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A BASIC GENE FOR MONO-GERM CHARACTER IN BEETS[1)]

By

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Introduction

It must be borne in mind that the so-called "beet seed" is in reality a fruit. The parts of the several flowers of beets stick together forming a flower cluster which develops into a several-seeded mass, the "seed ball or multi-germ seed." But if the flower stands by itself on the stem, the "mono-germ" seed is produced. Thus the multi-germ seed consists of several one-seeded fruits, and the mono-germ seed of one one-seeded fruit (Figure 1).

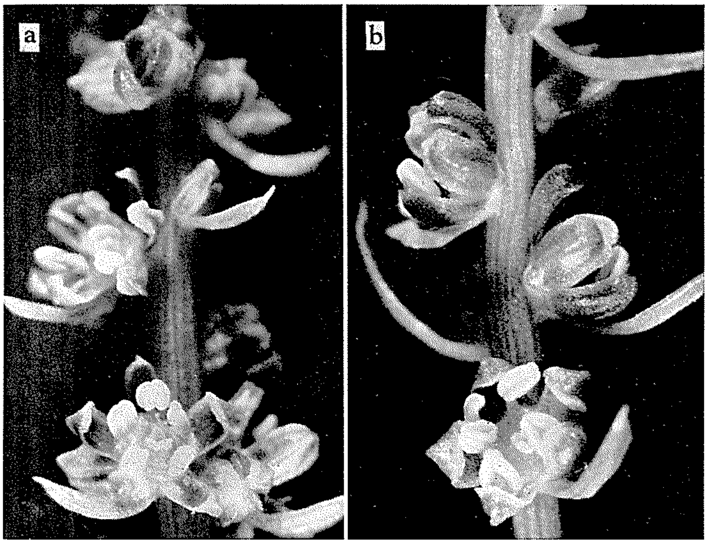

Fig. 1. Flower clusters of multi- and mono-germ sugar beets.
a, multi-germ; b, mono-germ.

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1) Contribution from the Plant Breeding Institute, Faculty of Agriculture, Hokkaido University, Sapporo, Japan.

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There have been studies having to do with the relative value of mono- and multi-germ beet seeds which show that mono-germ seeds are promising, not only in that they do much for labor saving in seeding and thinning work, but also in that they show superiority in the size of the germs themselves (Figure 2).

The first finding out of heritable mono-germ sugar beets was in the U.S.A. and U.S.S.R., about twelves years ago. This character is now being utilized in breeding work with sugar, fodder and table beets (SAVITSKY 1950, 1952, OWEN & RYSER 1959 etc.). Although no definitive explanation on the genic scheme of this character has been proposed, an explanation by SAVITSKY, the finder of this character from U.S. varieties, is generally accepted: that a single basic gene plays an important role and that the mono-germ is the phenotypic expression of homozygous recessive state of the causal gene, *mm* (SAVITSKY 1952).

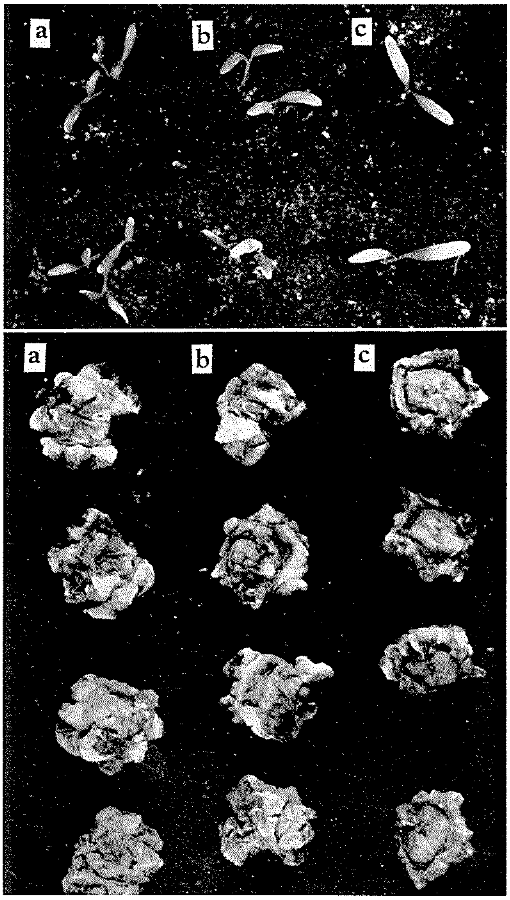

Fig. 2. Comparison of size in seeds and seedlings.
a, tetra- or tri-germ; b, di-germ; c, mono-germ

