

FIELD TRIAL

Seed of the parent, F_1, F_2, F_3 and backcross populations were planted in vermiculite and seedlings were transplanted into flats at cotyledon expansion. When the plants were 5-6 inches tall, they were transplanted in the field.

Summer 1969

The parents, F_1, F_2 and backcross populations for the crosses MSU 100 x Pennorange, MSU 100 x Apsory, and MSU 100 x MSU 200 were grown in the summer of 1969. F_2 selections from the following crosses were saved for observation in the F_3 generation:

a) single flower types from crosses MSU 100 x Pennorange
b) single flower, jointless pedicel types from the cross MSU 100 x Pennorange
c) compound inflorescence types from crosses MSU 100 x Apsory and MSU 100 x MSU 200

Cuttings were made from the single flower selections and the F_3 seed was produced in the greenhouse. Fruits from compound inflorescence individuals were selected in the field and the F_3 seed was saved.

Summer 1970

The F_3 selections made in 1969 and their parents were grown together with the parents, F_1 and F_2 of the cross MSU 100 (single flower) x MSU 180 (simple inflorescence) in the summer of 1970. This cross was made in order to learn the relationship of the single flower to the simple inflorescence character. Prior to the 1969 season, Pennorange was considered to be a typical simple inflorescence; however, the observed data suggested that Pennorange inflorescence was not representative of the simple inflorescence.

Summer 1971

The crosses, Apsory (compound inflorescence) x MSU 180 (simple inflorescence) and Pennorange (1-4 flowers) x Michigan State Forcing (simple inflorescence) were grown in the summer of 1971. The former was grown to investigate the abberant segregation ratios observed for the compound inflorescence phenotypes noted from the crosses MSU 100 (single flower) x Apsory (compound inflorescence) and MSU 100 (single flower) x MSU 200 (compound inflorescence). The cross Pennorange (1-4 flowers) x Michigan State Forcing (simple inflorescence) was observed in order to more fully investigate the relationship of the jointless pedicel phenotype to flower production and inflorescence morphology.

DATA

Data were recorded on an individual plant basis for all observations. Information was recorded on number of flowers and type of inflorescence as it appeared on the first cluster. Classification as to type of inflorescence was not limited to the first inflorescence, i.e., other inflorescences were observed to substantiate the phenotype of the first inflorescence.

In order to test the validity of sampling only the first inflorescence, a random sample of 50 F_2 plants from the cross MSU 100 x MSU 200 having phenotypes other than single flower per truss, compound inflorescence or the greater than 34 flowers per inflorescence class, were observed for the 10 consecutive clusters per plant and evaluated for number of flowers and branched inflorescence.

The mean number of flowers on the first inflorescence was 12.65 ± .361 and did not differ significantly from the 12.96 ± .207 mean number of flowers observed on the 500 inflorescences observed on the 50 plants.

The frequency of branched inflorescence on the first inflorescence was observed to be .462 and the frequency observed on the 500 inflorescences from the 50 plant sample was .442. The values were compared by the Chi-square test and no significant deviation between frequencies was observed (P = .95-.90).

The above sampling test for the number of flowers per inflorescence per plant suggests that information obtained from the first inflorescence is a valid estimate of phenotype for the plant.

The number of flowers on the first inflorescence were recorded for all plants except those segregates examplifying the phenotype of the compound inflorescence parents (Figure 3a,b). Due to the large number of flowers and the ability to produce flowers indeterminately, the compound inflorescence types were recorded only as to inflorescence type.

The inflorescence types referred to in this study are described by several basic terms. The terminology is after

Parkin (20). The following is a list of the terms used and a description of the inflorescence type they represent:

1) unbranched monochasial inflorescence (unbranched inflorescence) (Figure 1b) - All flowers originate from the primary axis of the inflorescence.
2) compound monochasial inflorescence (branched inflorescence) (Figure 1c) - The cluster has at least one branch originating from the primary axis of the inflorescence.
3) simple inflorescence - The simple inflorescence is composed of unbranched and compound monochasial inflorescence types.
4) compound dichasial inflorescence (Figure 1a) - The inflorescence forks, similar to dichotomous branching, and each axis exhibits branching.
5) compound inflorescence - The inflorescence exhibits the compound dichasial structure with a high degree of branching. Compound dischasial types with a low degree of branching (1-4 branches on each axis) were classified in a high flower number class (greater than 30 flowers or greater than 35 flowers).
6) primary monochasium - This term is used in relation to estimating the number of flowers per unbranched monochasium.

The number of flowers on the branched inflorescence was previously reported to be related to the number of branches and the flower number class of the unbranched monochasium from which the branch originated (11). The unbranched structure from which the branch originates is referred to as the primary monochasium.

The number of flowers per primary monochasium is estimated from the number of flowers and branches on a compound monochasial inflorescence. Since each branch replaces one flower on the primary monochasium, the total number of flowers (F) plus the number of branches (B) divided by the number of branches plus 1 (1 represents the primary monochasial structure) gives the estimated number of flowers for each primary monochasium ($\frac{F+B}{B+1}$). The flower number of the primary monochasial inflorescence is used as an estimate of the unbranched monochasial flower number. This is used to investigate the relationship between inflorescence branching and the number of flowers on an unbranched inflorescence.

Compound inflorescences similar to those observed on Apsory and MSU 200 exhibit a non-terminal flowering habit. This character is evidenced by continual production of young flower primordia on the inflorescence. The provisional symbol, <u>ntf</u>, will be used to describe this character.

Data were recorded for leafy inflorescences with indeterminant growth. This character is referred to as intercalary inflorescence (Figure 4) and is provisionally noted as <u>ini</u>. This information was obtained from the cross Pennorange x Michigan State Forcing.

Figure 4. Phenotype of intercalary inflorescence.

Figure 4

Data were recorded for the segregation of the jointless pedicel character (j) in the crosses MSU 100 x Pennorange and Pennorange x Michigan State Forcing. Data were also taken for the dwarf (d) character observed to segregate in the cross MSU 100 x Apsory. Both the j and d genes were investigated in order to determine linkage relationships with inflorescence types.

Segregating populations where families could be partitioned were tested for fit to expected ratios by the Chi-square test. Individual segregating families were tested for homogeneity prior to pooling data for analysis.

Population means were compared by use of the "t" test. Where more than two means are compared, Duncan's Multiple Range test was used (24).

The scaling test outlined by Mather (14) and Mather and Jinks (15) was used in the analysis of the cross Pennorange x Michigan State Forcing in order to test the distributions to an additive-dominance model. Methods of estimating the number of gene pairs differentiating the parents as described by Mather and Jinks (15) were used as well as methods described by Powers, Lock and Garrett (22) and Powers (21).

RESULTS AND INTERPRETATION

Inheritance of Inflorescence Type

Single Flower per Truss x Low-flower-number Inflorescence

The distribution for the parents F_1, F_2 and backcross populations from the cross MSU 100 (single flower) x Pennorange (low-flower-number) show three inflorescence types (Table 1). The types correspond to the MSU 100 (single flower), Pennorange (low-flower-number) and F_1 (simple inflorescence) phenotypes. Differentiation of the inflorescence types was based on the single flower type showing 1 flower per inflorescence and the low flower number type showing 1-4 flowers per inflorescence. The simple inflorescence type is composed of unbranched and compound monochasial inflorescences.

The presence of three inflorescence types, no expression of parental dominance and the frequencies of .181 for the single flower type and .266 for the low-flower-number type in the F_2 population suggest a digenic inheritance and the possibility that the parental types are controlled by recessive genes. The segregation of two inflorescence types in the backcross populations suggest that the inheritance of the single flower and low-flower-number inflorescence types may not be complex. Segregation in both backcross populations

Table 1. Distribution for inflorescence types in the different generations from the cross MSU 100 (P_1) x Pennorange (P_2).

Generation	Number of Plants	Inflorescence Type: Single flower	Low-flower-number	Simple inflorescence
MSU 100 (P_1)	40	40		
Pennorange (P_2)	40	4	36	
(P_1xP_2)F_1	27		3	24
(P_2xP_1)F_1	76		4	72
F_1 pooled	103		7	96
(P_1xP_2)F_2	290	57	86	147
(P_2xP_1)F_2	284	47	67	170
F_2 pooled	574	104	153	317
(P_1xP_2)xP_1	80	37	5	38
(P_2xP_1)xP_1	129	57	5	67
F_1xP_1 pooled	209	94	10	105
(P_1xP_2)xP_2	121	10	59	52
(P_2xP_1)xP_2	130	11	62	57
F_1xP_2 pooled	251	21	121	109

indicates that each parental genotype is homozygous recessive for one of the two pairs of genes concerned, e.g., MSU 100 (aaBB) and Pennorange (AAbb).

The F_2 population was tested for a two gene model of inheritance (Table 2). Chi-square analysis gave a good fit to a 9:4:3 ratio (simple inflorescence type : low-flower-number type : single flower type). The gene for low flower number type was epistatic to the gene for single flower. Chi-square analysis of the backcross populations gave a good fit to a 1:1 ratio of 1 single flower to 1 simple inflorescence in the backcross to MSU 100 and 1 low-flower-number to 1 simple inflorescence in the backcross to Pennorange. This suggests the single flower and low flower number inflorescence types are each conditioned by one recessive gene.

The expected frequencies for the F_2 and backcross to Pennorange were calculated on the basis of overlap values of .100 low-flower-number type in single flower type and .068 simple inflorescence type in the low-flower-number type. The overlap values were derived from the distributions of the MSU 100, Pennorange and F_1 populations (Table 1).

