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Genetics of the "umbrella" branching habit in *Capsicum annuum* L.*

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Summary. Three inbred lines, MSU 78-101, MSU 79-221 and MSU 74-230 were used to determine the inheritance of the "umbrella" branching habit in peppers. MSU 79-221, with the umbrella phenotype, was crossed with MSU 78-191 (dwarf) and MSU 74-230 (indeterminate growth habit). Segregating populations were separated on the basis of plant growth habit and fruit bearing habit. Genetic analyses suggested that the umbrella phenotype was controlled by three major recessive genes, *ct* and *dt* determining plant habit, and *fa* determining fruit bearing habit. When the dominant alleles *Dt* and *Ct* were in the dominant homozygous or heterozygous condition an indeterminate phenotype was produced. *Su,* a dominant suppressor gene, apparently acts to suppress the epistatic action of the *Ct* gene. Modifiers were involved in the control of branching in the umbrella plants. Linkage also was noted between the genes for indeterminate plant habit and non-clustered bearing habit. The information derived from this study will allow the plant breeder to design an efficient breeding program for the development of pepper cultivars suitable for mechanical harvesting systems.

Key words: Peppers – Inheritance – Linkage – *Capsicum*

Introduction

Problems associated with mechanical harvesting of peppers include difficulty in removing fruit from the plant, non-uniform maturity, and breakage of branches and uprooting of plants by the action of the harvester. Modifications of existing harvesters to overcome these problems would be a possible solution. Plant breeders have been charged with the responsibility of attempting to breed a plant adaptable to the harvester. This would require a plant architype exhibiting concentrated fruit set, uniform maturity, and with fruit set high off the ground. It also should possess the necessary horticultural characteristics, and resistance to diseases and insects.

Several investigations of the inheritance of growth habit in peppers (*Capsicum annuum* L.) have been reported. Dale (1931) studied the inheritance of a dwarf plant habit arising from a cross between the cultivars 'Coral Gem' and 'Anaheim', and determined the trait to be a simply inherited recessive character. Deshpande (1944) conducted an analysis of the inheritance of bunchy habit in chilli peppers. This mutant was described as bushy and compact with shortened internodes, and flowers and fruit produced in clusters. The bunchy character was shown to be recessive, and was later termed fasciculate (*fa*) by Lippert et al. (1965, 1966).

Kormos and Kormos (1956) crossed a fasciculate type of pepper with various non-fasciculate types and recovered F_2 progeny exhibiting completely determinate growth. In these plants, the main axis stopped growing early in the season and produced a cluster of fruit, after which no lateral shoots developed. This character was found to be recessive.

The inheritance of fruit bearing habit in *C. frutescens* L., a related species, was determined from a cross between two tabasco type cultivars, 'LP-1' and 'Almeda', in which the characters cluster versus non-cluster fruit set were studied. Results indicated that the cluster habit was controlled by a single recessive gene (Barrios and Mosokar 1972).

Two genetic studies have been conducted on branching in peppers. Bergh and Lippert (1975) studied three species, *C. baccatum* L., *C. chinense* Jacq. and *C. frutescens* L., for the inheritance of axillary shooting prior to the first bifurcation or point of branching. They observed mutant plants of *C. chinense* with extensive prebifurcation axillary shoots. Intra- and interspecific crosses with these plants indicated a monogenic reces-

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sive basis for the trait, which they termed compact (*ct*). Considerable environmental effects on the expression of axillary shooting were observed.

Shifriss and Hakim (1977) studied the inheritance of pre-bifurcation shooting in *C. annuum* L. They crossed 'Santaka', a Japanese cultivar with many axillary shoots developing acropetally along the main stem, and exhibiting the fasciculate bearing habit, with 'Csokros Fellalo', and Hungarian bush fasciculate cultivar, devoid of axillary shoots, and with 'Yolo-Wonder Y', with few axillary shoots prior to the first bifurcation. In the F_1 and F_2 from the 'Santaka' × 'Csokros Fellalo' cross, progenies showed partial dominance of many over few axillary shoots, while in the F_1 and F_2 from 'Santaka' × 'Yolo-Wonder Y', the opposite occurred, i.e, partial dominance of few over many shoots. They concluded that pre-bifurcation shooting, though a quantitative character, is controlled by relatively few genes with different action, and modified by environmental conditions.