The present paper is an outlined report of inheritance on this character transfered to some Japanese varieties and is limited to a confirmation of a basic gene postulated by SAVITSKY and co-workers.

Material and Methods

In 1955, nine sugar beet plants with typical "di-germ" flower clusters were grown together in the same field and their seeds were harvested separately. From these seeds nine mother lines were produced in the following year and their segregation modes on germ types were examined.[1] In every population,

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[1] The term "germ type" in the present paper is to mean the group of germs per flower cluster.

segregation of mono-, di- and tri-germ plants was formed in a ratio of approximately 1 : 2 : 1, respectively (Table 1). Segregates with multi-germ flower clusters were discarded before pollen shedding and the rest, that is segregates with monogerm clusters, were reserved for the following selfing and sib-mating. After additional breeding procedure of selfing and sib-mating in a two generation, several mono-germ strains, designated as m-1-1~m-2-8, were produced. Among them, the strain m-2-8 carried a cytoplasmic male-sterility character which character was of use for enforcing hybridization on a large scale in the present experiment.

TABLE 1. Segregation for germ type in progenies from di-germ beets

strain No.	germ type			total
	tri	di	mono	
m-1	1	11	6	18
m-2	3	8	4	15
m-3	5	15	1	21
m-4	5	7	6	18
m-5	5	8	2	15
total	19	49	19	87
C (1: 2 : 1)	21.75	43.50	21.75	87.00

$\chi^2 = 1.391$ d.f. = 2 p = 0.30–0.20

Five mono-germ strains were crossed with two multi-germ varieties from sugar beets, Hon-iku-192, and from table beets, Detroit dark red. Observation was carried out in F_1, F_2 and B_1 of each cross combination.

Experimental Results

A. Segregation Mode

Germ types of P_1s and their F_1s are as shown in Table 2. In this table it is pointed out that F_1s were multi-germ, and that the dominance was not complete, showing the range from di- to tri-germ in contrast with the range of di- to tetra-germ in their P_1s.

Seeds obtained from F_1s from selfing and sib-mating under paper bags were planted as separate progenies, viz. F_2 populations. In F_2s, there appeared all grades of germ types, ranging from mono- to tetra-germ; however, in all cross combinations, regardless of whether the F_2s were from selfing or sib-mating, the frequency of mono-germ segregates was found to be close to 25

TABLE 2. F_1s from mono-germ × multi-germ

	cross combination			germ type				total
	cross No.	♀ (mono)	♂ (multi)	tetra	tri	di	mono	
P_1		M-19 MS (m-1, m-2)					53	53
			Hon-iku-192 (192)	25	55	2		82
			Table beet (T)[1]	8	31	15		54
F_1	'56-94	m-1-3	192-2		7	5		12
	'56-106	m-2-8	192-5		1	6		7
	'57-34	m-2-1	192-1			6		6
	'57-35	〃	192-2		1	5		6
	'57-41	m-2-7	192-6			6		6
	'56-107	m-2-8	T-3		1	5		6
	'57-36	m-2-1	T-1			3		3
	'57-37	〃	T-2		6	10		16
	'57-43	m-2-7	T-1	1	10	5		16
	'57-44	〃	T-3		3	9		12
	'57-45	〃	T-4		6	2		8
	'57-46	〃	T-5		3	2		5
	'57-50	SLC-3[2]	〃		10	10		20

1) Variety name:—Detroit dark red.

