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A Population Genetic Analysis of Self- and Cross-Incompatibility in Sugar Beet (*Beta Vulgaris* L.)

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Summary. A population genetic model is proposed for the reproduction of self-incompatible inbred lines in which incompatibility is controlled by 1-4 loci. From theoretical considerations it was expected that: a) with the random matings of lines I_n, (obtained by self-pollination of n generations), some lines would be cross-incompatible (all the plants within these lines would be homozygous for *S*-genes) and the rest would be cross-compatible (retain heterozygosity for one or more *S*-genes); b) in the case of random matings of lines I_nG_m (obtained by self-pollination of n generations and by random pollination for m generations), some lines would be cross-incompatible (heterozygous for one *S*-gene) and the rest would be cross-compatible (retain heterozygosity for two or more *S*-genes); c) the relative proportion of sterile plants, obtained by random pollination of cross-compatible lines, would be related to the number of segregating S-loci and to the generation in which the lines are studied.

Forty-four inbred lines of sugar beet derived from self-incompatible plants of a population were analysed. Comparisons of the observed values with the theoretically expected ones demonstrated that: a) of 18 I_n (I_1-I_4) lines, 6 were cross-incompatible (homozygous for *S*-genes) and 12 were cross-compatible having one S-locus segregating in 7 lines and two S-loci segregating in 5 lines; b) of 22 I_nG_1 (I_2G_1 and I_3G_1) lines, one line was self-fertile, 7 lines were cross-incompatible (heterozygous for one S-loci) and 14 lines were cross-compatible (heterozygous for two S-loci).

No line was found to have three or more segregating S-loci. The results of this population genetics analysis of self- and cross-incompatibility in sugar beet comply with diallel analysis data on sugar beet incompatibility and indicates that it is under the gametophytic control of two basic S-loci.

Key words: Genetic analysis – Incompatibility – *Beta vulgaris* L. – Gametophytic control

Introduction

Self-incompatibility in plants, which is controlled by a single or several incompatibility genes (*S*-genes), prevents self-fertilization in populations in which all the individuals have normally functioning ovule and pollen. Genetic analysis of self-incompatibility is based on the interpretation of the results of inter-sib pollination performed according to a diallel scheme (East, Mangeslsdorf 1925; East 1929). Analysis of this kind includes either the F_1 offspring from crosses between two plants within a population or offspring obtained by selfing an individual plant.

Owen (1942) was the first to investigate the inheritance of incompatibility in beets (*Beta vulgaris* L.). The experimental design of the crosses used permitted Owen to conclude that incompatibility in beets is conditioned by two nonlinked genes with gametophytic control of pollen specificities. Owen's hypothesis implied that the allelic series at the two S-loci interact in a complementary manner. It has been assumed that the second S-loci resulted from the duplication of the first S-locus, and subsequently concluded that the two S-loci may have identical allelic series. Pollination has been considered to be incompatible when the pollen grain and the stigma carry identical alleles of the two S-loci. Lundqvist (1956, 1961, 1962) has described self-incompatibility in grasses within a similar hypothetical framework.

The results of Maletsky's investigations (Maletsky, Zhumabekov 1974 a,b) of self and cross-incompatibility in I_1 plants obtained by selfing a single plant within a population, have confirmed Owen's hypothesis of two loci gametophytically controlling incompatibility in beets. The assumption made has been that the interaction of the alleles of the two S-loci may be of complementary and epistatic types (Maletsky Zhumabekov 1974 a,b).

According to Lundqvist et al. (1973), in beets incompatibility may be controlled at more than two S-loci, perhaps three or perhaps four with complementary inter-

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action. This hypothesis helps to explain nonreciprocal incompatibility at three-four levels during inter-sib pollination of single offsprings. However, another explanation has been offered to elucidate this incompatibility by implying different types of interaction between the two S-loci (Maletsky 1976).

When testing alternative hypotheses regarding self- and cross incompatibility in beets, one encounters insurmountable difficulties. Experimental crossing of plants with emasculated flowers is very tedious work that cannot be carried out on a large scale.