The expected F_2 segregation was determined from the adjusted frequencies calculated with the overlap values and a theoretical segregation of .562 : .250 : .188 (simple inflorescence : low-flower-number type : single flower type). The calculations of the adjusted F_2 frequencies was accomplished as follows:

Table 2. Chi-square test for goodness of fit to a digenic inheritance for inflorescence type in the cross MSU 100 (P_1) x Pennorange (P_2).

Generation	Number of Plants	Inflorescence Type			(Ratio tested)	χ^2	P
		Single flower	Low-flower-number	Simple			
F_2	574	104	153	317	(9:4:3)	3.648	.20-.10
		exp.* 122.3	151.0	300.7			
BC to P_2	251		142	109	(1:1)	.999	.50-.30
		exp.*	134.1	116.9			
BC to P_1	209	94		115			
		exp. 104.5		104.5	(1:1)	2.110	.20-.10

*Expected values are calculated on the basis of the overlapping of simple and low-flower-number types and low-flower-number and single flower types.

single flower type = .188 + (.100 x .250) = .213

simple inflorescence type = .562 - (068 x .562) = .524

low flower number type = .250 + (.068 x .562) -
(.100 x .250) = .263

Low-flower-number inflorescence x Simple Inflorescence

The inheritance of inflorescence type in the cross Pennorange (low-flower-number type) x Michigan State Forcing (simple inflorescence) was investigated. Differentiation of parental inflorescence types could not be established from data on the number of flowers per inflorescence in the segregating generations (Table 3). Therefore, the data were analyzed quantitatively.

Expected F_2 and backcross generation means were calculated after the formulae described by Mather and Jinks (15): $\overline{F}_2 = \frac{1}{2}\overline{B}_1 + \frac{1}{2}\overline{B}_2$, $\overline{B}_1 = \frac{1}{2}\overline{P}_1 + \frac{1}{2}\overline{F}_1$ and $\overline{B}_2 = \frac{1}{2}\overline{P}_2 + \frac{1}{2}\overline{F}_1$ ($\overline{B}_1$ is the mean of the backcross to Pennorange and $\overline{B}_2$ is the mean of backcross to Michigan State Forcing). The calculated and observed mean flower number values were 4.41 and 4.35 ± .152 for the F_2, 3.65 and 3.37 ± .142 for the backcross to Pennorange and 4.90 and 5.44 ± .206 for the backcross to Michigan State Forcing. The predicted relationships between means and the assumption that the predicted means are based only on the additive and dominance effects of genes were tested by the scaling tests described by Mather (14) and Mather and Jinks (15).

Table 3. Frequency distribution for number of flowers on the inflorescence for different generations of tomato plants from reciprocal crosses of Pennorange (P_1) x Michigan State Forcing (P_2).

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	
Pennorange (P_1)	48	4	17	25	2												2.52 ± .103
M.S.F.(P_2)	45			6	9	15	10	3	2								5.02 ± .192
(P_1xP_2)F_1	52		2	7	11	18	12	1	1								4.73 ± .171
(P_2xP_1)F_1	71		3	9	15	21	17	5	1								4.83 ± .156
F_1 pooled	123		5	16	26	39	29	6	2								4.79 ± .116
(P_1xP_2)F_2	67	3	6	13	8	18	10	5	3		1						4.55 ± .228
(P_2xP_1)F_2	69	3	8	13	20	11	8	4	1	1							4.15 ± .202
F_2 pooled	136	6	14	26	28	29	18	9	4	1	1						4.35 ± .152
(P_1xP_2)xP_1	61	8	15	8	17	9	2	1	1								3.31 ± .205
(P_2xP_1)xP_1	59	3	18	14	6	12	5	1									3.42 ± .198
BC to P_1 pooled	120	11	33	22	23	21	7	2	1								3.37 ± .142
(P_1xP_2)xP_2	32		1	4	4	10	8	2	1	1						1	5.44 ± .406
(P_2xP_1)xP_2	66		4		12	24	15	7	1		1			2			5.44 ± .236
BC to P_2 pooled	98		5	4	16	34	23	9	2	1	1			2		1	5.44 ± .206

The scaling test is based on the following formulae:

$$\begin{array}{lcl} A = 2\bar{B}_1 - \bar{P}_1 - \bar{F}_1 & & V_A = 4V_{\bar{B}_1} + V_{\bar{P}_1} + V_{\bar{F}_1} \\ B = 2\bar{B}_2 - \bar{P}_2 - \bar{F}_1 & \text{and} & V_B = 4V_{\bar{B}_2} + V_{\bar{P}_2} + V_{\bar{F}_1} \\ C = 4\bar{F}_2 - 2\bar{F}_1 - \bar{P}_1 - \bar{P}_2 & & V_C = 16V_{\bar{F}_2} + 4V_{\bar{F}_1} + \\ & & \qquad V_{\bar{P}_1} + V_{\bar{P}_2} \end{array}$$

If the values of A, B and C do not deviate significantly from zero, then the additive-dominance model is suggested to be adequate.

The values $A = -.57 \pm .323$, $B = 1.07 \pm .471$ and $C = .23 \pm .612$ were calculated for cross Pennorange x Michigan State Forcing. They do not differ significantly from zero, suggesting that the additive-dominance model is adequate for analysis of variation.

The mean number of flowers per inflorescence 4.79 ± .116 (F_1) and 5.44 ± .206 backcross to Michigan State Forcing) did not differ from the Michigan State Forcing parental mean of 5.02 ± .192. This indicates that the Michigan State Forcing phenotype (simple inflorescence) was dominant to the Pennorange phenotype (low-flower-number).

The degree of dominance was investigated by analysis of variances according to Mather's formula (14):

$$V_{F_2} = \tfrac{1}{2}D + \tfrac{1}{4}H + E_1 \text{ and } V_{B_1} + V_{B_2} = \tfrac{1}{2}D + \tfrac{1}{2}H + 2E_1$$

where B_1 is backcross to Pennorange and B_2 is backcross to Michigan State Forcing. The non-heritable variation (E_1) was estimated as the mean variance of the Pennorange, Michigan State Forcing and F_1 populations.

The F_2 and backcross generation variances and non-heritable variance for these generations from the cross Pennorange x Michigan State Forcing are as follows:

$E_1 = 1.27$

$V_{B_1} = 2.42$

$V_{B_2} = 4.16$

$V_{F_2} = 3.16$.

The high value of V_{B_2} was due to the presence of compound monochesial inflorescences which exhibit flower numbers greater than 8 flowers per inflorescence.

By inserting these values into the above formulae, values of H (8.58) and D (-.506) were obtained. The negative value of D suggests zero variation due to additive effects and the 8.58 value of H suggests complete genotypic dominance.

The number of effective factors was estimated by the Mather and Jinks (15) formula $K_1 = \frac{\frac{1}{4}(\overline{P}_2 - \overline{P}_1)^2}{H}$; where $\overline{P}_2$ is the mean of Michigan State Forcing and $\overline{P}_1$ is the mean of Pennorange. A K_1 value of .18 was calculated ($\frac{\frac{1}{4}(5.02 - 2.52)^2}{8.58} = .18$) suggesting monogenic inheritance. The monogenic hypothesis is supported by the test described by Powers et al. (22) for gene pair estimation. The formulae $\frac{1}{4}\overline{P}_1 + \frac{3}{4}\overline{P}_2$ for 1-gene pair and $\frac{1}{16}\overline{P}_1 + \frac{15}{16}\overline{P}_2$ for 2-gene pair, with P_1 recessive (Pennorange) and P_2 as the dominant parent (Michigan State Forcing), were used to estimate the expected number of flowers per inflorescence in the F_2 population. Values of 4.40 for a 1-gene model and 4.86 for a

2-gene model were calculated. The observed F_2 mean of 4.35 ± .152 was similar to the 1-gene value, indicating monogenic inheritance.

The arithmetic mean of the two parents (3.77) suggests separation of the flower number distribution between the 3 and 4 flowers per inflorescence classes for Chi-square analysis, the 1-3 and 4-15 flower classes, corresponding to the low flower number type and simple inflorescence type respectively. They showed a good fit to a monogenic 3:1 ratio of simple inflorescence to low flower number in the F_2 and a 1:1 ratio in the backcross to Pennorange (Table 4).

Table 4. Chi-square test for goodness of fit to monogenic inheritance for inflorescence type in the cross Pennorange x Michigan State Forcing.

	Inflorescence Type			
	Low-flower-number	Simple	χ^2	P
F_2	obs. 46 exp.* 51.9 (3:1)	90	.522	.50-.30
Backcross to Pennorange	obs. 66 exp.* 75.6 (1:1)	54	3.292	.10-.05

*Expected values were calculated on the basis of the overlap of the simple and low-flower-number types.

Single Flower per Truss x Simple Inflorescence

The cross MSU 100 (single flower) x MSU 180 (simple inflorescence) was studied in order to determine the inheritance of the inflorescence type, single flower per truss. No reciprocal cross was made.

The F_2 population segregated for single flower and simple inflorescence types corresponding to the MSU 100 and MSU 180 population phenotypes respectively. The F_1 population exhibited simple inflorescence similar to that of the MSU 180 parent.

The data were tested for goodness of fit to a ratio of 3 simple inflorescence: 1 single flower (Table 5). The observed segregation did not show a significant deviation from the 3:1 ratio, suggesting single gene inheritance with the single flower per truss character being recessive.

Table 5. Chi-square test for goodness of fit to a monogenic inheritance for single flower per truss and simple inflorescence in the cross MSU 100 x MSU 180.

Generation	N	Single flower	Simple inflorescence	χ^2	P
MSU 100	37	37			
MSU 180	42		42		
F_1	62		62		
F_2	138	28	110		
		exp. (3:1) 34.5	103.5	1.633	.30-.20

Single Flower per Truss x Compound Inflorescence

The cross MSU 100 (single flower) x Apsory (compound inflorescence) was made to investigate the inheritance of single flower per truss, compound (s) and simple inflorescence types. The distribution of inflorescence types for the parents, F_1, F_2 and backcross populations are presented in Table 6. The F_2 segregation for inflorescence types suggests four classes--single flower per truss, compound, simple, and greater than 30 flowers.