The possibility of developing cultivars adaptable to existing harvesters was realized with the appearance of a particular plant habit among the MSU breeding population. These plants exhibited determinate growth, with a cluster of fruit at the apex, and a subsequent branching pattern which resulted in the production of additional clusters of flowers at the apex of each branch, all maturing at approximately the same time. This plant habit, designated "umbrella", produces its fruit at the periphery of the plant, away from the branch joints, and could be extremely useful in mechanical harvesting systems, allowing for an early hand harvest of the central cluster, followed by a once-over harvest of the remaining fruit at maturity.

Information on the genetic control of this branching pattern would be helpful in designing an efficient breeding scheme for the development of desirable phenotypes. The objective of the present study was to determine the inheritance of the "umbrella" branching habit in peppers.

Materials and methods

Three inbred *C. annuum* L. lines, MSU 78-101, MSU 79-221 and MSU 74-230 were used in this study (Fig. 1). MSU 78-101 is an upright, dwarf banana pepper carrying the "fasciculate" or clustered gene (*fa*). MSU 79-221 was a selection from the cross MSU 74-190, a yellow long banana pepper, × 'Csokros Fellalo', a Hungarian upright, yellow bell, also carrying the fasciculate gene. It was selected on the basis of its unique branching habit, termed "umbrella". Upon attaining a height of approximately 15 cm, the apex terminates in a cluster of 2–6 fruit followed by initiation of several lateral branches, each of which produces a terminal cluster of fruit, that mature uniformly. The umbrella phenotype has been designated (um).

MSU 74-230, a yellow, long banana, was an F_5 selection from the cross between 'Avelar', and a yellow long banana MSU selection. It is an indeterminate, non-clustered fruiting, yellow banana type, with a prolific branching habit, and produces fruit continuously and, therefore, matures over an extended period.

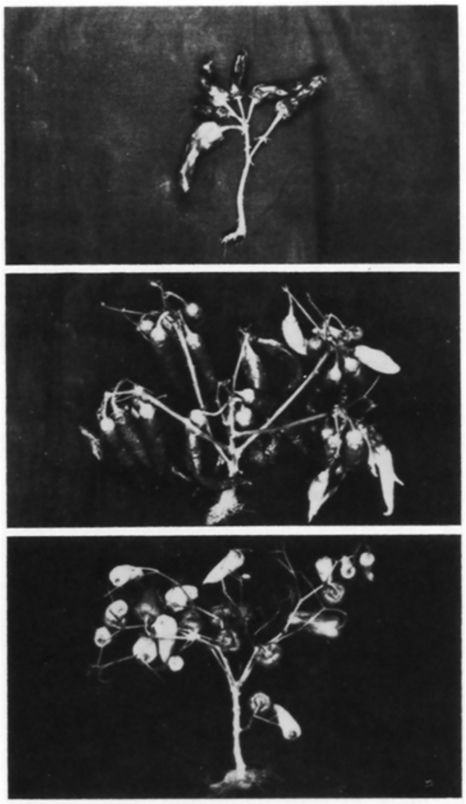

Fig. 1. Plant habit of the three parental lines. *Top* MSU 78-101, Dwarf (*CtCtdtdtfafaSuSu*); *center* MSU 79-221, Umbrella (*ctctdtdtfafasusu*); *bottom* MSU 74-230, Indeterminate (*CtCtDtDtFaFasusu*)

Hybridization

Crosses were made in the greenhouse to produce reciprocal populations for the genetic studies. One plant of each parental line was selected for hybridization with the other two parents. All generations were produced using these single plants and their F_1's. Flowering occurred in MSU 78-101 over a 10–14 day period, followed by very little vegetative development and occasional flowering. Therefore, it was impossible to obtain backcross progenies with MSU 78-101.

