Inheritance Studies of a Pollen Restorer from Ruby Queen Table Beet

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In Owen’s (4) original extensive studies concerning the inheritance of cytoplasmic male sterility (CMS) in sugarbeet (Beta vulgaris L.), he found that strong pollen-restorer genes were scarce in curly-top resistant material. He noted that normal hermaphrodite beets crossed to CMS frequently segregated male-sterile, partial-fertile, and at times, fertile offspring, but there were no lines having 100% fertile progenies. He attributed this to the fact that these pollinator lines carried sterile rather than normal cytoplasm. Contrariwise, Bliss and Gabelman (1) reported that a single monogenic factor in the presence of sterile cytoplasm restored complete pollen fertility to sugarbeet × table beet material.

Theurer and Ryser (7) isolated an inbred from the sugarbeet variety US 201 that carried strong pollen fertility restorer factors (Rf). Genetic studies with this restorer indicated that two complementary genetic factors govern male sterility, which confirms Owen’s (4) original premise. However, interaction of other modifying genes and possibly cytoplasts, and the influence of environmental factors, were also evident. Progenies of NB-1 CMS, 129 CMS, and CT9 CMS lines crossed with the US 201 Rf differed greatly in their fertility (7). This we attributed mainly to the interaction of genetic modifying factors, rather than differences in cytoplasm. However, the cytoplasm also could have had an influence on the fertility of these populations.

Savitsky (5) suggested that different expressions of male sterility in sugarbeets were caused by different genes, which influence the cytoplasm as well as by different types of male-sterile cytoplasm.

Hogaboam (3) proposed that a dominant fertility factor Sh enhanced the pollen-producing ability of plants with heterozygous Xx genotypes and altered the phenotypic ratios one would expect on the basis of Owen’s complementary gene hypothesis.

1 Cooperative investigations of the Plant Science Research Division, Agricultural Research Service, U.S. Department of Agriculture; the Beet Sugar Development Foundation; and the Utah Agricultural Experiment Station. Approved as journal paper no 1069, Utah Agricultural Experiment Station, Logan, Utah.

2 Research Geneticist, Crops Research Division, Agricultural Research Service, U.S. Department of Agriculture, Crops Research Laboratory, Utah State University, Logan, Utah, 84321.

3 Numbers in parentheses refer to literature cited.
Stein et al. (6) observed reversion of CMS to partial-fertile plants which was not caused by environmental factors alone. They proposed that reversion was due to an accumulation of a diffusible fertility substance or the exhaustion of a sterility substance and not to segregation of particulate sterility factors.

The present study was instigated to determine the inheritance of pollen fertility restoration in crosses of the annual tester SLC 03 CMS and a pollen fertility restorer line derived from the Ruby Queen variety of table beet.

Materials and Methods

In 1961 F. V. Owen crossed SLC 03 CMS with plants of the Ruby Queen variety of table beet. The F₁ (56 plants) were all classified as completely pollen fertile. However, segregation in subsequent generations gave varied ratios. The F₂ offspring fit a 9:7 ratio with a probability of .90, suggesting that pollen fertility restoration was governed by two complementary genetic factors. However, the BC₁ yielded 59 fertile : 53 male sterile, which definitely would not support the two gene model. Selection of the most fertile plants from this material for four selfed generations resulted in increased fertility each generation and ultimately in a line that was 100% fertile. Each plant of this line had over 90% stainable pollen. This selection having pollen-restorer genes from Ruby Queen and sterile cytoplasm from SLC 03 CMS was crossed to SLC 03 CMS to determine the inheritance of pollen fertility restoration in uniform cytoplasm. F₁, F₂, and BC₁ populations were grown in a 70 F greenhouse. A sample of pollen or anthers was collected at anthesis from each plant. Fertility was determined by visual observation of anther color and pollen dehiscence and by microscopic observation of the percentage of aceto-carmine stained pollen.

Results and Discussion

The F₁ progenies of the SLC 03 CMS × Rf crosses were all fertile having good dehiscence and 50% or better stainable pollen (Table 1). Seed production averaged .5 grams per plant. The F₂ generation for eight families showed monogenic inheritance when plants were classified into pollen-producing plants versus white-anther male steriles. However, there was wide variability in the degree of fertility. The BC₁ populations segregated 1 male sterile : 1 fertile plant and gave excellent fit to the expected ratio. Fertility based on pollen dehiscence showed a similar inheritance pattern.

These results support those of Bliss and Gabelman (1) that table-beet cultivars carry a strong pollen-restorer gene. However, we did not observe clear-cut segregation for pollen fertility
Table I.—F1, F2, and BC1 segregation for pollen fertility in the cross SLC 03 CMS × Ruby Queen Rf.

<table>
<thead>
<tr>
<th>No. families</th>
<th>F</th>
<th>MS</th>
<th>P&lt;sup&gt;²&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>F1</td>
<td>—</td>
<td>262</td>
<td>0</td>
</tr>
<tr>
<td>F2</td>
<td>8</td>
<td>2303</td>
<td>774</td>
</tr>
<tr>
<td>BC1</td>
<td>8</td>
<td>767</td>
<td>719</td>
</tr>
</tbody>
</table>

* Probability based on chi-square for 3:1 and 1:1 ratios in the F2 and BC1 generations respectively.

and male sterility as they did, but still noted considerable plant to plant variation.

In the F2 about 74% of the pollen-producing plants were highly fertile (Figure 1). Some plants, however, had 10% or less stainable pollen. About 11% of the total plants were in the 50% fertile class resulting in a second fertility peak.

![Figure 1.—Variation in fertility of 2303 pollen fertile plants in the F2 generation of SLC 03 CMS × Ruby Queen Rf.](image)

In the BC1 generation similar results were observed (Figure 2). About 78% of the plants had over 70% stainable pollen. A second peak was again observed at 50% stainable pollen with 10% of the total pollen-producing plants falling in this category. Only 9% of the plants had lower than 50% stainable pollen.

This wide variation in the percent of stainable pollen was observed regardless of the fact that both parents should have had the same cytoplasm, and that every plant of the S<sub>1</sub> pollinator was 90% or more fertile.
The influence of environmental factors is one possible explanation for the inter-plant fertility variation. These factors are probably micro-environmental conditions that affect the physiology and development of pollen within the anther during microsporogenesis, rather than macro-environmental factors. In other research work we have not been able to demonstrate that this type of variation in the greenhouse was caused by any specific environmental factor, such as temperature, light, nutrition, etc., per se. The uniform fertility of the parents and the F₁ in Owen’s original cross and in our later cross of SLC 03 X Rf tends to discredit environment as a major cause for the variation observed in segregating generations. Variation in fertility could be attributed to minor modifier genes of the two parents that are masked in the F₁, but interact and express themselves in the F₂ and the BC₁ generations. Alternatively, the observed variation may be due to segregation of plasmagenes; to the reversion of S to N cytoplasm as hypothesized by Cleij (2), or to change in diffusible cellular constituents suggested by Stein et al. (6). Additional research is planned with this material to further study these possibilities.

Summary

1. A strong pollen-restorer gene derived from the Ruby Queen variety of table beet, shows monogenic inheritance with the annual tester SLC 03 CMS.

2. The widely used tester line, SLC 03 CMS, possibly carries minor modifier genes which influence the degree of pollen fertility when this line is crossed to the Ruby Queen Rf inbred.
3. Segregation of plasmagenes or the reversion of S to N cytoplasm are other possible explanations for variation in pollen fertility of the sugarbeet and need to be further investigated.

Literature Cited