The simple inflorescence class includes both unbranched and compound monochasial inflorescences (Figure 1b,c), which account for the wide variability in number of flowers on the inflorescences observed (3-30 flowers per inflorescence).

Compound inflorescences (s) exhibit the compound dichasial inflorescence structure (Figure Ia). Recombinants that exhibit the compound dichasium, intense branching and nonterminal flowering (ntf) is defined as the capability to continually produce new flowers on an inflorescence. This character is detected by the presence of new flowers and the production of new flower primordia on old inflorescences.

Recombinants with a large number of branches on a compound monochasium were observed. They were noted in the class that had greater than 30 flowers per inflorescence. These highly branched segregates exhibited as many as 80 flowers per inflorescence and are easily discerned from compound inflorescence types. Phenotypes with up to 80 flowers

Table 6. Distribution for inflorescence types in the different generations from the cross MSU 100 (P_1) x Apsory (P_2).

Generation	Number of plants	Inflorescence Type			
		Single flower	Simple inflorescence	Greater than 30 flowers	Compound inflorescence
MSU 100 (P_1)	40	40			
Apsory (P_2)	40				40
$(P_1xP_2)F_1$	16		16		
$(P_2xP_1)F_1$	17		17		
F_1 pooled	33		33		
$(P_1xP_2)F_2$	365	67	227	17	54
$(P_2xP_1)F_2$	115	23	67	4	21
F_2 pooled	480	90	294	21	75
$(P_1xP_2)xP_1$	37	14	23		
$(P_2xP_1)xP_1$	43	15	28		
F_1xP_1 pooled	80	29	51		
$(P_1xP_2)xP_2$	56		30	2	24
$(P_2xP_1)xP_2$	25		14	2	9
F_1xP_2 pooled	81		44	4	33

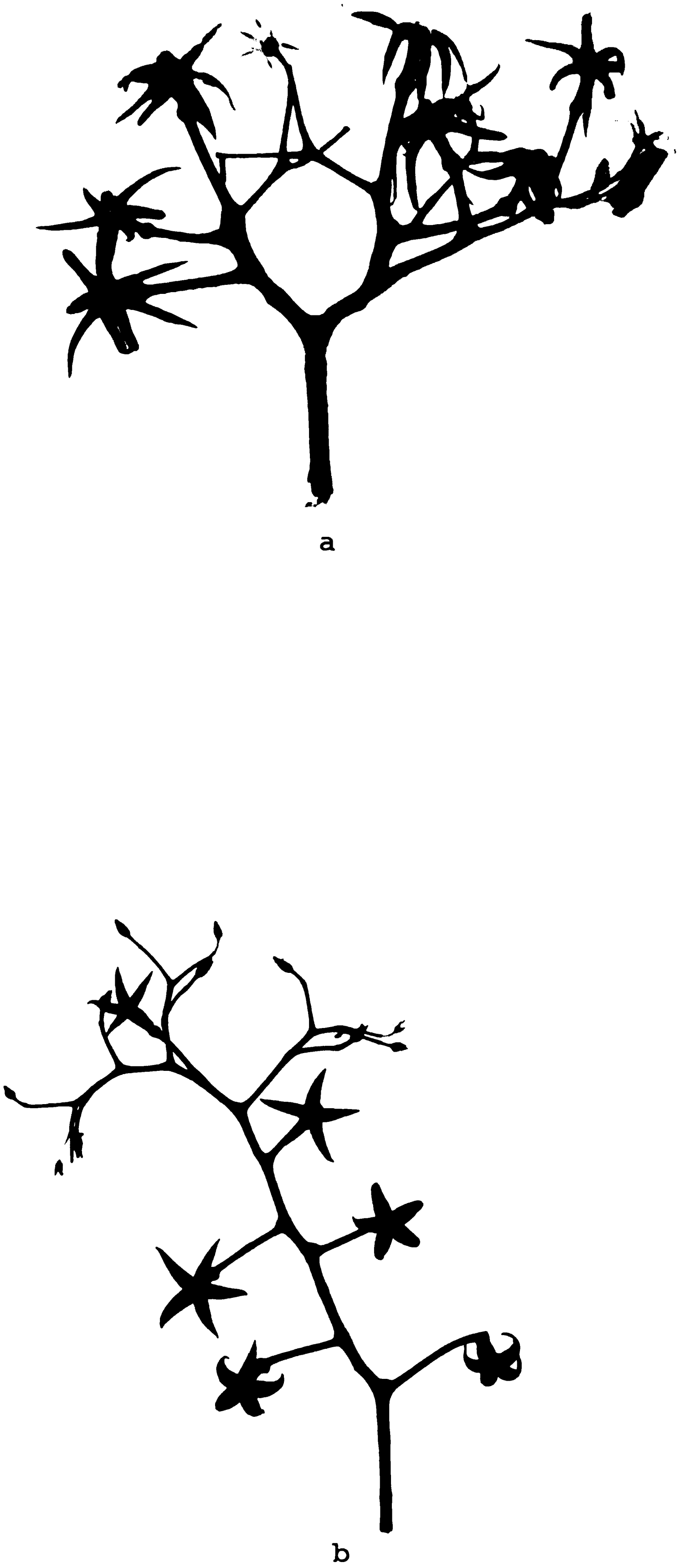
have been previously described as compound types (3,13). Individuals with this phenotype were observed in the F_2 and backcross to Apsory populations. The excessive branching may be due to factors affecting the degree of branching, intense branching (Figure 5a), and non-terminal flowering (Figure 5b).

The low frequency of segregates with single flower per truss .188 in the F_2 and .363 in the backcross to MSU 100 suggests that the inheritance of single flower was not simple. Two F_3 lines from eight F_2 selections with the single flower phenotype separated and each gave a good fit to a 15:1 ratio of single flower per truss to simple inflorescence (Table 7).

A low frequency (.156) of segregates with the compound inflorescence (s) phenotype was observed in the F_2 population. Three compound inflorescence F_2 lines were selected for observation in the F_3 generation. One line segregated and showed a good fit to a 3:1 ratio of compound inflorescence to single flower ($P = .70-.50$), suggesting that a recessive gene conditions the character single flower per truss. The single flower character appears to be epistatic to compound inflorescence (s). This epistatic activity may in part explain the deficiency of ss recombinants in the F_2 population.

Compound inflorescence was expected to segregate with a frequency of .25 in the F_2 population. Based on the epistatic relationship between the genes for single flower and compound

Figure 5. Phenotypes illustrating the characters a) intense branching and b) non-terminal flowering.



a

b

Figure 5

Table 7. Segregation in the F_3 generation from F_2 selections with the single flower per truss phenotype derived from the cross MSU 100 x Apsory.

Line	N		Single flower	Simple Inflorescence	χ^2	P
69-22	67		67			
69-23	71		71			
69-24	65		65			
69-25	89		89			
69-26	73		73			
69-27	69		69			
69-21	74		69	5		
		exp. (15:1)	69.4	4.6	.036	.90-.70
69-36	70		66	4		
		exp. (15:1)	65.6	4.4	.039	.90-.70

inflorescence, the expected frequency in the F_2 is .1875. The observed value of .156 representing 75 individuals in a population of 480 did not differ from the expected 90 individuals (P = .10-.05).

The expected frequency of compound types in the backcross to Apsory is .5. The observed frequency of .433 which represents 33 compound types in a population of 81 individuals did not deviate significantly from the expected (P = .10-.05).

Similar results to those observed in the cross MSU 100 x Apsory were obtained in the cross MSU 100 (single flower) x MSU 200 (compound inflorescence).

The distribution of inflorescence types for the parents F_1, F_2 and backcross populations are presented in Table 8. Four classes of inflorescence types were observed in the F_2 (single flower, simple, compound and greater than 34 flowers). The backcross to MSU 100 segregated for simple inflorescence and single flower and the backcross to MSU 200 segregated for greater than 34 flowers, simple and compound inflorescence types. The simple inflorescence types include both unbranched and compound monochasial inflorescences.

Table 8. Distribution for inflorescence types in the different generations from the cross MSU 100 (P_2) x MSU 200 (P_1).

		Inflorescence Type			
Generation	Number of plants	Single flower	Simple inflor- escence	Greater than 34 flowers	Compound inflor- escence
MSU 200 (P_1)	40				40
MSU 100 (P_2)	40	40			
F_1	34		34		
F_2	499	87	326	16	70
BC to P_1	84		44	6	34
BC to P_2	38	13	25		

The segregation for four inflorescence classes in the (MSU 100 x MSU 200) F_2 (Table 8) and (MSU 100 x Apsory) F_2 (Table 6) were tested for association by Chi-square analysis and no difference in segregation was suggested (P = .70-.50). Similarity in segregation of the backcross to the single flower parent (P = .90-.80) and the backcross to the compound inflorescence parent (P = .70-.50) were also observed. Frequencies for single flower per truss and compound inflorescence types are presented in Table 9.

Table 9. Comparison of observed single flower per truss and compound inflorescence frequencies in the F_2 and backcross populations for the crosses MSU 100 x Apsory and MSU 100 x MSU 200.

	Single flower	Compound inflorescence
(MSU 100 x Apsory) F_2	.188	.156
(MSU 100 x MSU 200) F_2	.174	.140
(MSU 100 x Apsory) x MSU 100	.363	
(MSU 100 x MSU 200) x MSU 100	.352	
(MSU 100 x Apsory) x Apsory		.433
(MSU 100 x MSU 200) x MSU 200		.405

The frequencies of single flower type .174 in the F_2 and .352 in the backcross to MSU 100 suggest again (as in the MSU 100 x Apsory cross), that the inheritance for single flower is not simple. While F_3 lines from single flower (MSU 100 x Apsory) F_2 selections segregated for simple inflorescence, none of the 7 F_3 lines from single flower (MSU 100 x MSU 200) F_2 selections segregated.

