Mendelian Male Sterility in Sugar Beets

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Introduction

Mendelianly inherited, or genie, male sterility in sugar beets offers different opportunities from those of cytoplasmic male sterility. Whereas the cytoplasmically inherited male sterility may be used to effect wholesale emasculation of entire populations (7)[2], and is useful for large-scale hybridization work, the Mendelian recessive gene is of more interest to the breeder in the intermediate steps of a breeding program. A point of importance is to recognize the wide occurrence of recessive genes for male sterility and to distinguish the Mendelian from the cytoplasmic type of inheritance.

To simplify terminology the recessive gene is designated *a* for abortion of pollen. From experience with other plants (3 and 9) several genes having somewhat similar effects on pollen abortion may be expected. This paper reports two different genes which are designated a_1 and a_2.

Mendelian Versus Cytoplasmic Inheritance

The anthers of the Mendelian male-sterile beets are usually smaller and more poorly developed than the anthers of the cytoplasmic male steriles. Artschwager (2) found that the microspores break down at an earlier stage in one case of Mendelian male sterility which he studied. Observations under a hand lens or low-power binocular usually make identification possible, but variations may be expected. There are particularly wide variations in case of the cytoplasm inheritance both in anther size and color and there are some variations in case of the Mendelian inheritance. Therefore, progeny tests constitute the most reliable diagnosis. When new male-sterile beets appear much can generally be learned regarding the inheritance by a progeny test from seed of individual plants harvested separately.

When Mendelian inheritance is encountered and *aa* beets are open pollinated, the offspring are all normal pollen producers, except when there are also heterozygotes in the parental population. A high-sugar selection (SL 824) from the curly-top-resistant variety U. S. 22/3 was found to be segregating for male sterility of the Mendelian type. Offspring from one open-pollinated *aa* beet produced 96 percent normal pollen producers and 4 percent male steriles, indicating a frequency of gene *a* in the parental population of about 4 percent.

In case of the cytoplasmically inherited male sterility, offspring grown from open-pollinated male-sterile beets are often 50 percent completely male sterile. A considerable percentage of semi-male steriles is also commonly observed and these constitute a relatively sure diagnosis of the cytoplasmic inheritance. Usually the percentage of normal pollen producers is relatively low but there are exceptions, depending upon the makeup of the parental populations.

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[2] Numbers in parentheses refer to literature cited.

No obvious association has been found in the inheritance of the genie or Mendelian male sterility and the cytoplasmic male sterility. Neither has any association been found between the gene a_1 for abortion of pollen and the genes tentatively designated *x* and z (7) which have a modifying effect on the cytoplasmic male sterility. Recessive a_1a_1 male steriles crossed to reliable type O, *Nxxzz*, pollinators (7) produced F, offspring all of which bore normal pollen. Selfing these heterozygous F_t plants produced F_2 populations which gave the usual 3:1 segregation for normal pollen producers and male steriles.

With cytoplasmic inheritance for which S cytoplasm is responsible, Mendelian segregation may be observed to some extent. *S X x* beets may bear more or less normal pollen and may be self-pollinated if they also carry a gene for self-fertility. However, the writer's experience has been that these F_2 populations do not give, clearcut 3:1 ratios and many intermediate or semi-male-sterile types appear. Whatever the cause of these intermediate types may be, they usually constitute a clear indication of the cytoplasmic inheritance. It may be that eventually isogenic populations can be produced in which self-pollination of S X *x* beets will produce populations with clearcut 3:1 segregation.

Table 1.—Backcross Populations, Identifying Different Sources of the Gene *ai*for Abortion of Pollen.