2) A newly introduced mono-germ strain of sugar beets.

percent, when the germ type was classed into two groups, mono- vs. multi-germ (Table 3). This indicates the possibility that the expression of the mono-germ character is mostly connected with a single Mendelian gene.

To ascertain the monohybrid type of inheritance, F_1s from two cross combinations were crossed back to their respective mono-germ parents. The segregation mode of B_1s from one combination came up to the authors' expectation, segregating as multi-germ : mono-germ = 1 : 1. In the other combination, however, the segregation mode was not a close fit to the ratio of 1 : 1, but was closer to the relation 3 : 1, which is a ratio in which two pairs of duplicate genes are concerned and in which the double recessive genotype causes the character expression of mono-germ (Table 4).

Thus, by the experimental results of B_1 generation no verification of the correctness of the mono-genic scheme was obtained, however, the majority of the segregation modes in F_2 and B_1 generations lead the authors to the opinion

TABL 3. F_2 segregations from the crosses mentioned in Table 2

cross combination		germ type					goodness of fit		
		tetra	tri	di	mono	total	χ^2	d.f.	p
'56-106	-1	9	105	51	42	207			
	-2	1	22	15	12	50			
	-3	6	33	13	14	66			
	total	16	160	79	68	323			
	0	255			68	323			
	C (3:1)	(237.25)			(85.75)	(323.00)	2.684	1	0.20-0.10
'56-107	total	3	104	138	68	313			
	0	245			68	313			
	C (3:1)	(234.75)			(78.25)	(313.00)	1.790	1	0.20-0.10
'57-37	total	3	37	6	11	57			
	0	46			11	57			
	C (3:1)	(42.75)			(14.25)	(57.00)	0.988	1	0.50-0.30

$\sum\chi_i^2 = 5.642$ d.f. = 3 p = 0.20-0.10

TABLE 4. Segregations from mono × (mono- × di-germ)

cross combination	germ type					goodness of fit		
	tetra	tri	di	mono	total	χ^2	d.f.	p
H-19 MS '56-106 F_1-6		5	11	16	32			
0		16		16	32			
C (1:1)		(16.00)		(16.00)	(32.00)	0		
H-19 MS '56-106 F_1-4		10	19	12	41			
0		29		12	41			
C (1:1)		(20.5)		(20.5)	(41.0)	7.049	1	<0.01
C (3:1)		(30.75)		(10.25)	(41.00)	0.397	1	0.70-0.50

that in respect to germ type, at least, a single basic gene may be concerned and that the phenotypic expression of "mono-germ" seems to be caused by the recessive homozygous state of the basic gene.

With regard to germ numbers per cluster in the multi-germ segregates of F_2s in Table 1 and 2, it is noteworthy that plants with maximum germ number were found in F_2s of Table 3, and then that the frequency of highly multi-germ F_2 plants was relatively high in Table 3, when it was compared with that of highly multi-germ segregates in Table 1. A similar tendency was also observed in the comparison of two kind of plants, between the introductory di-germ plants and the F_1s in Table 2. Thus, it may follow from this fact that the different germ number per cluster was observed in either different F_1 combinations or their derived multi-germ segregates in F_2.

In this connection, the reports by SAVITSKY (1954 a, 1958) and BUROCKA (1960) are worthy of consideration. According to SAVITSKY's opinion, some modifiers may take part in the development of multi-germ besides the basic gene, and/or, the basic gene may consist of multiple alleles which are responsible for expression of several grades of germ type, from highly multiple- to typical mono-germ. However, in applying this explanation to the authors' data, further detailed examinations should be conducted.

Therefore, at present, the authors will only give the following interpretation, that the mono-germ character is produced by, at least, one recessive basic gene in the homozygous state. After SAVITSKY's gene symbol, this gene is designated as "*m*".

B. Linkage and Correlation

Analysing the genotype of the mono-germ, and recovering linked genes will facilitate the breeding of mono-germ varieties. Linkage or correlation between mono-germ and some other accompanying character such as late-bolting tendency, male sterility, sucrose contents, and type of branching and leaf development have been reported by some workers (SAVITSKY 1950, 1952, SAVITSKY & RYSER 1954 c, HOGABOAM 1957).