The frequency of compound inflorescence recombinants, .140 in the (MSU 100 x MSU 200) F_2 population, was lower than expected for a single recessive gene (s) inheritance. F_3 lines from compound inflorescence F_2 selections exhibited segregation for single flower types in 1 of 4 lines grown (Table 10). Line 69-37 gave a good fit to a 3:1 ratio of compound inflorescence to single flower. The single flower gene is suggested to be epistatic to the gene for compound inflorescence.

Table 10. Segregation of F_3 populations from F_2 selections of compound inflorescence individuals derived from the cross MSU 100 x MSU 200.

			Inflorescence Type			
Line	N		Compound	Single Flower	χ^2	P
69-38	68		68			
69-39	75		75			
69-40	73		73			
69-37	66		54	12		
		exp. (3:1)	49.5	16.5	1.636	.30-.20

The segregation of compound inflorescence (s) progeny observed in the (MSU 100 x MSU 200) F_2 population was tested to an expected segregation frequency of .1875. The expected value is based on epistasis between single flower per truss and compound inflorescence. The observed frequency .140

representing 70 compound types in 499 F_2 individuals was tested to the expected frequency of .1875 representing 93.5 compound types in 499 F_2 individuals. The observed compound inflorescence frequency showed a poor fit to the expected frequency (P = less than .01), suggesting the two gene, epistatic hypothesis to be inadequate.

Compound inflorescence types are expected to occur with a frequency of .5 in the backcross to MSU 200. The observed frequency of .405 which represents 34 compound types in a population of 84 individuals does not differ from the expected .5 or 42 compound types in a population of 84 (P = .10-.05).

Inheritance of single flower per truss. A hypothetical model for the inheritance of the character single flower per truss is based on the following observations:

1) Low frequencies of single flower types were observed in (MSU 100 x MSU 200) F_2 (.174), (MSU 100 x Apsory) F_2 (.188), (MSU 100 x MSU 200) x MSU 100 (.352) and (MSU 100 x Apsory) x MSU 100 (.363) (Table 9).
2) F_3 generations from compound inflorescence (MSU 100 x MSU 200) F_2 and (MSU 100 x Apsory) F_2 selections segregated 3:1 (compound *vs*. single flower), suggesting a recessive gene controlling the character single flower and that gene to be epistatic to the gene for compound inflorescence.

3) Segregation for simple inflorescence types in the F_3 generations of single flower types from (MSU 100 x Apsory) F_2 selections.

The frequency of single flower per truss segregates observed in the backcross (MSU 100 x Apsory) x MSU 100 gave a poor fit (P = .05-.01) to a 1:1 segregation; while the backcross (MSU 100 x MSU 200) x MSU 100 showed no significant deviation from an expected 1:1 ratio (P = .10-.05).

Since results from the previous crosses, MSU 100 x Pennorange and MSU 100 x MSU 180, suggested the character single flower per truss was controlled by a single recessive gene, the low frequency of single flower types in single flower x compound inflorescence crosses probably is a result of factors transmitted by the compound inflorescence parents. The repressive effect on single flower expression in the backcross to MSU 100 suggests the factor or factors to be dominant.

The 3:1 segregation of compound vs. single flower for the F_3 lines from the F_2 compound inflorescence selections suggests no inhibitor of single flower expression. Yet, the 15:1 segregation for single vs. simple inflorescence in F_3 lines from single flower (MSU 100 x Apsory) F_2 selections suggest segregation of inhibition factors.

A model is proposed to explain the observed single flower segregations (Table 11) for the single flower x compound inflorescence crosses. The model is based on three major genes--a for single flower per truss, I - inhibitor of

Table 11. Proposed model for single flower per truss (*a*) inheritance as affected by *I*, single flower inhibitor and *R*, restorer of single flower expression.

MSU 100	x	Apsory or MSU 200
aa ii rr		*AA II RR*

F_1 *Aa Ii Rr*

BC to MSU 100	Female gametes and frequency			
	a i r	*a i R*	*a I r*	*a I R*....
male gamete	.125	.125	.125	.125 ....
a i r	single	single		single

F_2		Female gametes and frequency			
		a i r	*a i R*	*a I r*	*a I R*....
male gametes and frequency		.125	.125	.125	.125 ....
a i r	.125	single	single		single
a i R	.125	single	single	single	single
a I r	.125		single		single
a I R	.125	single	single	single	single
.	.				
.	.				
.	.				
.	.				

single flower expression and R - restorer of single flower expression.

I inhibits the expression of aa in the absence of R. In the presence of R, the single flower character segregates as a single gene. The genotype of MSU 100 is a i r and the genotype of compound inflorescence lines is A I R.

The calculated frequencies of single flower types, based on the model (Table 11), in the backcross and F_2 populations are .375 and .203 respectively. These values were used to calculate expected segregations for single flower in segregating generations from the crosses MSU 100 x MSU 200 and MSU 100 x Apsory. No significant deviations were observed in the (MSU 100 x MSU 200) F_2 (P = .20-.10), (MSU 100 x MSU 200) x MSU 100 (P = .80-.70), (MSU 100 x Apsory) F_2 (P = .50-.30) and (MSU 100 x Apsory) x MSU 100 (P = .90-.80) suggesting a good fit to the proposed model.

From this model, the following would be expected in the F_3 generations of single flower lines selected from F_2 populations of either MSU 100 x MSU 200 or MSU 100 x Apsory crosses: 4 with 13:3 ratios; 2 with 3:1 ratios and 10 with no segregation; however, the 2 (MSU 100 x Apsory) F_3 lines that showed segregation, each segregated with a 15:1 ratio of single flower to simple inflorescence. This suggests that other factors may be involved in the expression of the single flower character.

Inheritance of compound inflorescence. The inheritance of the compound inflorescence (s) as noted in the crosses MSU 100 x MSU 200 and MSU 100 x Apsory was quite similar to that previously reported (12). The apparent epistasis between the single flower gene and compound inflorescence gene may account for the observed deficiency of compound inflorescence types in these F_2 populations. The epistasis however, did not compensate for the deficiency of the ss types in the (MSU 100 x MSU 200) F_2 population. The (MSU 100 x Apsory) F_2, backcross to Apsory and backcross to MSU 200 did not deviate significantly from expected segregation at the 5% level; however, all these populations showed P values of .10-.05. The low P values were due to low number of compound inflorescence types.

Previous investigations concerning the compound inflorescence reported on deviations in expected segregation (4), variation in degree of compounding (4), and descriptions of the phenotype ranging from 80 flowers (3,13) to 200-300 flowers (11,26) per compound inflorescence. Based on these observations, the low frequency of compound inflorescence segregates may be the result of a more complex inheritance. The presence of recombinants with high flower number and moderate branching or non-terminal flowering may be considered a form of compound inflorescence. The low frequency of recombinants in the greater than 30 flower class (greater than 34 in the MSU 100 x MSU 200 cross) (hereafter to be referred to as 30 flower class) and the deficiency of compound inflorescence types suggest that this class may be associated with compound inflorescence.

The possible association of the compound and 30 flower class was investigated by observing the dwarf gene (d) known to be linked to the s locus (3). The dwarf character was transmitted by the Apsory parent. The segregation for dwarf (d), single flower, compound and simple inflorescence and the 30 flower class are presented in Table 12.

Assuming that the 30 flower class is associated with compound inflorescence, the frequency of dwarf types within the compound inflorescence class and the 30 flower class should indicate linkage. There were 48% dwarf, compound inflorescence types, 47.6% dwarf, 30 flower types and 12.3% dwarf simple inflorescence recombinants (Table 12).

Table 12. Segregation of the F_2 population of MSU 100 x Apsory for 4 phenotypic classes of inflorescence types, and dwarf plant habit (d).

	Number of plants	Single flower	Simple inflorescence	Greater than 30 flowers	Compound inflorescence
Total obs	480	90	294	21	75
Dwarf obs	102	20	36	10	36
Percent dwarf		22.2	12.3	47.6	48.0

The 22.2% dwarf types in the single flower class exceeded the frequency observed for simple inflorescence types. The increased frequency does not suggest linkage of single flower to dwarf but probably is a result of the epistatic relationship of single flower and compound inflorescence. The high frequency of combinations of dwarf with compound and dwarf with 30 flower types which was observed in the (MSU 100 x Apsory) F_2 suggest that dwarf is probably linked to both compound inflorescence and the 30 flower class.

The compound inflorescence phenotypes of the Apsory and MSU 200 parents exhibit very intense branching and non-terminal flowering. The 30 flower class plants shows many branches per inflorescence but few exhibit non-terminal flowering. Based on these observations, the intense branching and non-terminal flowering (<u>ntf</u>) are suggested to be linked and compose the compound inflorescence phenotype exhibited by the parents. The intense branching phenotype exhibits high flower number and the compound dichasial structure suggesting that the intense branching gene may be the <u>s</u> gene.

Recombination values between genes for intense branching and non-terminal flowering were estimated from the backcrosses (MSU 100 x MSU 200) MSU 200 and (MSU 100 x Apsory) Apsory. Recombination values 10.89% for (MSU 100 x MSU 200) MSU 200 and 6.17% for (MSU 100 x Apsory) Apsory were calculated according to the methods outlined by Immer (9) (Table 13).

Table 13. Recombination values for intense branching and non-terminal flowering (*ntf*) as components of compound inflorescence from backcross populations of MSU 100 x Apsory and MSU 100 x MSU 200.