Population number	Classification of offspring: Normal	Male sterile	Total	♀	♂
4533	19	11	30	Inbred 2668	Annual 841-1
4554	10	14	24	Inbred 2668	Annual 841-1
5618	32	34	66	Annual 841-1	Inbred 2668
5619	26	21	47	Annual 841-1	Inbred 2668
5621	15	21	36	Annual 841-1	Inbred 2668
5622	24	19	43	Annual 841-1	Inbred 2668
5624	8	16	24	Annual 841-1	Inbred 2668
6850	44	49	93	Annual 841-1	Inbred 2668
6836	29	24	53	Annual 841-1	Annual 841-4
7700	21	17	38	X-rayed 3700-1	Annual 841-1
7701	29	23	52	X-rayed 3700-2	Annual 841-1
7703	31	28	59	X-rayed 3700-4	Annual 841-1
9435	9	7	16	Inbred 8T9.19	Annual 841-1
9439	9	8	17	Inbred 8T9.19	Inbred 5201
9440	6	12	18	Inbred 8T9.19	Inbred 5201
9441	15	8	23	Inbred 8T9.19	Inbred 5201
0.402	48	57	105	Inbred 5201	Annual 841-1
1.414	10	6	16	Inbred 5201	Annual 01480-4
Totals	375	385	760		
1.1 ratio	380	380	760		

The Gene a_x From Different Sources

The recessive gene a_x for abortion of pollen was first identified in Munerati's annual beet (1) population number 841. From this race the gene was identified in progeny from beet No. 1 in 1945 (Table 1). In 1946 the same gene was identified in progeny from beet No. 4. In 1951 the same gene was identified in a new population, 04480, of the same annual beet. The parentage of population 04480 had been carried three years

without any sign of male sterility, so it is assumed that its appearance in the offspring in 1951 represents a new mutation. Additional male steriles have appeared in other populations from this annual beet and may have been due to the same gene but progeny tests would be required for a definite answer.

Seed from Munerati's annual beet, which arose from progenies which had been X-rayed at the University of Missouri, was received in 1943 from Dr. Luther Smith. In this material 21 percent of the plants were observed to show male sterility, a much higher percentage than that observed in previous populations. The X-ray treatment may have been responsible for new mutations. Test crosses (Table 1) with beets taken from the X-rayed material indicated the presence of the same identical *gene* a_1 as observed in previous material.

Table 2.—F_2 Data

Population number	Classification of offspring: Normal	Male sterile	Total	X^2
3851	113	29	142	1.6
4535	69	10	79	6.4
4536	76	23	99	0.2
4855	18	8	26	0.6
4856	43	9	52	1.6
4858	146	52	198	0.2
4859	110	28	138	1.6
5850	51	14	65	0.4
6839	55	17	73	0.1
7709	24	8	32	0
7710	11	3	14	0.1
02.13	120	40	160	0
	5% point of probability			3.8
	1% point of probability			6.6

Observations of inbred lines showed that the appearance of occasional male-sterile beets was a common phenomenon. Progeny from male-sterile beets taken from three entirely separate lines (Table 1) gave good 1:1 ratios in hybrids to known pollinators heterozygous for a_1, which is proof that the gene a_1 was responsible for all these cases of male sterility from the widely separated sources. The 1:1 ratios shown in Table 1 would not be possible if a different gene were involved.

A Second Gene a_2

In 1948 open-pollinated seed from a single male-sterile beet was furnished by Dr. Sidney Ellerton from England. The offspring grown from this seed were all completely normal pollen producers, indicating that the inheritance was of the Mendelian type instead of the cytoplasmic type. However, test crosses made in 1950 and observed in 1951 showed that a new gene, a_2, must be involved.

Examination of Genetic Ratios

Table 1 lists 18 different backcross populations which segregated for the gene a_1. The observed results in each of these populations were com-

pared with expected 1:1 ratios by using Mather's method (6). No highly significant deviations from expected 1:1 ratios were observed.

Table 2 shows F_2 data from 12 different populations. With one exception, the observed results agree well with expected 3:1 ratios. A poor 3:1 ratio of normals to male steriles is shown for population 4535. Here the deviation from expectancy represents the 1 percent point of probability.

Linkage Tests

Previous studies (8) have shown only one well-established linkage group in beets. The gene *R* for red hypocotyl color was found to be linked with several other genes, including the gene *Tr* for trout or spotted leaves. Table 3 shows results with one backcross population which indicates no linkage between the gene *R* and the gene a_1. Three backcross populations failed to show linkage between the genes *Tr* and a_1. These results indicate that the gene a_x is not located in the same linkage group with *R* and *Tr*.

A test for linkage between the gene a_1 for pollen abortion and the recessive gene *m* for the monogerm character (10) is shown in Table 3. In an F_2 population of 160 plants there is no evidence of linkage between these two genes.