In the present experiment of the authors, a linkage between the gene for mono-germ and a gene for male sterility was confirmed, together with a character correlation between germ type and fasciation tendency.

Of male sterility, detailed accounts on analyzing causal genes, being not the principal subject on the present paper, are abridged here, however, as the conclusive but brief statement it was ascertained that this character was controlled by the same type of genes which had been reported by OWEN (1945), HOGABOAM (1957) or KNAPP (1955). Adapting OWEN's gene symbols, the present genes are *S* (sterile plasma), *X* (a chromo-gene for restoration of pollen fertility in sterile cytoplasma by *S*) and *Z* (same as *X*); and the genic constitution of the completely male-sterile, the semi-male-sterile and the fertile are postulated as *Sxxzz*, *SXxzz* (and *SxxZz*, *SXxZz*) and *N* (*N*-plasma; irrespective of *X* and *Z* loci), respectively (NAGAO, TAKAHASHI & KINOSHITA 1960).

The genotypes of the parents of the cross from which a linkage was found out, were considered to be (♀) *Sxxzzmm* and (♂) *NXXZZMM*. As shown in Table 5, the result of F_2 segregation indicates a possible linkage between *m* and *x* or *m* and *z*, with a recombination value of 21.7±5.6%.

TABLE 5. Linkage between genes responsible for mono-germ (*m*) and male sterility (*x*)

F_2 from'56-107: m-2-8 (complete sterile)×192-5

germ type	multi (tetra-di) germ		mono-germ		total
male sterility	normal to semi-male-sterile	complete male-sterile	normal to semi-male-sterile	complete male-sterile	
0	156	9	32	10	207
C (R.C.V. 21.7%)	(150.24)	(5.01)	(43.82)	(7.93)	(207.00)

Recombination value (R.C.V.) 21.7 5.58%

$\chi^2 = 7.134$ d.f. = 3 p = 0.10–0.05

	d.f.	χ^2	p
segregation of multi- vs. mono-germ. (3:1)	1	2.449	0.20–0.10
segregation of normal semi-male-sterile vs. complete-sterile. (15:1)	1	3.030	0.10–0.05
combined segregation	1	15.097	<0.01
total	3	20.576	

TABLE 6. Character correlation between mono-germ and fasciation tendency of stems

F_2 from '56-107: m-2-8×T-3

	germ type				total
	tetra	tri	di	mono	
normal	2	64	85	23	174
fasciated			2	18	20
total	2	64	87	41	194
0	153			41	194
C (3:1)	(145.50)			(48.50)	(194.00)

However, further tests are needed to determine which of the genes, *x* or *z*, is linked with *m*; the linkage between *m* and *x*, that is *M* and *X*, is considered to be more reasonable, because a linkage of *m* and *x* has already been suggested by HOGABOAM (1957), even though the linkage intensity calculated by him was rather weak (37.5%).

With regard to character correlation, the authors have recognized a remarkable association between the mono-germ and fasciation tendency of stems, on which examination results are given in Table 6 and Figure 3.

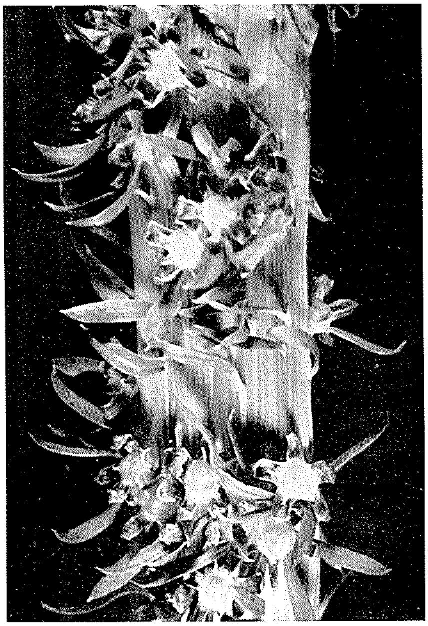

Fig. 3. Fasciated stem with mono-germ fruit clusters.

