A Genetic Study of Monogerm and Multigerm Characters in Beets

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Introduction

Monogerm beets were found in the variety Michigan Hybrid 18 in Oregon in 1948. Two of these monogerm plants, SLC **101** and SLC **107,** proved to be self-fertile and two inbred lines were produced from them (8 and 9).[2] These original inbred lines had apparently been selfed for five to seven previous generations because of uniformity shown in many characters. They were homozygous for the monogerm character, self-fertility and red hypocotyl color. The monogerm character remained constant in different environments for the inbred line SLC 101 during three additional generations of controlled selfing or crossing offspring inter se.

The Basic Gene *m* for the Monogerm Character

F_1 Generation

All F_1 hybrids were multigerm from numerous crosses between SLC 101 with different multigerm varieties of sugar beets, fodder beets, red table beets and Swiss chard. The multigerm character was dominant, but dominance was not complete in F_1 hybrids (7). The number of flowers per flower cluster was less in the F_1 hybrids than in the multigerm parents (Table 1).

The number of highly multiple flower clusters decreased in F_1 hybrids when compared with the multigerm parents. F_1 plants also developed some monogerm fruits. The percentage of monogerm fruits in F_1 hybrids increased rapidly when SLC 101 was crossed to double-germ plants (Table 1). In F_1 beets derived from hybridization to the double-germ clone 4, the percentage of monogerm fruits reached 51 percent of the total (Table 1). However, these heterozygous plants always developed seedballs in the axils of lateral branches while in the homozygous monogerm SLC **101** the seedballs were never located in the floral axils.

Table 1.—Number of Flowers Per Flower Cluster in F_1 Hybrids and Their Parents.

Parental varieties and offspring	Generation	Flowers per flower cluster						Flowers per 100 flower clusters
		1	2	3	4	5	6	
		%	%	%	%	%	%	Number
Monogerm SLC 101	P	100	—	—	—	—	—	100
Monogerm SLC 107	P	100	—	—	—	—	—	100
Multigerm SL 92	P	3	55	28	13	1	—	254
SLC 92 × SLC 101	F_1	6	81	13	—	—	—	207
SLC 92W × SLC 107	F_1	65	19	1	—	—	—	206
Clone 4, double-germ	P	7	93	—	—	—	—	193
Clone 4 × SLC 101	F_1	51	49	—	—	—	—	149

F_2 Generation

Seed obtained from F_1 plants from self-pollination under paper bags was planted as separate progenies. These different F_2 populations were

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[2] Numbers in parentheses refer to literature cited.

Table 2.—Segregation for Multigerm and Monogerm Beets from F_2 Hybrids, Salt Lake City, 1950 and 1951.

1950 greenhouse and field experiment				1951 field experiment				1952 field experiment Reciprocal hybrids			
	Classification of offspring				Classification of offspring				Classification of offspring		
Population Number	Multigerm	Monogerm	Total	Population number	Multigerm	Monogerm	Total	Population number	Multigerm	Monogerm	Total
	No.	No.	No.		No.	No.	No.		No.	No.	No.
1 G[1]	22	6		6	28	13	41	37	26	8	34
1 F[2]	24	8	60	7	24	11	35				
				8	25	7	32	38	22	7	29
2 G	25	8		9	38	8	46				
2 F	61	30	124	10	21	8	29	39	21	6	27
				11	47	17	64				
3 G	23	7		12	28	10	38	40	40	16	56
3 F	59	14	83	13	7	2	9				
				14	17	5	22	41	15	6	21
4 G	23	7		15	15	6	21				
4 F	79	24	133	16	17	5	22	42	10	3	13
				17	13	3	16				
5 G	25	10		18	23	8	31	43	21	8	29
5 F	57	18	110	19	16	8	24				
				20	12	12	24	44	16	6	22
				21	15	4	19				
				22	21	6	27	45	26	8	34
[1]G indicates grown in greenhouse				23	19	8	27				
				24	15	3	18	46	12	5	15
[2]F indicates grown in the field				25	38	13	51				
				26	5	1	6	47	27	13	40
				27	26	8	34				
				28	6	1	7	48	27	8	35
				29	23	10	33				
				30	18	5	23	49	25	7	32
				31	23	7	30				
				32	20	5	25	50	19	6	25
				33	33	9	42				
				34	13	4	17				
				35	38	13	51				
				36	19	6	25				
Total	378	132	510		663	226	889		307	105	412
3:1 ratio	382.5	127.5	510		666.75	222.25	889.0		309.0	103.0	412.0
Deviation	—4.5	+4.5	.....		—3.75	+3.75	.....		—2.0	+2.0	.....
X^2	0.2117				0.8436				0.05174		
Probability	0.70 to 0.50				0.5 to 0.3				0.9 to 0.8		

studied for two years in the field and the greenhouse at Salt Lake City. The number of monogerm segregates in all cases was close to 25 percent (Table 2).