Pedigree	Intense branching *ntf*	Intense branching +	+ *ntf*	++	Percent ± S.E.
(MSU 100 x Apsory) x Apsory	35	4	1	41	6.17 ± .020
(MSU 100 x MSU 200) x MSU 200	34	3	6	39	10.89 ± .019

The recombination values were used to estimate the expected segregation frequency of compound inflorescence types in the F_2 and backcross populations of MSU 100 x Apsory and MSU 100 x MSU 200 (Table 14). All calculated values were similar to the observed values.

Table 14. Comparison of observed compound inflorescence frequencies and expected frequencies based on epistatis of single flower character and linkage between intense branching and non-terminal flowering for the crosses MSU 100 x Apsory and MSU 100 x MSU 200.

	Backcross to Compound Parent		F_2	
Cross	obs.	exp.	obs.	exp.
MSU 100 x Apsory	.433	.469	.156	.165
MSU 100 x MSU 200	.405	.455	.140	.149

Compound Inflorescence x Simple Inflorescence

The cross Apsory (compound inflorescence) x MSU 180 (single inflorescence) was made in order to support the proposed mode of inheritance of the compound inflorescence character (s) noted in the MSU 100 x Apsory and MSU 100 x MSU 200 crosses. The F_2 distribution showed segregation for simple and compound inflorescence. Segregates showing high flower number and many branches or the non-terminal flowering habit were also observed.

The F_2 segregation 74 simple : 14 compound inflorescences gave a poor fit ($P = .05-.02$) to an expected 3:1 ratio, and suggested that more than one factor of linkage affected the inheritance of the compound inflorescence. Recombinants with many branches and non-terminal flowering were observed. The intense branching and ntf loci were suggested to be linked and comprise the compound inflorescence phenotype. This linkage is similar to that proposed in the MSU 100 x Apsory and MSU 100 x MSU 200 crosses.

A recombination value for intense branching and ntf of 5.97 ± .017 was calculated from the F_2 data. This value is similar to that observed in the single flower x compound inflorescence crosses (Table 13). The chi-square analysis suggests the observed compound inflorescence segregation shows a good fit ($P = .20-.10$) to the expected segregation based on linkage.

Inheritance of Flower Number on the Unbranched Monochasial Inflorescence

Single Flower per Truss x Low-flower number Inflorescence

In the cross MSU 100 (single flower) x Pennorange (low-flower-number), the simple inflorescence types showed segregation for number of flowers per inflorescence. The segregation was observed in the distribution for number of flowers on the unbranched inflorescence (Table 15). A high proportion of individuals in the 8-9 flower range were noted

Table 15. Distribution of number of flowers on the unbranched monochasial inflorescence in different generations from the cross MSU 100 (P_1) x Pennorange (P_2).

Generation	Total unbranched types	Number of flowers									Mean ± S.E.
		3	4	5	6	7	8	9	10	11	
F_1	94	2	5	27	26	20	9	5			6.10 ± .137
F_2	288	7	13	82	68	61	33	20	1	1	6.19 ± .085
BC to P_1	103	6	4	5	14	19	25	25	5		7.29 ± .177
BC to P_2	105	2	4	58	29	7	2	1	1	1	5.06 ± .234

in the backcross to MSU 100 while a high number of individuals were present in the 5-6 flower range in the backcross to Pennorange.

The mean number of flowers for the F_1 and F_2 populations were 6.10 ± .127 and 6.19 ± .085, respectively. The mean flower number of the backcross to MSU 100 was 7.29 = .177 and the backcross to Pennorange was 5.06 ± .234. The observed F_1 mean (6.10) and F_2 mean (6.19) did not differ.

Using the formula described by Mather (14), $\overline{F}_2 = \frac{1}{2}\overline{B}_1 + \frac{1}{2}\overline{B}_2$, where $\overline{B}_1$ is the mean of the backcross to MSU 100 and $\overline{B}_2$ is the mean of the backcross to Pennorange, the expected F_2 population mean of 6.17 flowers per unbranches inflorescence was calculated. The formula can be written as $0 = \frac{1}{2}\overline{B}_1 + \frac{1}{2}\overline{B}_2 - \overline{F}_2$ and the deviation from 0 can be tested: $t = \frac{\text{deviation}}{s_{\overline{\text{dev}}}}$ where $s_{\overline{\text{dev}}} = \sqrt{\frac{1}{4}V_{\overline{B}_1} + \frac{1}{4}V_{\overline{B}_2} + V_{\overline{F}_2}}$. No significant difference between the observed and calculated F_2 means was observed. The similarity of the F_1 and F_2 means and the F_2 mean being the midpoint between the two backcross means suggest no dominance effect in the inheritance of flower number classes within the unbranched monochasial inflorescence phenotype.

A single gene model is proposed and the gene is symbolized as c. The genotype of Pennorange is cc and MSU 100 is CC. The flower number expressed by the cc and CC genotypes were estimated by assuming the F_1 mean to be the midpoint in a no dominance situation. The flower number values were calculated as follows:

cc = 5.06 - (6.10 - 5.06) = 4.02 flowers

CC = 7.29 + (7.29 - 6.10) = 8.48 flowers

The phenotype *cc* is expressed as 4-flower class, *CC* as 8-flower class, and *Cc* as 6-flower class.

Assuming that the backcross populations are composed of ½ 6-flower class (*Cc*) plus ½ parental type (*CC* or *cc*), the model was tested by comparing the skewed portion of the backcross population to the corresponding classes in the F_1. The skewed portions, 3, 4 and 5 flowers in the backcross to MSU 100 and 7, 8, 9 and 10 flowers in the backcross to Pennorange (Table 15), were assumed to arise from the effect of the *Cc* genotype. The expected value for the backcross to MSU 100 was calculated as follows:

$$\begin{array}{l} \text{frequency of } F_1 \\ \text{population with} \\ \text{3, 4 and 5 flowers} \end{array} \times \frac{\begin{array}{l} \text{total 6-flower class} \\ \text{(unbranched) in the} \\ \text{BC to MSU 100} \end{array}}{2} = \begin{array}{l} \text{expected individ-} \\ \text{uals with 3, 4 and} \\ \text{5 flowers in the} \\ \text{BC to MSU 100} \end{array}$$

$$34/94 \times 103/2 = 18.6$$

The same formula was used to calculate the expected number of individuals in the 7, 8, 9 and 10 flower class in the backcross to Pennorange. The total number of unbranched inflorescences was estimated on the basis of the overlap of the Pennorange and F_1 populations. The observed values show no deviation from the expected (Table 16) indicating a good fit to the no dominance hypothesis for inheritance of flower number on the simple inflorescence.

Table 16. Chi-square test for goodness of fit to a no-dominance model controlling the number of flowers on unbranched monochasial inflorescences for backcross populations from the cross MSU 100 (P_1) x Pennorange (P_2).

Generation	Number of Unbranched Inflorescences	Partial 'F_1 Types'	Parental + 'F_1 Types'	χ^2	P
BC to P_1	103	15	88	.849	.50-.30
		exp. 18.6	84.4		
BC to P_2	105	12	93	3.072	
		exp. 18.9	86.1		.10-.05

Single Flower per Truss x Compound Inflorescence

Simple inflorescence types in the F_1, F_2 and backcross populations of the cross MSU 100 (single flower) x MSU 200 (compound inflorescence) showed variability with regard to the number of flowers on the unbranched inflorescence (Table 17). Mean flower number values for the F_1 and backcross to MSU 200 were 10.65 ± .41 and 10.43 ± .47, respectively. Means of 8.27 ± .66 for the backcross to MSU 100 and 8.65 ± .21 for the F_2 were observed. The similarity of the F_1 and backcross to MSU 200 means suggest that the high flower number individuals (8-16 flowers) make up the dominant class. The high flower number class is referred to as the 10-flower class.

The F_2 distribution for number of flower on the unbranched monochasium does not indicate any distinction between the 10-flower class and the low flower class (3-7 flowers). The low flower number class is described as the 7-flower class.

The unbranched populations were analyzed using a formula similar to that proposed by Powers (21) and illustrated by Leonard, Mann and Powers (10). The formula $\frac{F_2}{P}$ x 100 was used to estimate the number of genes involved. The frequency in the F_2 for a given class is divided by the parental frequency for the same class, the result multiplied x 100 for conversion to percent to give an estimate of the proportion of parent types in the F_2 population.

Table 17. Distribution for flower number on unbranched monochasial inflorescence in segregating populations from the cross MSU 100 (P_2) x MSU 200 (P_1).

Generation	Total Un-branched Types	Number of Flowers														Mean ± S.E.
		3	4	5	6	7	8	9	10	11	12	13	14	15	16	
F_1	14							3	5	3	1	1	1			10.65 ± .41
F_2	142	2	7	5	8	26	21	23	17	14	12	5	1			8.65 ± .21
BC to P_1	21						5	4	2	4	3	1	1		1	10.43 ± .47
BC to P_2	15	1		1	1	2	4	1	2	1	2				1	8.27 ± .66

Since MSU 100 and MSU 200 are assumed to be of the recessive phenotypes single flower and compound inflorescence respectively, the F_1 and F_2 unbranched inflorescence populations were tested by the formula $F_2/F_1 \times 100$ (Table 18). This formula gives an estimate of the frequency (in percent) of F_1 phenotypes (dominant class) in the F_2 population.

Table 18. Calculated percentage values of F_1 (dominant) phenotype expressed for each flower number class and the cumulative mean for the cross MSU 100 x MSU 200.