Seeds of parents and progenies were shown in vermiculite and seedlings were transplanted two weeks later into peat pots, and into the field a month later. A completely randomized design with three replications was used. Rows were spaced 1.07 m apart, with plants spaced at intervals of 0.60 m in the row. Cultural practices utilized were those recommended for pepper production in Michigan.

Plants were classified for growth habit (indeterminate versus determinate) and fruit bearing habit (non-cluster versus cluster). The means of reciprocal populations were tested for homogeneity prior to analysis of the data.

MSU 78-101 × MSU 79-221. Due to a short period of flowering of the MSU 78-101 parent, it was impossible to obtain reciprocal generations for this study. Using the dwarf as the female parent, F_1, F_2 and BC_2 populations were produced. Each replication consisted of 12 plants of each parent, 12 of each F_1 family, 72 of the backcross to MSU 79-221, and 96 of the F_2 population.

MSU 79-221 × MSU 74-230. Each replication consisted of 12 plants of each parent, 24 of each F_1 family, 72 of each backcross population of 96 of each F_2 family. The possibility of linkage necessitated the use of a χ^2 contingency test in which the test is separated into three components using the following formulae (Bonnier 1942):

$$\text{Aa segregation component } \chi^2 = \frac{(a+b-3(c+d))^2}{3N},$$

$$\text{Bb segregation component } \chi^2 = \frac{(a+c-3(b-d))^2}{3N},$$

$$\text{Linkage component } \chi^2 = \frac{(a-3b-3c+9d)^2}{9N},$$

Where N is the total number of plants per test component and classes a, b, c and d = phenotypes AB, Ab, aB, and ab, respectively. There is one degree of freedom for each χ^2 test. Linkage intensities were calculated using the product method (Fisher and Balmukand 1928).

MSU 78-101 × MSU 74-230. Reciprocal populations of F_1 hybrids and F_2 families were produced for use in this study. However, the F_1 was backcrossed only to MSU 74-230 due to an absence of flowers caused by the short duration of flowering in the dwarf parent (MSU 78-101). Each replication consisted of 12 plants of each parent, 12 of each F_1 family, 72 of the backcross to MSU 74-230, and 96 of each F_2 population.

Results and discussion

MSU 78-101 × MSU 79-221

The segregating populations were separated on the basis of plant habit prior to genetic analysis. The F_2 generation segregated into 103 dwarf : 40 indeterminate : 47 umbrella, approximating a 9 : 3 : 4 ratio (P = 0.80–0.70, Table 1). The expected ratio for the backcross to the umbrella parent would be 2 umbrella : 1 dwarf : 1 indeterminate. A ratio of 99 : 49.5 : 49.5 would be expected among 188 plants. The data show good fit to the expected ratio (P = 0.30–0.20, Table 1). Nine umbrella plants were observed in the F_1 population; however, the observed F_1 ratio could not be tested due to the zero expectation for the umbrella class.

It appears that four major genes are involved in the expression of the umbrella habit. The genes *dt* and *ct* control plant habit; *dt* conditions determinte growth, while *ct* controls the number of axillary shoots (Bergh and Lippert 1975). *Dt* and *Ct* condition indeterminate growth, and are epistatic to one another, such that, in the homozygous dominant or heterozygous conditions, *Ct* is epistatic to the expression of *dt*, while *Dt* is epistatic to the expression of *ct*. A third gene, *fa*, controls the fasciculate or clustered fruit bearing habit. *Fa* causes non-clustered fruit set. A fourth gene, *Su*, acts to suppress the epistatic action of *Ct*.