All X^2 values in Table 2 are low and show good agreement between observed and expected ratios. This indicates that the monogerm parental lines were homozygous *mm* with respect to a single gene for the monogerm character. With reciprocal hybridization, when the monogerm SLC 101 was used as the female parent and multigerm beets as pollinators, there was no change in type of segregation. F_2 hybrids obtained from hybridization of the monogerm SLC 101 to multigerm fodder beets, red table beets and Swiss chard also showed segregation in agreement with the monohybrid scheme.

Table 3.—Segregation for Monogerm and Multigerm Character in the First Backcross Generation.

Parentage of hybrids	Classification of offspring		
	Multigerm	Monogerm	Total
	Number	Number	Number
$F_1 Mm$ x SLC 101 *mm*	43	42	85
mm x F_1 *Mm*	28	27	55
do.	16	18	34
do.	19	20	39
Total observed	106	107	213
Expected 1:1 ratio	106.5	106.5	213
Deviation from expectation	0.5	0.5	
X2	0.0023		
Probability	0.0047		

First Backcross Generation and F_3 Lines

The monohybrid type of segregation was apparent also when F_1 hybrids were crossed back to the recessive monogerm parent SLC 101 (Table 3). The segregation for type of fruits in h_x backcross populations gave results close to the 1:1 monohybrid ration.

In 19 F_3 lines, derived from selfing monogerm F_2 plants from hybrids between SLC 101 and multigerm beets, about 400 plants were produced in 1951. All of these F_3 plants appeared to be monogerm. This indicates that the monogerm character is caused by one recessive gene in the homozygous condition *(mm)* (10).

Genes Which Modify the Effect of the Basic Gene *m*

The different number of flowers per flower cluster in different F_1 hybrid combinations indicates that some other genes take part in the development of multigerm seedballs besides the gene which is responsible for the monogerm character. Some homozygous monogerm *mm* plants in the F_2 generation produced a few double-germ fruits on the basal part of the main floral axis just above the lateral branches. Sometimes solitary double-germ fruits were observed on the basal part of some lateral branches while other branches produced only monogerm fruits.

Population studies of the F_2, F_3 and the first backcross generation showed that in many cases the appearance of the few double fruits is caused by genes which modify the action of the basic *m* gene.

From 201 monogerm plants derived as F_2 segregates at Salt Lake City in 1951 (Table 4), 65 plants or 32.3 percent developed such solitary double-germ fruits. A few solitary double fruits were also observed on 29.7 percent of the monogerm plants grown in the greenhouse during 1950 and 1951.

Segregation of these modifying genes is distinct from the segregation of the basic *m* gene. The percentage of monogerm segregates carrying the basic *m* gene is always very close in different F_2 families and approaches the expected 3:1 ratio. The percentage of monogerm segregates with a few double-germ flowers is irregular in different F_2 progenies. Hybrids receive the genes modifying the action of the basic *m* gene from the genotype of the multigerm parent. Therefore in some hybrids monogerm plants in the

F_2 generation develop very few of the solitary double-germ fruits or none at all. In other F_2 families 30 to 70 percent of the monogerm plants produced a few double fruits.

The F_2 segregates which were absolutely pure for monogerm seed and monogerm segregates with a few double-germ fruits produced different F_3 lines after selfing. From 28 F_3 lines derived from pure monogerm F_2 plants about 400 offspring were grown, all of which appeared to be pure monogerm. From 11 F_3 lines, derived from monogerm F_2 plants bearing a few double-germ fruits, about 150 plants were grown of which 31.81 percent bore some double-germ fruits. The total percentage of these double-germ fruits on monogerm plants was never high. Usually there were not more than about two to five doubles per 1,000 monogerm fruits. It is highly probable that the action of the basic *m* gene is modified by other genes with less influences. In some cases these modifying genes are dominant and in other cases recessive. Special crosses have been made to study this question.

Table 4.—Differences Between F2 Populations Concerning Development of a Few Double-germ Fruits on Homozygous Monogerm *mm* Plants.