However data on the inheritance of self- and cross-incompatibility in plants may be obtained by population analysis of the random mating of sibs produced by selfing or crossing two plants. Some plants derived from random mating of lines are sterile, while others are fertile. Those plants which are incompatible for all the genotypes of the pollen formed by plants of the population, are sterile (cross-incompatible). The relative proportion of fertile and sterile plants is related to the number of heterozygous S-loci.

The purpose of this paper is to assess the results of a random pollination of 44 lines of sugar beet which we have derived earlier by selfing self-incompatible plants at high altitude localities of Tien-Shan. The development of these plants has been described elsewhere (Maletsky et al. 1970; Maletsky, Denisova 1974). Based on the comparisons of experimental results with those yielded by population models, the possible number of basic genes controlling incompatibility specificities in beet is discussed.

Materials and Methods

The material for this study comprised 44 different inbred lines of sugar beet. Two types of regular systems of inbreeding were used to obtain these lines: a) selfing, b) random intersib pollination. The selfed offspring was designated as I (inbreeding) and the sib-pollinated generation as G (generation). The analysis included: a) two I_1 lines; b) five I_2 lines; c) ten I_3 lines; d) one I_4 line; e) eighteen I_2G_1 lines (two successive generations obtained by selfing and one generation obtained by random intersib pollination); f) four I_3G_1 lines (three successive selfed generations and one random sib-pollinated generation); g) four I_2G_2 lines (two successive selfed generations and two random sib-pollinated generations). Random pollination was done under isolating cloth bags enclosing 8-15 plants and in isolated plots where 25-120 plants were pollinated simultaneously. The investigation was conducted using a standard method developed in 1974-1976. The localities chosen were the high altitude vicinities of Prjevalsk (Tien Shan mountainous regions, the Kirghiz Republic), and areas where sugar beet is commonly grown (Alma Ata regions, the Kazakhstan Republic). The plants were pollinated under isolating cloth bags in Prjevalsk and random pollination was used in Alma-Ata.

Seed productivity was expressed by the number of full seed balls per plant. Plants with seed balls having 2-3 seeds were taken into account. The total number of seed balls collected was recorded. To estimate the portion of full seed balls, i.e., those with normal embryos, 100 seed balls were sampled and embryo presence was determined visually (all the seed balls were examined in plants with small ball number). The number of full seed balls per plant (x_i) was obtained by multiplying the total number of seed balls per plant by a correction factor (the portion of full seed balls). The values (x_i) calculated were subjected to statistical treatment.

Definitions

1) In conformance with the genetic concept of incompatibility, pollination is defined as incompatible when the absence of seed set is due to the interaction between the identical alleles of *S*-genes in the pollen grain (pollen tube) and stigma. Plants with identical genotypes for *S*-genes are cross incompatible, i.e., they cannot be self- or cross-pollinated.

2) Compatible is that type of pollination which produces a large number of seeds close to the potential seed productivity of the given plant. In the case of cross pollination, pollen compatibility is due to the interaction between nonidentical S-alleles in the pollen grain (pollen tube) and stigma. Self-fertility means compatibility of the pollen grain of selfed plants. Total self-fertility (selfing produces about the same number of seeds as cross-pollination) results from mutations of *S*-genes (S_f mutations). It is pertinent to note that Owen (1942) has described self-fertility resulting from mutation as determined by a single genetic factor, S_f. Incompatibility may be partially a result of the possible selection of modifier genes which affect the expression of incompatibility genes. Pseudocompatible is that type of pollination which produces a relatively small number of seeds under the modifying influence exerted by environmental factors on basic *S*-genes. Pseudocompatibility may be observed during self-pollination and cross-pollination.