Table 1. Chi-square (χ^2) goodness of fit test for pooled generations from the cross *MSU* 78-101 × *MSU* 79-221

Generation	Observed ratio	Expected ratio	χ^2	P^a
Pooled F_1	34:9	1:0	–	–
Pooled F_2	103:40:47	9:3:4	0.682	0.80–0.70
Pooled BC to P_2	89:59:50	2:1:1	2.838	0.30–0.20

[a] P = probability of obtaining as large or larger deviation than observed

Assuming that the genotype of MSU 79-221 is *ctctdtdtfafa*, and that of MSU 78-101 is *CtCtdtdtfafa*, the expected F_2 ratio is 3 dwarf : 1 umbrella. However, the appearance of indeterminate plants in the F_2 population suggests the presence of an additional gene(s) in determining the umbrella habit. The addition of gene *Su*, to the genotype of the dwarf plant would result in a 9 : 3 : 4 segregation pattern in the F_2 generation. In this case, the genotype of MSU 79-221 would be *ctctdtdtfafasusu*, that of MSU 78-101, *CtCtdtdtfafaSuSu*. The *Su* gene would act to suppress the epistatic action of *Ct*, the genotypes *Ct – – dtdtfafaSu – –* would produce dwarf plants, genotypes *ctctdtdtfafaSu – –* and *ctctdtdtfafasusu* would produce umbrella types, and genotypes *CtCtdtdtfafasusu* and *Ctctdtdtfafasusu* would produce indeterminate types.

The presence of 9 umbrella plants out of 43 F_1 plants may be due to the effect of modifiers on the expression of the *ct* gene. The genotype of the F_1 would be *CtctdtdtfafaSusu*. Assuming the suppressor gene inhibits the action of the *Ct* gene, modifiers affecting the expression of the *ct* gene could alter the amount of branching in a given plant, resulting in a misclassification of a plant as an umbrella type. The proposed genotypes, phenotypes and expected ratios from this cross are presented in Table 2.

MSU 79-221 × MSU 74-230

Plant type and fruit bearing habit were used to separate the F_2 and backcross progenies into distinct classes for genetic analysis. The F_1 plants were indeterminate and

Table 2. Proposed genotypes, phenotypes and expected ratios from the cross *MSU* 78-101 × *MSU* 79-221

Genotype	Expected ratio	Phenotype
CtCtdtdtfafaSuSu *CtctdtdtfafaSuSu* *CtCtdtdtfafaSusu* *CtctdtdtfafaSusu*	9/16	Dwarf
CtCtdtdtfafasusu *Ctctdtdtfafasusu*	3/16	Indeterminate
ctctdtdtfafaSuSu *ctctdtdtfafaSusu* *ctctdtdtfafasusu*	4/16	Umbrella

non-clustered, suggesting that the umbrella habit was a recessive character. In the F_2, the plants segregated into four classes: indeterminate, non-clustered; indeterminate, clustered; determinate, non-clustered and determinate, clustered. Plant habit appeared to be under a 2 gene dominant epistatic control, resulting in a segregation of 15 indeterminate : 1 determinate. The non-clustered versus clustered characters however did not fit the expected 3 : 1 ratio. A preponderance of parental types suggested linkage between the determinate and fasciculate genes. This was supported by the poor fit of the data to the proposed (15 : 1) (3 : 1) model ($P=0.001$, Table 3). This model gave the best fit of all models tested.

The backcross of the F_2 to the umbrella parent also showed a poor fit to the expected ratio ($P=0.001$, Table 3). The preponderance of parental types over recombinants in the backcross generation further suggested linkage between the gene determining plant growth habit and bearing habit. The backcross of the F_1 to the dominant parent showed a good fit to the expected ratio.

Separation of the χ^2 test into its components showed a good fit to the expected 15 : 1 segregation for plant habit ($P=0.50$–0.10), but a poor fit to the expected 3 : 1 segregation for bearing habit ($P=0.001$). A significant value was also obtained for the linkage component ($P=0.001$). Linkage studies using the product method indicated a crossover value of 10.45 ± 3.82%. Therefore, it appears that the poor fit of the data to the proposed model may be due to the tight linkage between the genes conditioning indeterminate plant habit and non-clustered fruit bearing habit.