Flower Number Class	Frequency F_2	Frequency F_1	Calculated Percentage for Each Class ($F_2/F_1 \times 100$)	Cumulative Mean
12-16	.134	.214	62.6	
11	.099	.214	46.3	54.5
10	.119	.357	33.3	47.1
9	.162	.214	75.7	54.2

The comparisons of individual classes show some variability (33.3%-75.7%) which may be due to sampling size of the F_1 and F_2 populations. The cumulative mean for the 4 individual comparisons was 54.2%, suggesting that the F_2 population is composed of 54.2% F_1 types. This frequency (54.2%) of dominant flower number class 10-flower class suggests digenic inheritance for unbranched inflorescence flower number class with the dominant class comprising 9/16 (56.2%) of the total population. The mean of 4 individual values (54.2%) did not differ from the expected 56.2% for a digenic model (P = .90-.70).

The digenic inheritance assumes that unbranches inflorescence classes are independent of the parental phenotypes and that branching can occur with equal frequency in the 10-flower class and 7-flower class. The latter assumption can be noted by observing the segregation of compound monochasial inflorescences with one and two branches (Table 19).

The relationship between number of flowers per unbranched inflorescence and the number of flowers on one-branches compound monochasia has been previously reported (11). Specific flower number classes of unbranched inflorescences give a predictable number of flowers when the inflorescence branches.

The low frequency of one-branched inflorescences in the 12-flower class of the (MSU 100 x MSU 200) F_2 population and the 13 flower class being the low flower number limit of the F_1 and backcross to MSU 200 distributions (Table 19) (dominant class) suggest the 12-flower class to be the point of separation between the two classes. Using this as the point of separation, a segregation ratio of 22 (8-12 flowers--low flower class) : 36 (13-23 flowers--dominant class) is noted. The observed segregation was not significantly different from an expected 7:9 ratio (Table 20), suggesting the higher flower class to be dominant.

Table 19. Frequency distributions of individuals segregating for number of flowers per inflorescence in populations of one-branched and two-branched compound monochasial inflorescences from MSU 100 (P_2) x MSU 200 (P_1).

Generation	No. of Plants	Number of flowers											
		8&9	10	11	12	13	14	15	16	17&18	19&20	21&22	23
One-branch													
F_1	17					3	1	4	4	2	2	1	
F_2	58	4	8	6	4	6	10	6	4	2	3	4	1
BC to P_1	13					1	2	3	1	2	2	2	
BC to P_2	5	1			1		1			2			

Generation	No. of Plants	Number of flowers								
		13	14	15	16	17	18&19	20&21	22&23	>23
Two-branches										
F_1+BC to P_1	8					1	1	1	3	2
F_2	27	2	2	4	2		4	4	3	6

Table 20. Chi-square test for goodness of fit to a digenic model for number of flowers on the inflorescence in 1 branch and 2 branched populations from the cross MSU 100 x MSU 200.

Distribution	Number of Plants	Low Flower Class	Dominant Class	χ^2	P
1 branch	58	22	36		
		exp. (9:7) 25.4	32.6	.808	.50-.30
2 branches	27	10	17		
		exp. (9:7) 11.8	15.2	.465	.50-.30

The absence of segregates in the 17-flower class in the two-branched compound monochasial inflorescence of the (MSU 100 x MSU 200) F_2 distribution and the 17-flower class being the lowest observed individual in the F_1 and backcross to MSU 200 distribution, suggests 17 flowers to be the separation point between the two flower number classes.

A ratio of 10 (13-16 flowers) : 17 (18 and greater flowers per inflorescence) was observed. The 18 and greater number of flowers correspond to the distributions of the F_1 and backcross to MSU 200 and is considered the dominant class. Sixty-two and nine-tenths percent of the two-branched inflorescences are of the dominant type. The observed segregation gives a good fit to the digenic 7:9 ratio of 13-16 flowers to the dominant class (Table 20).

The segregation for flower number on both one-branched and two-branched compound monochasial inflorescences show agreement to the digenic inheritance as suggested in the analysis of flower number on the unbranched monochasial inflorescences.

Other crosses. No segregation for number of flowers on the unbranched monochasial inflorescence was noted in the crosses Pennorange x Michigan State Forcing and MSU 100 x Apsory.

Inheritance of Compound Monochasial Inflorescence

Single Flower per Truss x Low-flower-number Inflorescence

The frequency of compound monochasial inflorescences observed in the F_1, F_2 and backcrosses for the cross MSU 100 (single flower) x Pennorange (low-flower-number) are presented in Table 21. The frequency of branching in the F_1 (8.7%) is approximately 2 times that observed in the backcross to Pennorange (3.6%). Assuming that the backcross to Pennorange is composed of $\frac{1}{2}$ F_1 frequency + $\frac{1}{2}$ P_2 frequency, where P_2 is Pennorange, the 3.6% of the branched inflorescences in the backcross to Pennorange are probably due to a factor or factors transmitted by the F_1. The degree of branching contributed by the Pennorange parent is suggested to be small. The compound monochasial inflorescence frequencies of the F_2 (11.9%) and the backcross to MSU 100 (10.4%) are greater than that observed in the FL, suggesting a factor or factors for increasing branching frequency may have been transmitted by the MSU 100 parent.

Table 21. Distribution of mean flower number per primary monochasium, and frequency (percent) of compound monochasia in populations from the cross MSU 100 (P_1) x Pennorange (P_2).

Generations	Number of Branched and Unbranched Inflorescences	Percent Branched	Flowers per Primary Monochasium 3-5	6	7-10	Mean ± S.E.*
BC to P_1	115	10.4	3	3	6	6.33 ± 3.69 a
F_2	327	11.9	18	9	12	5.97 ± .318 ac
F_1	103	8.7	8	1		4.77 ± .075 b
BC to P_2	109	3.6	3		1	4.75 ± .755 bc

*Different letters indicate significant deviation at the 5% level.

Assuming the relationship reported by Lewis (11) between the number of flowers per unbranched monochasium and the frequency of branched inflorescence, the gene regulating flower number class (*c*) and the frequency of branched inflorescence may be considered to be the same. The *cc* genotype would have little effect on branching, the *Cc* genotype would produce branched inflorescences at a frequency of 8.7% and the *CC* genotype would have an increased branching frequency which was estimated from the F_2 and backcross to MSU 100 to be 30.4% and 12.2% respectively. The estimates were based on monogenic segregation frequencies as follows: backcross to MSU 100 $= \frac{1}{2}\ \underline{Cc} + \frac{1}{2}\ \underline{CC} = .104$, $\underline{CC} = \frac{.104 - (.5 \text{ x } .087)}{.5} = .122$ $F_2 = \frac{1}{4}\ \underline{cc} + \frac{1}{2}\ \underline{Cc} + \frac{1}{4}\ \underline{CC} = .119$, $\underline{CC} = \frac{.119-(.25\text{x}.00)-(.5\text{x}.087)}{.25} = .304$. The difference between estimated effect of *CC* may be due to population size of branched types.

Primary monochasial flower number values were used to estimate the unbranched flower number class from which branching occurred. The distribution of primary monochasial flower number (Table 21) exhibited three classes--3-5 flowers, 6 flowers and 7-10 flowers.

The mean number of flowers per primary monochasium for the F_1 (4.77 flowers) and the backcross to Pennorange (4.75 flowers) do not differ significantly and suggest branching ~~to~~ occur predominantly of 3-5 flower individuals. The mean number of flowers for the F_2 (5.97 flowers) and the backcross to MSU 100 (6.33 flowers) differed significantly from the F_1 mean. The higher mean values indicate that the F_2 and backcross to MSU 100 tend to exhibit branching on higher flower number types.

If the F_1 genotype (Cc) onIy effects the 3-5 and 6 flower classes and the CC genotype effects only the 6 and 7-10 flower classes, then the effect of CC on branched inflorescence frequency can be estimated relative to the Cc (F_1) branching frequency. The $\overline{6}$-flower class segregates are partitioned into either the 3-5 or 7-10 flower classes on the basis of the F_1 segregation.

The two 6 flower types observed in the backcross to MSU 100 were partitioned with one individual to each class. An adjusted ratio of 4 (3-5 flowers, Cc) : 8 (7-10 flowers, CC) was obtained. With a monogenic segregation of 1 Cc : 1 CC, the CC effect was 2 times ($\frac{8CC}{4Cc} = 2$) the effect of the F_1 on branching. An adjusted F_2 segregation of 20 (3-5 flowers, Cc) : 19 (7-10 flowers, CC), was obtained. With a monogenic segregation of 1 cc : 2 Cc ; 1 CC and cc giving no effect on branching, the effect of CC was estimated as 1.9 times ($\frac{19\ CC}{20\ Cc/2} = 1.9$) the effect of the F_1. Two times effect of the F_1 gives an estimated CC effect on branching of .174, (2 x .087), which approximates the mean of the values estimated above from the F_2 (.304) and backcross to MSU 100 (.122).

The F_1 phenotype showed unbranched inflorescences with a range of 3 to 11 flowers. Compound monochasial inflorescence was suggested to arise from unbranched inflorescences with 3-6 flowers. The absence of branching on individuals with a higher number of flowers (7-10) suggest that the production of branched inflorescences is not based on the number of flowers but may be related to the specific genotype.

Single Flower per Truss x Compound Inflorescence

The frequency distribution of the number of branches on each of the compound monochasial inflorescences for the cross MSU 100 (single flower) x MSU 200 (compound inflorescence) is shown in Table 22. Individuals with greater than 4 branches per inflorescence were associated with either the compound dichasial structure or non-terminal flowering and a high number of flowers.

Table 22. Frequency distribution of number of branches per compound monochasial inflorescence and the frequency of compound monochasia in the simple inflorescence segregates for different generations from the cross MSU 100 (P_2) x MSU 200 (P_1).