Classification

We then proceeded to the classification of plants as compatible or incompatible. It is difficult to distinguish compatible plants from incompatible ones, because the incompatibility reaction may be affected by both genotypic conditions in the cell and environmental factors. One has to determine the number of seeds which would under particular environmental conditions permit the assignment of each plant either to the compatible or the incompatible group. In this way seed productivity would be expressed as a qualitative character, not as a quantitative one. Based on theoretical expectations (see following Section), all the lines may be designated to either of the two groups: a) cross-compatible or b) cross-incompatible. All the plants of cross-incompatible lines may be considered identical with respect to *S*-genes. Seed productivity in plants of cross-incompatible lines was 9-14% that of cross-compatible lines (See Results). It was also expected that some plants of the cross-compatible lines would be sterile due to the segregation of *S*-genes. Standard methods of biological statistics were applied to make this distinction. Distribution series of the X_i values for the cross-incompatible lines were arranged. The mean geometric values ($\bar{X}$) and mean square deviations (σ) of the x_i values were calculated. The right limit of the distribution series was calculated by using formula (1) in which Z (P = 0.99) is the critical number separating compatible lines from incompatible ones

$$Z = k\bar{X}\,(1 + t\,2.3026\,\sigma_y) \qquad (1)$$

where t = 2.58, σ_y is the value of the square deviation in the logarithmic series (2.3026 is the factor used to convert common logarithms into natural logarithms) and k is the proportionality coefficient and expresses the ratio of the maximum values of x_i of the actually observed distribution to the maximum values of x_j ($x_j = \bar{X} + 3\,\sigma_x$). The mean geometric value ($\bar{X}$), not the mean arithmetic value, was determined because seed productivity is a character which conforms to logarithmic normal distribution, i.e., we treated the series $y_i = \lg x_i$, where x_i denotes the observed number of seeds per plant.

The confidence interval for the distribution mean of the function $X = 10^{\bar{y}}$ is calculated as follows:

$$\bar{X}(1 - t\,2.3026\,\sigma_y/\sqrt{n}) < 10^{\bar{y}} < \bar{X}(1 + t\,2.3026\,\sigma_y/\sqrt{n}) \quad (2)$$

Population-Genetical Models for the Reproduction of Self-Incompatible Diploid Inbred Lines in Sugar Beet

In diploid sugar beet, incompatibility is of the gametophyte type and for this reason the probable number of basic genes controlling incompatibility does not exceed four (Owen 1942; Lundqvist et al. 1973; Maletsky and Zhumabekov 1974 a,b). Lines homozygous and heterozygous for *S*-genes occur with a definite frequency (determined by the number of preceding self-pollinated generations and by the genotype of the initial population) in generation G_1 among those subjected to intersib pollination after self-pollination for the preceding I_n generation. By definition, the term incompatibility implies that lines homozygous for *S*-genes are sterile because plants genotypically identical with respect to *S*-genes cannot be cross-pollinated. Thus, in the first generation of randomly pollinated lines I_n, only lines (of which) all the plants are homozygous for *S*-genes will be assigned to the group of sterile lines. The group of sterile lines will now be designated as 'low fertile lines' or cross incompatible lines, owing to the fact that little seed is formed under the effects of factors (internal and external) altering the incompatibility reaction.

After random pollination, lines I_n, which retained heterozygosity at a single *S*-locus, are assigned to the group of high fertile (cross-incompatible) lines. Table 1 sum-

Table 1. Random Pollination within a Line Heterozygous at a Single S-Locus

Genotype ♀ I_n	Frequencies I_n	Gamete compatibility ♂* 1	2	Offspring genotype in I_nG_1
11	0.25	–	+	12
12	0.50	–	–	–
22	0.25	+	–	12

* The genotypes are denoted by numbers 1 and 2 which stand for the respective number of alleles at the incompatibility locus

Designation + : compatible pollination
– : incompatible pollination

Table 2. Genotype Frequencies in the First Generation of Randomly Pollinated lines and Gamete Compatibility in Lines Heterozygous at two S-loci (England 1974)

Genotype ♀	Frequencies	Gamete compatibility				Genotype frequencies in offspring of various random pollinated plants (generation I_1G_1)				
I_1	I_1	1.1	1.2	2.1	2.2♂	11.12	12.11	12.12	12.12	22.12
11.11	1/16	–	+	+	+	1/3	1/3	1/3	–	–
11.12	1/8	–	–	+	+	–	1/4	1/2	1/4	–
11.22	1/16	+	–	+	+	1/3	–	1/3	1/3	–
12.11	1/8	–	+	–	+	1/4	–	1/2	–	1/4
12.12	1/4	–	–	–	–	–	–	–	–	–
12.22	1/8	+	–	+	–	1/4	–	1/2	–	1/4
22.11	1/16	+	+	–	+	–	1/3	1/3	–	1/3
22.12	1/8	+	+	–	–	–	1/4	1/2	1/4	–
22.22	1/16	+	+	+	–	–	–	1/3	1/3	1/3
						5/36	5/36	6/36	5/36	5/36