Within the determinate class of the F_2 and BC_1 populations, both umbrella and dwarf types were recovered. The following genetic model is proposed: 3 major genes are involved in the inheritance umbrella habit in this cross. The proposed genotype of the umbrella parent is *ctctdtdtfafasusu,* where *ct* controls the number of axillary shoots (Bergh and Lippert 1975). The *dt* and *fa* genes control determine growth and clustered bearing habit, respectively. The proposed genotype of MSU 74-230 is *CtCtDtDtFaFasusu, Dt* and *Ct* causing indeterminate growth. It appears that, in the homozygous or heterozygous conditions, *Ct* is epistatic to the expression of *dt,* while *Dt* is epistatic to the expression *ct.* However, both dominant genes may be inherited independently, resulting in a 9 : 3 : 3 : 1 segregation ratio for plant habit, but due to an inability to distinguish the intermediate classes from the dominant class, a 15 : 1 ratio was observed. Since the *su* gene was in the recessive condition in both parents, it did not affect the expression of these characters in this cross. The proposed genotypes and phenotypes of the F_2 generation are given in Table 4.

Table 3. Chi-square (χ^2) goodness of fit test for the cross *MSU* 79-221 × *MSU* 74-230, based on a 4-gene, epistatic model

Generation	Observed ratio	Expected ratio	χ^2	P^a
Pooled F_1	136:0	1:0	–	–
Pooled F_2	440:31:19:20	45:15:3:1	106.45	< 0.001
Pooled BC to P_1	245:43:30:94	3:3:1:1	203.26	< 0.001
Pooled BC to P_2	394:0	1:0	–	–

[a] $P=$ see Table 1

Table 4. Proposed genotypes, phenotypes and expected ratios from the cross *MSU* 79-221 × *MSU 74-230*

Genotype	Expected ratio	Phenotype
CtCtDtDtFaFasusu	45/64	Indeterminate, non-clustered
CtCtDtDtFafasusu		
CtCtDtdtFaFasusu		
CtCtDtdtFafasusu		
CtCtdtdtFaFasusu		
CtCtdtdtFafasusu		
CtctDtDtFaFasusu		
CtctDtDtFafasusu		
CtctDtdtFaFasusu		
CtctDtdtFafasusu		
CtctdtdtFaFasusu		
CtctdtdtFafasusu		
ctctDtDtFaFasusu		
ctctDtDtFafasusu		
ctctDtdtFaFasusu		
ctctDtdtFafasusu		
CtCtDtDtfafasusu	15/64	Indeterminate, clustered
CtCtDtdtfafasusu		
CtCtdtdtfafasusu		
CtctDtDtfafasusu		
CtctDtdtfafasusu		
Ctctdtdtfafasusu		
ctctDtDtfafasusu		
ctctDtdtfafasusu		
ctctdtdtFaFasusu	3/64	Determinate, non-clustered (Umbrella and dwarf)
ctctdtdtfafasusu	1/64	Determinate, clustered (Umbrella and dwarf)

Dwarf plants arising from this cross would have the genotype *ctctdtdtfafasusu* or *ctctdtdtFa – – susu* and would have reduced axillary shoots due to the action of modifier genes. Recombination of modifiers associated with *ct* would allow for varying numbers of axillary shoots in different genetic backgrounds, resulting in dwarf plants with few or no axillary branches.

MSU 78-101 × *MSU 74-230*

The plants in the segregating generations were classified by plant type and fruit bearing habit. The F_1 plants

Table 5. Chi-square (χ^2) goodness of fit test for the cross *MSU* 78-101 × *MSU* 74-230

Generation	Observed	Expected	χ^2	P^a
Pooled F_1	72:0	1:0	–	–
Pooled F_2	363:68:70:53	39:13:9:3	48.27	<0.001
Pooled BC to P_2	428:0	1:0	–	–

[a] P = see Table 1

Table 6. Proposed genotypes, phenotypes, and expected ratios from the cross *MSU 78-101* × *MSU* 74-230