Generation	Number of Simple Inflorescence Types	1	2	3	4	>4	Total Frequency
F_1	34	17	2	1			.588
F_2	264	58	27	10	4	23	.462
BC to P_1	50	13	6	3	2	5	.580
BC to P_2	25	5	2	2			.360

The frequency of branched inflorescences for the F_1 population was observed to be .588. The similarity in the frequency of inflorescence branching in the F_1 and backcross to MSU 200 populations suggest that the high frequency was due to a dominant gene.

Based on a dominant gene expression giving .588 frequency of compound monochasial inflorescences, the frequency of branched inflorescences attributable to the MSU 100 parent is estimated from the backcross to MSU 100. Assuming the backcross to MSU 100 is composed of the frequencies transmitted by MSU 100 and the F_1 populations with a proportion $\frac{1}{2}$ MSU 100 + $\frac{1}{2}$ F_1. The estimated frequency of compound monochasial types produced by MSU 100 is .132 ($P_2 = \frac{.360-(.5x.588)}{.5}$). This value is in close agreement with the frequency of branching attributed to the MSU 100 that was estimated from the backcross (MSU 100 x Pennorange) x MSU 100 (.122).

Using the dominant expression as 58.8% branched inflorescences and the recessive as 13.2% branched inflorescences, the expected F_2 segregation of branched inflorescences was calculated. The segregation in the F_2 population was tested for goodness of fit to an expected monogenic segregation and a good fit was obtained (P = .90-.80).

The relationship between compound monochasial inflorescences and the flower number class of unbranched monochasium was investigated. In the F_2 and backcross to MSU 100, segregation for number of flowers per unbranched monochasium was noted (Table 17). Two flower number classes were hypothesized--a 7-flower class and 10-flower class (F_1 type). They segregated with a ratio of 9:7, 10-flower class to 7-flower class.

According to Lewis (11), the high flower number class (10 flowers) should exhibit a greater frequency of branched inflorescences than the 7-flower class.

The distributions of one-branch and two-branched compound monochasial inflorescence types (Table 19) were previously partitioned into two classes. The 8-12 and 13-16 flower classes correspond to 7-flower class individuals, and the 13-23 and 17 and greater flower classes correspond to 10-flower class individuals. The segregation observed in one and two-branched inflorescences did not differ significantly from the digenic segregation observed in the unbranched monochasial population (Table 20).

The similarity of the segregation ratios for the one and two-branched types to the unbranched inflorescence population suggests that the 7-flower class and the 10-flower class have the same capacity to produce branched inflorescences.

Single Flower per Truss x Compound Inflorescence

The distribution of number of branches per branched inflorescence and the frequency of branching for segregating generations from the cross MSU 100 (single flower) x Apsory (compound inflorescence) are presented in Table 23.

Table 23. Frequency distribution of number of branches per compound monochasial inflorescence and the frequency of compound monochasia in the simple inflorescence segregates for different generations from the cross MSU 100 (P_1) x Apsory (P_2).

Generation	Number of Simple Inflorescence Types	Number of Branches					Total Frequency
		1	2	3	4	Greater than 4	
F_1	33	5	2				.212
F_2	315	59	20	6	1	30	.368
BC to P_2	48	16	3		1	4	.500
BC to P_1	51	15	3	3			.420

Individuals with greater than 4 branches per inflorescence may be either compound monochasial or compound dichasial inflorescences. Compound dichasial types may arise from individuals expressing the intense branching phenotype (Figure 5a). The branching frequencies include all branched individuals.

The frequency of compound monochasial inflorescences for the backcross populations (42.0% for the backcross to MSU 100 and 50.0% for the backcross to Apsory) exceeded the F_1 (21.2%) and the F_2 population frequency (36.8%). The backcross values suggest that each parent contributed to increased branching.

The F_1 value (21.2%) is assumed to be the dominant expression. If the backcross branched inflorescence frequencies are due to recessive genes, each parent (MSU 100 and

Apsory) must carry independent genes for increased compound monochasial inflorescence.

The branching effect of MSU 100 estimated in the cross MSU 100 x Pennorange was 12.2%. The effect of MSU 100 on branching in the cross MSU 100 x Apsory appears to be much greater. The increased branching effect is probably due to an interaction of loci. The low branching frequency (21.2%) of the F_1 population suggests that the interaction may be due to recessive genotypes.

Jointless Pedicel *vs.* Number of Flowers per Inflorescence

Single Flower per Truss (jointed pedicel) x Low-flower-number Inflorescence (jointless pedicel)

The close association of the jointless pedicel (*j*) character and a low number of flowers per inflorescence was suggested by Rick and Sawant (23) and Emery and Munger (6).

Data obtained on jointless pedicel and flower per inflorescence from the cross MSU 100 (single flower, jointed pedicel) x Pennorange (low-flower-number inflorescence type, jointless pedicel) also suggest a strong association between the two characters. Recombination values of 1.99 ± .002 and 1.80 ± .005 were observed in the backcross to Pennorange and F_1 populations respectively. F_2 linkage values were calculated according to the methods described by Immer (9).

Information regarding the relationship of the jointless pedicel to the character single flower (a) and to the low-flower-number type was obtained from the segregation of F_3 populations derived from F_2 selections of jointless and jointed pedicel single flower plants.

F_3 Populations

Fifteen F_2 individuals with jointed pedicel (J) and single flower (a) were observed. Three of the selections segregated for flower number and for the jointless pedicel character (Table 24). Assuming the recessive genotype (b) governing the Pennorange phenotype (low-flower-number type) to be epistatic to the single flower genotype (Table 2), segregation was expected.

Table 24. Segregation of F_3 populations for flower number and jointless pedicel from jointed pedical (J), single flower F_2 selections from the cross MSU 100 x Pennorange.

Line	Number of Plants	Single Flower	Low-flower-number	Jointless Pedicel (j)
69-8	54	42	12	15
69-10	68	58	10	13
69-15	74	60	14	19

Four lines from jointless pedicel (j) and single flower (a) F_2 individuals were also grown. Two lines showed a distribution for flower number similar to Pennorange and two lines bred true for single flower.

Two single flower and jointless pedicel F_2 selections, reverted to the Pennorange phenotype when grown in the greenhouse.

The relationship between jointless pedicel and the low-flower-number class was observed in the F_3 generations. All segregates for number of flowers in lines 69-8, 69-10 and 69-15 (Table 24) were jointless; therefore, pleiotropy or tight linkage was suggested.

Assuming linkage or pleiotropy between jointless and low flower number, jointless, single flower selections are expected to segregate similar to the Pennorange parent. However, jointless single flower selections were observed to breed true for the single flower character in 2 of 6 F_3 selections. F_3 lines segregating for jointless pedicel only were also observed.

The fact that jointless segregates from F_3 populations of jointed pedicel F_2 selections both breed true for single flower and segregate for number of flowers suggest that a gene or genes other than the single flower gene, a, is necessary for jointless types to exhibit the character single flower per truss.

Leafy Indeterminant Inflorescence

Low-flower-number Inflorescence (leafy indeterminant) x Simple Inflorescence

While the jointless pedicel, leafy inflorescence relationship has been well-investigated (16,23), the relationship of jointless pedicel and leafy indeterminant inflorescence has not. Leafy indeterminant inflorescence is associated with non-terminal growing of the inflorescence. Such growth is characterized by the production of flowers followed by leafy growth then flowers followed by growth, etc. This pattern continues indefinitely. Parkin (20), in his discussion on inflorescence evolution, describes this character as intercalary inflorescence, provisionally referred to as *ini* in this study (Figure 4).

The frequency of intercalary inflorescence in the parents, F_1, F_2 and backcross populations of the cross Pennorange x Michigan State Forcing is presented in Table 25. Assuming the .155 frequency of Michigan State Forcing to be due to a dominant factor, since both the F_1 and backcross to Michigan State Forcing exhibit similar frequencies. The Pennorange expression (.875) was suggested to be due to a recessive factor. The expected intercalary inflorescence frequencies for the F_2 and backcross to Pennorange populations were estimated from the formula $\frac{1}{4}P_1 + \frac{3}{4}P_2$ for the F_1 and $\frac{1}{2}P_1 + \frac{1}{2}P_2$ for the backcross to Pennorange where P_1 is the frequency observed in Pennorange and P_2 is the frequency observed

Table 25. Segregation for intercalary inflorescence (ini) in the various populations of the cross Pennorange (P_1) x Michigan State Forcing (P_2).

Generation	Number of Plants	ini	Normal (+)	ini Frequency
Pennorange	48	42	6	.875
M.S.F. (P_2)	45	7	38	.155
F_1	71	12	59	.169
F_2	136	50	86	.367
BC to P_2	98	16	82	.163
BC to P_1	120	62	58	.517

in Michigan State Forcing. The expected frequencies for the F_1 and backcross to Michigan State Forcing equal that observed in the Michigan State Forcing population. The expected frequencies were used to determine the theoretical segregation of different generations for chi-square analysis. The observed intercalary inflorescence segregation suggests a good fit to a monogenic inheritance (Table 26), with low frequency of occurrence the result of a dominant gene.

Intercalary Inflorescence *vs.* Jointless Pedicel

The relationship between intercalary inflorescence and the jointless character was also investigated. The frequency of *ini* types with the jointless (*j*) and jointed (*J*) characters

Table 26. Chi-square test for goodness of fit to a monogenic inheritance for intercalary inflorescence for the F_1, F_2 and backcross populations from the cross Pennorange (P_1) x Michigan State Forcing (P_2).