Table 3.—Linkage Tests Between Gene a_1 for Abortion of Pollen and the Color Genes *R* and *Tr* and the Gene *m* for Monogerm Character.

Population number	Designations[1]			Classification of offspring				
	X	x	y	XY	xY	Xy	xy	Total
			Backcross populations					
6850	R	r	a_1	22	22	25	24	93
6836	Tr	tr	a_1	19	10	13	11	53
7700	Tr	tr	a_1	9	12	9	8	38
7701	Tr	tr	a_1	16	15	11	12	52
			Total	66	57	58	55	236
			Expected	59	59	59	59	236
			F_2 population					
02.13	M	m	a_1	85	35	32	8	160
			Expected	90	30	30	10	160

[1] Genie designations are as follows:
R = Red hypocotyl and crown color
r = recessive to *R*
Tr = Trout leaf (closely linked to *R)*
tr = recessive of *Tr*
M = multigerm
m = monogerm (independent of *R)*

Discussion

As more attention is given to developing inbred lines of sugar beets it will be more and more important to give serious consideration to the genetic principles involved and to learn as much as possible from experience with other plants, including naturally self-fertile plants. During the process of inbreeding the breeder automatically narrows the base of the germ plasm. This makes it necessary from time to time to make outcrosses to incorporate new genes. Fisher (5) has discussed the advantages of maintaining heterozygosity for a few selected genes during the process of inbreeding. This involves the production of larger populations than can conveniently be

obtained by artificial emasculation. Therefore, Mendelian male sterility should be an invaluable tool in accomplishing the desired heterozygosity in self-fertile inbred lines of beets.

The utilization of a backcross procedure in convergent improvement work in self-fertile crop plants, as advocated by Briggs (4), offers many advantages. As homozygosity is approached in successive backcrosses, the important gene or genes which are being transferred from one line to another are subjected to more careful study than they receive in any other way. The method is particularly applicable to the genetic study of disease resistance and for the practical production of disease-resistant varieties.

To facilitate future work, the gene a_1 for abortion of pollen has been retained or introduced into several curly-top-resistant inbred lines of beets, including some monogerm lines. Now, in addition to using a gene for pollen abortion, the possibility of utilizing the gene *B* for bolting or annual habit is also being investigated. With the gene *B* present, thermal induction is no longer necessary and three or four generations can be grown in a single year under warm temperatures and continuous illumination. After the desired degree of homozygosity has been reached in successive backcrosses and the desired gene or genes have been transferred from the non-recurrent parent to the recurrent parent, genes *B* for bolting and *a* for abortion of pollen may be eliminated by selfing. No injury should result to the final inbred by carrying gene *B* for bolting up to the last backcross operation. So long as the bolting or annual habit is produced by a single gene and segregation is clearcut, this should not influence the bolting tendency of the final inbred.

The gene a_1 for abortion of pollen is most useful if it can be found in the choicest inbreds without taking time to incorporate the gene. Evidence indicates that by a consistent search in populations of a few hundred plants this may often be possible. Male-sterile mutants have appeared in a wide variety of material. Whether the mutation rate is so high that the gene may be found in any inbred is a point of much interest which needs investigation.

Summary

A gene, designated a_1 for abortion of pollen, was identified in four widely different races of beets. A second gene a_2 was found in material obtained from Dr. Sidney Ellerton in England. No linkage was found between the gene a_1 and other genes tested which included the color genes *R* and *Tr* and the gene *m* for the monogerm character.

The recessive gene a_1 apparently bears no relation to previously described examples of cytoplasmic male sterility. In F_2 populations 3:1 ratios of normal to male-sterile beets were observed and in backcross populations the expected 1:1 ratios were obtained. The frequent occurrence of the gene a_1 in widely different sources of material, including one source which had been X-rayed, indicates a relatively high mutation rate.

Mendelian male sterility is useful for emasculation of individual plants in various genetic investigations and improvement programs, especially in

connection with convergent improvement of inbred lines or incorporation of desirable genes into established inbreds. To facilitate backcross operations, a suggestion is made that the gene *B*, for bolting or annual habit, may be used in connection with a gene *a* for abortion of pollen. In the final product genes *B* and *a* are both eliminated.

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