C. Size of Seedling

In order to clarify the relation between seedling size and germ type, fruits from open pollinated F_2 plants of these crosses were harvested separately by individuals and seeded in the design of split plots.

As presented in Figure 4, throughout all cross combinations, mono-germ seedlings had larger cotyledons than multigerm seedlings from the same cross had. In an average the cotyledon length of the mono-germ was 13% and 22% longer than that of the di-germ and tri-germ respectively, showing that the size of cotyledons increases in inverse proportion to the number of germs per fruit cluster.

The initial advantage of the mono-germ seed in weight has been already recognized by SAVITSKY (1954 a), and therefore it is natural to conclude that good growth of seedlings is mainly resulted from the increase in size of the germs themselves.

Summary

1. In crosses of mono-germ sugar beets with multi-germ type of sugar and table beets, their F_1s were multi-germ, but the dominance was not complete.
2. In F_2 from these crosses, a 3 : 1 ratio was observed for segregates

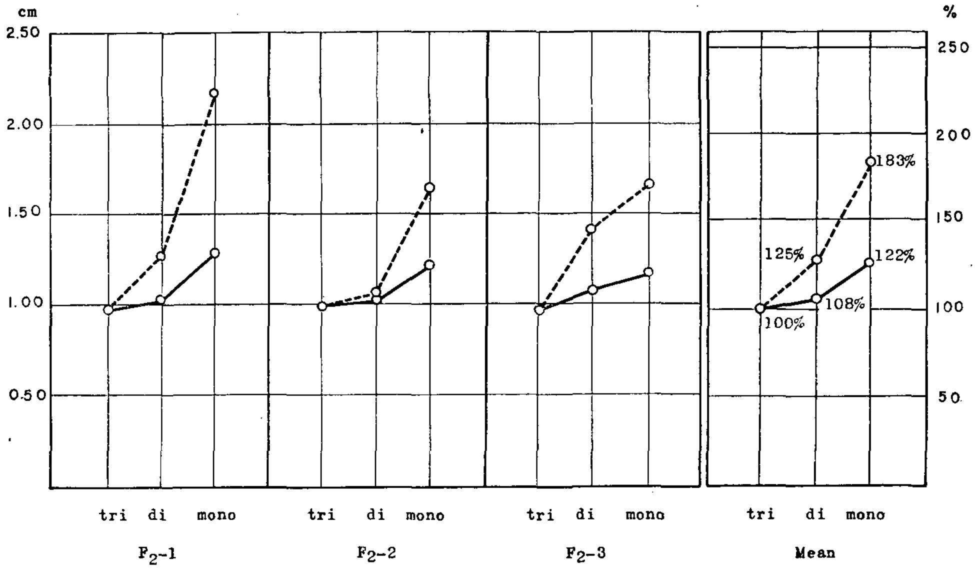

Fig. 4. Comparison of cotyledon size from tri-, di- and mono-germ segregates in F_2 of crosses, '56–106 in Table 3.

a, tri-germ; b, di-germ; c, mono-germ

Unbroken line; length of cotyledon in cm. Broken line; estimated volume (length^3) of cotyledon.

F-test of length:

germ type (tri~mono) $F=12.04$ $(F_{0.01}=6.01)$

cross combination (F_2–1~F_2–3) $F=1.08$ $(F_{0.01}=10.92)$

germ type×cross combi. $F=1.52$ $(F_{0.01}=4.58)$

with multi-germ vs. mono-germ type. The mono-germ character is mainly caused by one recessive basic gene in a genotype of *mm*.

3. Besides this gene, there remain some possibilities of the existence of some other alleles or genes which control the number of germs per cluster in the multi-germ.

4. A gene *m* is linked with one of the genes which are responsible for restoration of pollen fertility, in the intensity of about 21% recombination value.

5. Character correlation was also observed between germ type and fasciation tendency of stems.

6. Seedlings from mono-germ fruits show remarkable increase in their size, and thus it will be possible to combine high stand number with good growth of plants.

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