Origin of F_2 hybrids	Classification of offspring: Monogerm plants bearing double-germ fruits		Pure *monogerm*	Total *mm* plants	Multi-germ plants	Total plants
	Percent	Number	Number	Number	Number	Number
F_3 hybrids in which most monogerm plants did not bear double-germ fruits						
Oberndorf x SLC 101	0.0	....	11	11	32	43
Peragis x SLC 101	0.0	..	6	6	15	21
SL 92 x SLC 101	0.0		10	10	19	29
SL 92 x SLC 101	7.14	1	13	14	51	65
SLC 100 x SLC 101	11.11	1	8	9	31	40
LSR sugar beet x SLC 101	12.50	1	7	8	31	39
Mammoth x SLC 101	16.67	1	5	6	15	21
Barrès x SLC 101	18.18	2	9	11	26	37
Total		6	69	75	220	295
F_2 hybrids in which many monogerm plants produced a few double-germ fruits						
SL 92 x SLC 101	27.27	3	8	11	29	40
Swiss chard x SLC 101	33.33	3	6	9	24	33
Egyptian x SLC 101	33.33	4	8	12	29	41
Clone 4 x SLC 101	38.47	5	8	13	29	42
SL 92 x SLC 107	45.45	5	6	11	21	33
Red table beet x SLC 101	46.15	6	7	13	42	55
Ovana x SLC 101	50.00	7	7	14	47	61
SL 941 x SLC 101	52.00	13	12	25	62	87
Klein E x SLC 101	72.22	13	5	18	49	67
Total		59	67	126	352	457

The monogerm character was found to be clear-cut and constant, whereas the secondary character with regard to development of a few double-germ fruits was highly variable. Some F_2 monogerm plants like the original monogerm beet SLC 101 developed fasciated floral axes. These fasciated floral axes often bear phenotypic double-germ fruits, double-germ fruits with two bracts, single flowers with a sepal number higher than five, or monogerm fruits with two bracts. Monogerm F_2 plants as well as monogerm plants from the inbred line SLC 101 may show these abnormalities and may pro-

duce pure monogerm progenies in which some plants may develop the same abnormalities caused by fasciation.

Linkage Between a Gene for Late-Bolting Tendency and the Gene *m*

Monogerm inbred lines derived from SLC 101 and SLC 107 are very late bolting. They usually started to flower 15 to 20 days later than ordinary sugar beets. The original monogerm plants from which SLC 101 and SLC 107 were derived (Table 5) were also late bolting. When found in Oregon they were only in blossom when the seed crop for the variety Michigan Hybrid 18 was ripe and ready for harvest. The monogerm beet seed would have been lost if this seed crop had been harvested by the usual harvesting machinery. The concentration of genes responsible for the monogerm character is very low in populations of sugar-beet varieties because of elimination of late-bolting plants by natural and artificial selection. This explains the scarcity of monogerm mutants in beet populations and the difficulty of their discovery.

When SLC 101 was crossed with ordinary sugar beets, some very late-bolting plants appeared in F_2 which with usual storage conditions did not bolt even the second year. To avoid the appearance of non-flowering plants, all F_1 and F_2 hybrids and their parents were exposed to very prolonged thermal induction. Through the advice from Dr. F. V. Owen, all potted plants were placed in the cold frame for the entire winter. After this prolonged low-temperature treatment with plants held in the cold frame, all F_1 and F_2 plants developed seedstalks within 30 to 50 days. The F_1 hybrids, in spite of the large genetic diversity of their multigerm parents and their derivation from various crosses with different varieties of sugar beets, fodder beets and red table beets with the monogerm self-fertile line SLC 101 flowered

Table 5.—Linkage Intensities in Fa and Backcross Populations for Genes Responsible for Type of Fruit and Earliness of Flowering, Salt Lake City, 1950 and 1951.

Year	Classification of offspring					
	Multigerm		Monogerm			
	Early	Late	Early	Late	Total	Crossing over[1]
	Number	Number	Number	Number	Number	Percent
			F_2 Populations			
1950 Observed	215	44	37	56	352	
Expected 9:3:3:1	198	66	66	22	352	
						25.3 ± 1.86
1951 Observed	586	61	79	86	612	
Expected 9:3:3:1	344.25	114.25	114.25	38.25	612	
						25.8 ± 1.45
	Population from First Backcross Generation					
1951 Observed	30	14	15	26	85	
Expected 1:1:1:1	21.25	21.25	21.25	21.25	85	
						34.2 ± 3.46

[1] Crossing over calculated from Immer's product method (2).

at the same time as ordinary multigerm varieties and significantly earlier than the monogerm line SLC 101 (Figure 1) .