Genotype	Expected ratio	Phenotype
CtCtDtDtFaFaSuSu *CtCtDtDtFaFaSusu* *CtCtDtDtFaFasusu* *CtCtDtDtFafaSuSu* *CtCtDtDtFafaSusu* *CtCtDtDtFafasusu* *CtCtDtdtFaFaSuSu* *CtCtDtdtFaFaSusu* *CtCtDtdtFaFasusu* *CtCtDtdtFafaSuSu* *CtCtDtdtFafaSusu* *CtCtDtdtFafasusu* *CtCtdtdtFaFasusu* *CtCtdtdtFafasusu*	39/64	Indeterminate, non-clustered
CtCtDtDtfafaSuSu *CtCtDtDtfafaSusu* *CtCtDtDtfafasusu* *CtCtDtdtfafaSuSu* *CtCtDtdtFafaSusu* *CtCtDtdtfafasusu* *CtCtdtdtfafasusu*	13/64	Indeterminate, cluster
CtCtdtdtFaFaSuSu *CtCtdtdtFaFaSusu* *CtCtdtdtFafaSuSu* *CtCtdtdtFafaSusu*	9/64	Determinate, non-clustered
CtCtdtdtfafaSuSu *CtCtdtdtfafaSusu*	3/64	Determinate, clustered

were indeterminate and non-clustered. This suggested that these characters were dominant to the dwarf clustered habit, as previously reported. The F_2 segregated into 363 indeterminate, non-clustered: 53 determinate, clustered plants. Analysis of each of these two characters showed a segregation ratio of 13:3 for plant type (P=0.05–0.01) and 3:1 for bearing habit (P=0.10–0.05). This suggested that bearing habit was controlled by a single gene, as reported by Deshpande (1944), while plant type appeared to be controlled by two genes. As discussed in the previous crosses, the compact (*ct*) and suppressor (*su*) genes were present in both parents and were presumably involved in determining plant habit in this cross. The proposed genotype of MSU 78-101 is *CtCtdtdtfafaSuSu,* that of MSU 74-230 is *CtCtDtDtFaFasusu.*

A cross involving parents with these genotypes would result in a segregation ratio of 39 indeterminate, non-clustered; 3 indeterminate, clustered; 9 determinate, non-clustered; 1 determinate, clustered. A chi-square test for this model gave a poor fit (P=0.001, Table 5).

The preponderance of parental types in the segregating generations suggested the presence of linkage between the genes for determinate plant habit and fasciculate fruit set. In separating the χ^2 test into its components, a significant value was obtained for the linkage component (P=0.001). Linkage studies using the product method indicated a crossover value of 31.70±2.58%. The proposed genotypes, expected ratios are given in Table 6.

The information gained from this study will aid efforts to develop pepper cultivars suitable for mechanical harvesting. A program of crosses to various cultivars exhibiting different fruit types, followed by recurrent backcrosses to the umbrella parent, will be the most efficient technique for achieving this goal.

References

Barrios EP, Mosokar HI (1972) The inheritance of pod color and bearing habit in *Capsicum frutescens* L. J Am Soc Hortic Sci 97:65–66

Bergh BO, Lippert LF (1975) Inheritance of axillary shooting in *Capsicum.* Bot Gaz 136:141–145

Bonnier G (1942) The X^2 linkage test. Hereditas 28:230–232

Dale EE (1931) Inheritance of dwarf in *Capsicum.* Pap Mich Acad Sci, Arts Lett 13:1–4

Deshpande RB (1944) Inheritance of bunchy habit in chilli (*Capsicum annuum* L.). Indian J Genet Plant Breed 4:54

Fisher RA, Balmukand B (1928) The estimation of linkage from the offspring of selfed heterozygotes. J Genet 20: 79–92

Kormos J, Kormos J (1956) Determinate growth in red pepper (in Hungarian, English summary). Noventytermeles 5:1–10

Lippert LF, Bergh BO, Smith PG (1965) Gene list for the pepper. J Hered 56:30–34

Lippert LF, Smith PG, Bergh BO (1966) Cytogenetics of the vegetable crops. Garden Pepper, *Capsicum* sp. Bot Rev 32: 24–55

Shifriss C, Hakim Y (1977) Segregation of prebifurcation shooting, stem length and leaf number of main stem in two crosses of *Capsicum annuum* L. Euphytica 26:491–495