Total genotype frequencies in offspring of random pollinated plants. The numbers were weighted for parental genotypes in I_1.

marizes the data pertaining to crosses within lines heterozygous at a single S-locus. As seen from this table, 50% of generation I_n is composed of cross-compatible plants (homozygotes 11 and 22) and 50% is represented by cross-incompatible plants (heterozygote 12). Offspring from random pollinations are represented only by one genotype (12), and, consequently, generation I_nG_1 will be cross-incompatible.

We then analysed pollination in lines retaining heterozygosity for two-four genes. The model considers incompatibility of the gametophytic type with only complementary interaction between alleles. When other types of genes are taken into account, the results are, in principle, the same (Maletsky 1976). In this connection, it is worthwhile to recall the theoretical results of England (1974) obtained with self-incompatible I_1 inbred lines of forage grasses possessing a similar incompatibility control.

Table 3. Generation Matrix A for Genotype Frequencies in Random Pollinated Lines Heterozygous at two S-loci

		Genotypes in generation f_n		
		hom^2	hom^1	hom^0
Genotypes in generation f_{n+1}	hom^2	0	0	0
	hom^1	2/3	1/2	0
	hom^0	1/3	1/2	0

Table 4. Expected Frequencies of Genotypes Grouped according to *S*-genes in Successive Generations of Randomly Pollinated Lines (1-4 loci segregate)

	I_n	G_1	G_2	G_3	G_4 and subsequent generations
One locus					
hom^1	0.500	0.000	0.000	0.000	0.000
hom^0	0.500	1.000	0.000	0.000	0.000
Two loci					
hom^2	0.250	0.000	0.000	0.000	0.000
hom^1	0.500	0.556	0.500	0.500	0.500
hom^0	0.250	0.444	0.500	0.500	0.500
Three loci					
hom^3	0.125	0.000	0.000	0.000	0.000
hom^2	0.375	0.311	0.282	0.280	0.280
hom^1	0.375	0.500	0.500	0.500	0.500
hom^0	0.125	0.199	0.218	0.220	0.220
Four loci					
hom^4	0.0625	0.000	0.000	0.000	0.000
hom^3	0.2500	0.175	0.161	0.159	0.159
hom^2	0.3750	0.408	0.404	0.403	0.403
hom^1	0.2500	0.327	0.339	0.341	0.341
hom^0	0.0625	0.090	0.096	0.097	0.097

The results of random pollination within a generation heterozygous at two loci are presented in Table 2. This is the same type of incompatibility that Owen (1942) originally described for beets. Plant genotypes and pollen grain genotypes, with respect to the two S-loci, are designated by numbers. In this case, pollination will be termed incompatible when pollen and stigma carry identical alleles at the two S-loci.

Nine genotypes (Table 3) fall into three genotypic groups: 1) hom^2; those with two homozygous loci: namely, 11·11, 11·22, 22·11, and 22·22, 2) hom^1; those with a single homozygous locus: 11·12, 12·11, 22·12 and 3) hom^0; double heterozygote: 12·12.

From Table 2 it is evident that hom^2 plants are compatible with three pollen types, hom^1 plants are compatible with two types of pollen and hom^0 plants are incompatible with four pollen types. As a result, offspring from random pollination are represented by only five genotypes belonging to two groups – hom^1 and hom^0 (Table 2).

Genotype frequencies change in successive generations of randomly pollinated lines which are heterozygous for two-, three- and four S-loci systems. Genotype frequencies were calculate by using formula (3) of Kempthorne (1957):

$$f_{n+1} = A \cdot f_n \quad \text{or} \quad f_{n+1} = A^n \cdot f_1 \,. \tag{3}$$

f_1, f_n and f_{n+1} are the genotype frequencies in the first n and n+1 generations respectively; A denotes the generation matrix.