In the F_2 generation both multigerm and monogerm segregates showed great variability in time of flowering (Figure 2) , but most of the multigerm plants flowered earlier than the monogerm plants. A few F_2 multigerm

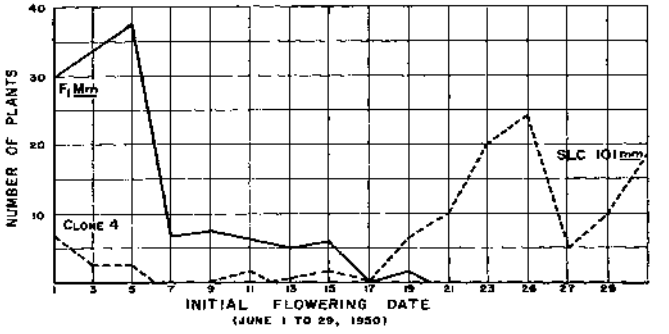

Figure 1.

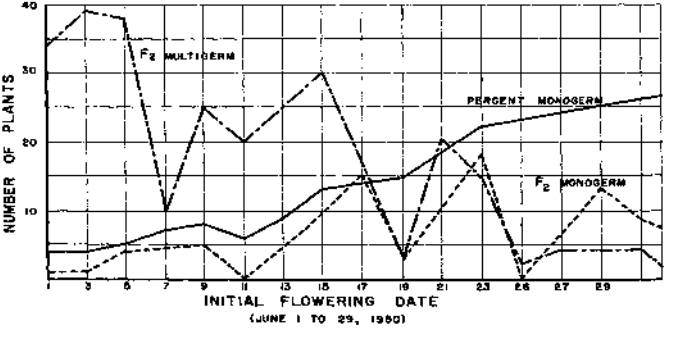

Figure 2.

segregates flowered very late. The majority of the monogerm F_2 **plants** flowered late and only a small proportion of these flowered early (Figure 2). The F_2 offspring were classified into four classes: multigerm early, multigerm late, monogerm early and monogerm late (Table 5). Assuming an independent single dominant gene for early flowering, the expected and observed number of plants did not coincide in all four classes. The parental classes, multigerm early and monogerm late, were in considerable excess. The two new classes, multigerm late and monogerm early, accounted for by genie recombination, contained fewer plants than expected. Therefore, the monogerm character is linked with a gene responsible for a late-bolting tendency and late flowering. The linkage intensity in F_2 was calculated to be 25.3 ± 1.86 percent for a field experiment in 1950 and 25.8 ± 1.43 percent in 1951. The linkage intensity for a backcross population was calculated to be 34.2 ± 3.46 percent for a test in the greenhouse (Table 5) (3,4).

A similar linkage was observed in hybrids between monogerm beets and an annual beet from California which grows wild near San Jose. When F_2 hybrid seed from the cross, multigerm California annual beet x monogerm SLC 101, was planted June 21 at Salt Lake City, some of the annual plants started to bolt in July. But most of these early bolters were multigerm and by August 25 only five percent of them appeared to be monogerm. Then the percentage of monogerm plants increased gradually, reaching 10.3 percent at the end of October. The enormous deficiency of mono germ plants by October indicates that most of the potential monogerm segregates did not flower during the first year. Unpublished results obtained by F. V. Owen indicate that the late-bolting tendency in SLC 101 is not allelic to the gene *B* for bolting described by Abegg (1, 5, 6) and obtained from Munerati's annual beet, but by another allelomorph which is directly related with bolting tendency in biennial beets. The inbred line SLC 101 represents a very valuable breeding stock for development of non-bolting varieties for such areas as California where fall or winter plantings are made for commercial sugar beet production.

Summary

When the monogerm race SLC 101 was crossed with multigerm beets, the multigerm character was dominant in F_t hybrids, but the dominance was not complete. In F_2 populations derived from hybridization of SLC 101 with multigerm sugar beets, red table beets, fodder beets and Swiss chard, a 3:1 ratio was observed for segregates with multigerm versus monogerm fruits.

The monogerm character is produced by one recessive basic gene in the homozygous *mm* condition. Some other genes may modify the manifestation of the gene m causing the appearance of a few double-germ fruits on the monogerm plants.

Gene m was linked with a gene causing late-bolting tendency. The linkage intensity in F, was calculated to be 25.3 ± 1.86 in 1950 and 25.8 ± 1.43 in 1951.

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