Generation	Number of Plants	Intercalary Types		Normal Types		χ^2	P
		Obs.	Exp.	Obs.	Exp.		
F_1	71	12	11.0	59	60	.1075	.80-.70
F_2	136	50	53.7	86	82.3	.4213	.70-.50
BC to P_2	98	16	15.2	82	82.8	.0499	.90-.80
BC to P_1	120	62	61.7	58	58.3	.0029	.98-.95

were recorded from the F_2 and backcross to Pennorange. Frequencies of .939 and .935 for jointless progeny in the F_2 and backcross to Pennorange respectively were not significantly different from the .875 frequency observed in the Pennorange population. The frequency of ini J progeny observed in the F_2 (.181) did not differ from the frequency observed in the Michigan State Forcing parent (.155), but the .061 ini J frequency observed in the backcross to Pennorange was significantly different from the Michigan State Forcing.

These data suggest that the expression of intercalary inflorescence may be a function of the jointless and jointed pedicel characters. The apparent single gene segregation for intercalary inflorescence may be segregation for jointless and jointed pedicel.

If intercalary inflorescence is linked to jointless pedicel, recombinants of jointless and low ini frequency and jointed and high ini frequency would be apparent in the F_2 and backcross to Pennorange population frequencies. Jointed high ini recombinants are expected to cause the ini frequency to be greater than that exhibited by the Michigan State Forcing parent and jointless low ini recombinants are expected to cause the ini frequency to be lower than that exhibited by Pennorange (.875). However, the only significant deviation was the low jointed pedicel ini frequency (.061) observed in the backcross to Pennorange. Since no effects of linkage were observed, pleiotropy or close linkage between intercalary inflorescence (ini) and jointless pedicel (j) is suggested.

DISCUSSION

The inheritance of the inflorescence types, single flower per truss (a), compound (s), simple and low-flower-number was determined. Inheritance studies were conducted for flower number on the unbranched simple inflorescence and the occurrence of the compound monochasial (branched inflorescence) characters.

Single Flower per Truss

The character single flower per truss was suggested to be controlled by a single recessive gene from crosses to a simple inflorescence line (MSU 180), and a low-flower-number per inflorescence line (Pennorange) (Table 2). The crosses of single flower (MSU 100) to compound inflorescence lines (MSU 200 and Apsory) showed segregations that suggested a more complex inheritance. A model (Table 11) composed of the single flower per truss gene (a), an inhibitor (I) gene which inhibits the expression of a and a restorer gene (R) which restores the expression of a in the presence of I was proposed. The segregation for single flower in the F_2 and backcross to single flower parent for both crosses of single flower x compound inflorescence showed a good fit to the expected base on this model. The proposed model could not explain the 15:1 ratio of single flower to simple inflorescence noted in the F_3 generations from single flower F_2 selections.

Low Flower Number per Inflorescence

The low flower number phenotype of the Pennorange variety is suggested to be controlled by a single recessive gene (Tables 2,5). The 9 'F_1 class' : 4 low flower class : 3 single flower per truss segregation observed in the (MSU 100 x Pennorange) F_2 (Table 2), suggests the gene for low flower class to be epistatic to the gene single flower per truss.

Compound Inflorescence

Compound inflorescence was previously reported to be controlled by a single recessive gene (s) (5,14). Deviations from monogenic inheritance (4) were reported. In the present study segregation for compound inflorescence types deviated from the expected in (MSU 100 x MSU 200) F_2 and (Apsory x MSU 180) F_2 populations. Segregation of the (MSU 100 x Apsory) F_2, backcross to Apsory and (MSU 100 x MSU 200) x MSU 200 populations did not differ from the previously reported segregation.

Individual plants with high flower numbers (30-80 flowers) and many branches on the inflorescence were observed in crosses involving compound inflorescence. An association between the high flower number segregates and compound inflorescence (s) is suggested from the following evidences:

a) The deficiency of ss recombinants in the F_2 populations.

b) Both high flower number and compound inflorescence were suggested to be linked to the dwarf plant habit (d) (Table 12).

c) Previous reports suggested that 200-300 flowers per inflorescence is not a prerequisite for compound inflorescence (3,13).

The phenotype of compound inflorescence expressed by the MSU 200 and Apsory parents (200-300 flowers) is the result of intense branching of the inflorescence and a non-terminal flowering habit. Recombinants with either intense branching or non-terminal flowering were observed in segregating populations, suggesting the MSU 200 and Apsory to carry genes for intense branching and non-terminal flowering. The intense branching character exhibits high flower numbers, suggesting that this may also be conditioned by the s gene.

Linkage values between intense branching and non-terminal flowering were calculated from the backcrosses (MSU 100 x Apsory) Apsory and (MSU 100 x MSU 200) MSU 200, and the F_2 of Apsory x MSU 180. Recombination values ranged from 6% to 11%. The observed segregation frequencies of compound inflorescence show close agreement to the expected values based on the linkage model (Table 14).

Flower Number on the Unbranched Monochasial Inflorescence

The F_1 phenotype (simple inflorescence) was suggested to be the dominant class. The mean number of flowers on the simple inflorescence progenies from the backcross to Pennorange and the backcross to MSU 100 suggested segregation of modifiers which affected the number of flowers on the unbranched monochasial inflorescence.

The modifier or modifiers contributed to Pennorange is suggested to give a phenotype of 4-flowers per unbranched infloresence, and the modifier or modifiers transmitted by MSU 100 were suggested to give a phenotype of 8-flowers per unbranched inflorescence. The two phenotypes exhibited no dominance and the F_1 phenotype showed a mean of 6 flowers.

Segregation for flower number class within the simple inflorescence was observed in the cross MSU 100 x MSU 200. The classes, 10-flowers and 7-flowers, exhibited a digenic 9:7 ratio of 10-flowers to 7-flowers.

Compound Monochasial Inflorescence

The occurrence of compound monochasial inflorescences in the different generations from the cross MSU 100 x Pennorange was investigated (Table 21). The factor(s) transmitted by Pennorange and MSU 100 was suggested to contribute less than 3.6 percent and from 12.2 to 30.4%, respectively. The F_1 showed 8.7 percent compound monochasial types and their occurrence was suggested to be related to the genotype conditioning number of flowers per inflorescence.

The estimated frequency of compound monochasial inflorescences transmitted by the MSU 100 parent in the cross MSU 100 x MSU 200 was 13.2 percent and is similar to the value estimated in the cross MSU 100 x Pennorange. The frequency of the F_1 was 59 percent and the backcross to MSU 200 was 58 percent suggesting that the higher frequency is due to a dominant factor. The observed frequencies of the F_1, F_2 and backcross generations gave a good fit to a monogenic hypothesis.

The frequency of compound monochasial inflorescences noted in the cross MSU 100 x Apsory suggest that the MSU 100 parent contributed an effect greater than was previously noted in the MSU 100 x Pennorange and MSU 100 x MSU 200 crosses. The high frequencies in the backcross populations (42% and 50%) and the low frequencies of the F_1 (21.2%) and F_2 (36.8%) may be due to an interaction or recombination of several genes.

Intercalary Inflorescence

The character intercalary inflorescence, indeterminant vegetative growth in the inflorescence, was suggested to be conditioned by a single recessive gene, ini (Table 26).

Studies on the relationship of the jointless pedicel (j) to intercalary inflorescence (ini) suggest the jointless gene to be either closely linked to the gene for intercalary inflorescence or the genes are pleiotropic.

SUMMARY AND CONCLUSIONS

1. The results of crosses between single flower per truss (MSU 100), compound inflorescence (Apsory and MSU 200) simple inflorescence (MSU 180 and Michigan State Forcing) and low-flower-number per inflorescence (Pennorange) were evaluated to determine the mode of inheritance for these characters. The simple inflorescence phenotype was evaluated for inheritance of number of flowers on the unbranched inflorescence and for the occurrence of compound monochasial inflorescences.

2. Single flower per truss was suggested to be conditioned by a single recessive gene, designated as a, from the crosses MSU 100 x Pennorange and MSU 100 x MSU 180.

Single flower inheritance in the crosses MSU 100 x Apsory and MSU 100 x MSU 200 was suggested to be more complex. A three gene model was proposed to explain the probable mode of inheritance:

a - conditions single flower per truss
I - inhibitor of a (single flower) expression
R - restores a (single flower) expression in the presence of I.

3. Low-flower-number inflorescence, as found in the Pennorange parent, was suggested to be conditioned by a single recessive gene, from crosses MSU 100 x Pennorange and Pennorange x Michigan State Forcing.

The low flower gene was suggested to be epistatic to the gene for single flower per truss.

4. Compound inflorescence, as expressed by the parents, Apsory and MSU 200, was suggested to be conditioned by two linked genes, intense branching and non-terminal flowering (<u>ntf</u>), with recombination values between genes for intense branching and non-terminal flowering of 6 percent in the crosses MSU 100 x Apsory and Apsory x MSU 180 and 11 percent in MSU 100 x MSU 200.

5. Simple inflorescence phenotypes exhibited segregation for number of flowers on the unbranched inflorescence. Modifiers were proposed to condition the 4-flower class and 8-flower class observed in the cross MSU 100 x Pennorange and the 7 and 10-flower classes observed in the MSU 100 x MSU 200 cross. The modifiers conditioning the 4 and 8-flower classes were suggested to show no dominance while the digenic 9:7 ratio of 10-flower class to 7-flower class suggests dominance of the 10-flower class.

6. The occurrence of compound monochasial inflorescences in the cross MSU 100 x Pennorange was suggested to be conditioned by a single recessive gene, designated as <u>c</u>. The gene was suggested to behave as follows:

<u>cc</u> - conditions low frequency of compound monochasial types (3.6 percent or less)

<u>Cc</u> - conditions 8.7 percent compound monochasial types

<u>CC</u> - conditions 12-30 percent compound monochasial types.

7. Compound monochasial inflorescence, as noted in the cross MSU 100 x MSU 200, was thought to be inherited as a single gene.

8. Intercalary inflorescence was suggested to be conditioned by a recessive gene, <u>ini</u>, which is either closely linked or pleiotropic with the jointless pedicel gene, <u>j</u>.

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