The generation matrix A for the two loci may be constructed from the the data of Table 2. Two-thirds of the offspring of hom^2 plants are represented by hom^1 and one-third by hom^0 groups. Hom^0 plants produce no offspring. The generation matrix is presented in Table 3.

In a similar way, generation matrices can be built from the data of randomly pollinated lines heterozygous for three- and four *S*-genes. As a matter of fact, a generation matrix can be constructed for any number of segregating loci using a formal mathematical method (England 1974), Table 4 presents the expected changes in the frequencies of genotypic groups in successive generations of randomly pollinated self-incompatible lines with 1-4 segregating S-loci.

From the Table 4 it is evident that lines heterozygous for two or more loci may be randomly pollinated per se through an unlimited number of generations. During this random process the heterozygous genotypes are maintained and an equilibrium between these genotypes is attained after 2-3 generations of random pollination.

Table 2 shows that hom^0 plants (genotype 12·12) are incompatible with all pollen. Lines heterozygous for 2 loci produce offspring of which 50% have hom^0 genotype: i.e., half of the population would be sterile and their total seed productivity would be 50% of that of a population with a low probability of cross-incompatible pollination.

According to Table 4, the percentage of hom^0 plants is 22 among lines heterozygous for 3 genes and as low as 9.7 among those heterozygous for 4 genes. Thus, comparisons of the numbers of fertile (hom^k + .. + hom^1) and sterile plants (hom^0) among randomly pollinated lines give an estimate of the number of segregating S-loci (k).

Experimental Results

The genetic-population model developed predicts that random inter-sib pollination produces sterile (homozygous or heterozygous for *S*-genes) as well as fertile lines retaining heterozygosity for at least two S-loci. The relative proportions of these two groups of lines in generation I_n depends on the ratio of plants belonging to different genotypic groups in the initial population (hom^0, hom^1 and so on).

The results of the random pollination of 44 inbred lines of sugar beet were analysed. Of these 44, one line proved to be self-fertile; 28 lines fell into the group of self-compatible lines and 12 were assigned to the cross-incompatible group.

The cross-compatible plants were distinguished from the cross-incompatible ones using the following method: Lines of all plants which showed low seed productivity were singled out and in each of the four experimental series such identified lines were grouped into one. Four distribution series of the values of seed productivity were arranged. It was found that seed productivity has a normal logarithmic distribution: i.e., the logarithms of the values characterizing seed productivity of an individual plant were treated statistically (See Methods). The data for 15 cross-compatible lines are summarized in Table 6.

Comparisons of the mean values of seed productivity obtained in two independent experiments performed in Prjevalsk in 1974 and 1975 demonstrated no significant differences. However, the mean values for this character obtained in Alma Ata in 1975 and 1976 differed significantly and reflected the marked effect of environmental conditions on the seed productivity of cross-pollinated plants. It should be mentioned that in Alma Ata it was hot and dry in the summer of 1975 and it was cool and rainy in the summer of 1976.

The right of the confidence interval (Z) of the distribution of the low fertile lines (Table 6) was accepted as the limit of seed productivity in self- and cross-compatible plants. Consequently, plants with a seed number smaller than this limit value were cross-incompatible, while those with a seed number larger than this number were cross-compatible.

Based on seed productivity, the plants were classified as shown in Table 7. This table includes the statistical data for four experiments. Lines in which all the plants had seed numbers exceeding the accepted limit were self-fertile. The occurrence of such lines is possibly due to their

Table 5. A Classification of Sugar Beet Lines Based on Population Compatibility

Generation of random pollinated lines	No. of lines	Of these		
		Self-fertile	Cross-compatible	Cross-incompatible
I_1	2	–	2	–
I_2	5	–	2	3
I_3	10	–	7	3
I_4	1	–	1	–
I_2G_1	18	–	12	6
I_3G_1	4	1	2	1
I_2G_2	4	–	2	2
Total	44	1	28	15

Table 6. Random Pollination of 15 Low-Fertile (cross-incompatible) Sugar Beet Lines at two Different Localities

Locality	Year	No. of lines	Total no. of plants	X ± tm	(Z)
Prjevalsk	1974	6	66	101 ± 25	378
Prjevalsk	1975	3	34	129 ± 37	405
Alma-Ata	1975	3	162	83 ± 14	477
Alma-Ata	1976	3	158	192 ± 18	734

X – mean geometric number of full seed balls per plant
Z – right limit of the distribution series (P = 0.99)

Table 7. A Classification of Sugar Beet Plants Based on Seed Productivity (1974-1976)

Classification	No. of lines	No. of plants	Of these		$\bar{X}$ ± t'm	(P = 0.95)
			Cross-compatible	Cross-incompatible	Cross-compatible	Cross-incompatible
Self-fertile	1	30	30	–	877 ±	–
Cross-compatible	28	740	417	323	1315 ± 75	157 ± 15
Cross-incompatible	15	420	–	420	–	121 ± 12

selection from the population during the process of inbreeding. Lines partly composed of plants with high seed productivity (5500 seeds per plant) and partly consisting of plants with low seed productivity were assigned to cross-compatible lines. Lines in which all the plants had low seed productivity were referred to cross-incompatible lines. Seed productivity of cross-incompatible plants was 9-14% of that of the cross-incompatible plants, determined by comparing the mean values for this character (Table 7). It may be suggested that this level of partial compatibility is inherited in the inbred lines used in the experiments.

Table 8 presents the segregation patterns of seed productivity in cross-compatible lines differing in the degree of inbreeding. As already noted, the theoretically expected ratio of sterile to fertile plants is expressed as the ratio of genotype frequencies hom^0 to the sum of the frequencies of all the other genotypes ($hom^k + .. + hom^1$). This ratio depends on the number of loci in the population and the generation in which seed productivity was estimated (Table 4). To illustrate: in randomly pollinated lines I_n, the segregation of a single S-locus results in an 1:1 (0.5:0.5) ratio of fertile to sterile plants; in the case when two loci segregate, the ratio is 3:1 (0.75:0.25); the three-loci system segregation results in a 7:1 (0.875:0.125) ratio. Comparisons of the observed and expected demonstrated that 7 I_n lines have a genotype with a single segregating S-locus and 5 I_n lines have a genotype with two segregating loci (Table 8). Of the 18 lines belonging to generation I_n (Table 5), 6 are cross-incompatible (the plants within these lines are presumably homozygous for the *S*-genes) and in 12 lines there occurs a segregation of one, two S-loci.

The ratios of fertile to sterile plants are quite different from those of the lines belonging to group I_nG_1. It may be inferred from the theoretical models (Table 1) that populations heterozygous for a single S-locus may be randomly pollinated in generation I_n, although in generation I_nG_1 these populations become cross-incompatible (all the plants within such populations are genetically identical with respect to *S*-genes). Therefore, two or more S-loci may be expected to segregate in lines belonging to generations I_nG_1 (Table 4). Theoretically, the expected ratio of fertile to sterile plants with two segregating loci is 5:4 (0.556:0.444); 4:1 (0.801:0.199) when three loci segregate. From comparisons of the expected ratios with the observed ratios it emerges that only two loci segregate in line I_nG_1. Thus, of the 22 lines belonging to group I_nG_1, 18 of which were of generation I_2G_1 and 4 of generation I_3G_1, 7 lines were cross-incompatible (Table 5), 1 line was self-fertile, and the remaining 14 lines were cross-compatible.

The results of the random pollination of four I_2G_2 lines were also analysed. In lines of this group with two S-loci segregating (lines retaining homozygosity at a single locus should be cross-incompatible), the expected ratio of

Table 8. Fertile to Sterile Plant Ratios in Randomly Pollinated (cross-compatible) Sugar Beet Lines Differing in Degree of Inbreeding

Generation in which seed productivity was estimated	No. of lines involved	Total No. of plants estimated	Of these		Expected ratios of fertile to sterile plants	χ^2
			Fertile	Sterile		
	Segregation of one locus					
I_1	1	53	26	27	1 : 1	0.02
I_2	2	21	12	9	1 : 1	1.26
I_3	4	58	23	35	1 : 1	2.48
Total No. in I_n	7	132	61	71	1 : 1	0.82
	Segregation of two loci					
I_1	1	68	55	13	3 : 1	1.26
I_3	3	38	28	10	3 : 1	0.04
I_4	1	55	43	12	3 : 1	0.29
Total No. in I_n	5	161	126	35	3 : 1	0.91
I_2G_1	12	302	156	146	5 : 4	1.87
I_3G_1	2	33	21	12	5 : 4	0.892
Total No. in I_nG_1	14	335	177	158	5 : 4	1.00
I_2G_2	2	112	53	59	1 : 1	0.32

sterile to fertile plants would be 1:1 (0.5:0.5); when segregation involves three S-loci the expected ratio would be 3.6:1 (0.782:0.128). Having compared the expected and observed ratios, it is clear that two loci segregate in lines I_2G_2. Thus, of the 4 I_2G_2 lines analysed, there is no segregation in 2 lines (these are homozygous for one or two S-loci) and in the other 2 lines there is segregation of two loci.

Discussion

In randomly pollinated populations of self-incompatible plants such as sugar beet, incompatible pollination is a rare event because *S*-genes as a rule consist of a series of multiple alleles. For this reason, many 'pollen specificities' arise during the random pollination of populations and the stigma of any flower may be pollinated with compatible pollen grain. However, in offspring derived from selfing or crossing of sibs, the number of 'pollen specificities' does not exceed that inherent in an individual plant from a randomly pollinated population. Models simulating reproduction at the population-genetic level demonstrated that only a portion of inbred lines can be randomly pollinated and retain heterozygosity at two or more S-loci. However, in such populations, some plants are sterile because they are incompatible with all 'pollen specificities'. The relative proportion of sterile plants is related to the number of segregating loci and the generation in which seed productivity was examined.

The randomly pollinated 44 inbred lines we analysed comprised two well-defined groups: in one group one or two *S*-genes segregate and in another group the gene does not. The results obtained with the random pollination of inbred lines are in full agreement with the hypothesis of the two loci gametophytical control of incompatibility in sugar beet (Owen 1942; Maletsky, Zhumabekov 1974 a,b). As shown in Table 4, this hypothesis postulates that either one or two loci may segregate. Segregation of one loci results in a 1:1 ratio of fertile to sterile plants, while segregation of two loci gives rise to a 3:1 ratio of fertile to sterile plants. Both types of segregation were observed in our experiments. In subsequent generations I_nG_1 and I_nG_2, only two loci are expected to segregate and the ratios of fertile to sterile plants would be 5:4 and 1:1, respectively. In these experiments there was also a good fit between the observed and expected ratios (Table 8). Segregation never involved 3-4 loci, as might be expected from the hypothesis proposed by Lundqvist et al. (1973).

Environmental conditions had a strong effect on seed productivity and seed set. However, differences in the level of seed set in pseudocompatible plants, observed through different years, as a rule do not make plant classification on the basis of their fertility (sterility) difficult. The level of seed set in randomly pollinated pseudocompatible plants amounted to 9-14% of that of compatible cross-pollinated plants. This surpasses by far the level observed in artificially self-pollinated plants (Maletsky et al. 1970; Maletsky, Denisova 1974).

Our population-genetic approach is advantageous when compared with the method of diallel crosses because analysis of large plant samples are feasible. This approach could be combined with diallel cross analysis. In fact, based on ratios of fertile to sterile plants, judgments about the interaction of *S*-genes are precarious. Let us assume, for example, that allele S_1^1 inhibits epistatically the expression of S_1^2 and S_2^2 in the pollen and that the allele S_2^1 interacts with the alleles of the second locus in a complementary manner (the top symbol stands for locus number and the bottom symbol stands for allele number). In this case, the ratio of fertile to sterile plants would be 3:1 in generation I_n; 19:17 in generation I_nG_1 and 1:1 in generation I_nG_2 (by way of comparison, it should be reminded that, when two alleles of two loci interact in a complemenatry fashion, the expected fertile to sterile plant ratios in the respective generations are 3:1, 5:4 and 1:1) (Maletsky 1976). These alternative hypotheses can be tested only in I_nG_1 under the stipulation that the plant samples are sufficiently large.

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