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Genetic studies of self-fertility in rye (*Secale cereale* L.). 1. The identification of genotypes of self-fertile lines for the *Sf alleles* of self-incompatibility genes

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Abstract. Segregation for self-fertility has been studied in progenies from the crosses of self-sterile (SS) plants with interline hybrids obtained by a diallel scheme of pollinations between seven self-fertile (SF) lines (nos. 2–8) and with F_1 (SS plant × SF line) hybrids. All the offspring families from the SS plant × F_1 (SS plant × SF line) crosses demonstrated a 1SF:1SS segregation. The crosses of SS plants with some interline hybrids gave only self-fertile plants, whereas the crosses with other interline hybrids gave a segregation of 3SF:1SS expected in the case of digenic segregation. The data obtained permitted us to identify three different S loci (*S1*, *S2*, *S5*) and to estimate the genotypes of self-fertile lines for their *Sf* alleles: lines 5, 6, 7 and 8 are *S1f/S1f S2n/S2n S5m/S5m*, line 4 is *S1n/S1n S2f/S2f S5m/S5m*, and lines 2 and 3 are *S1n/S1n S2m/S2m S5f/S5f* (*Sn*, *Sm* designate active alleles of the incompatibility genes). The identification of the particular *S* gene which is presented by the *Sf* allele in each line has been made on the basis of our data concerning the linkage of the *Sf* mutation with isozyme markers of particular rye chromosomes, which is reported in an accompanying paper.

Key words: *Secale cereale* L. – Incompatibility genes – Self-fertility

Introduction

According to the classical data of Lundqvist (1956, 1958) self-fertilization in rye (*S. cereale* L.) is prevented by a gametophytic incompatibility system which is controlled by two multiallelic loci *S* and *Z*. However, more recent data have shown the existence of more than two loci involved in the determination of self-incompatibility in rye. Melz and his coworkers have revealed four genes, *S1*, *S2*, *S3*, and *S4*, the mutations of which (*Sf*) control self-fertility in rye (Melz et al. 1987, 1990).

In the present paper the genotypes of seven self-fertile lines have been established in terms of mutant alleles (*Sf*) of S genes by genetical analysis of segregation for self-fertile and self-sterile plants in the progenies from the two kinds of crosses: self-sterile plants × interline hybrids, and self-sterile plants × F_1 (self-sterile plant × self-fertile line).

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Materials and methods

Plant material

Seven self-fertile (SF) inbred lines from a genetic stock collection have been used in this study. The origin of the lines is shown in Table 1.

The interline hybrids have been obtained by a diallel scheme of pollinations between these lines. Plants from the recently-obtained Russian variety Volkhova have been used as a source of self-sterility. Our data obtained over several years have shown that this variety possesses less than 2% of self-fertile plants. F_1 hybrids have been obtained from the crosses of Volkhova's self-sterile (SS) plants with self-fertile lines.

Eight plants from the Volkhova variety (V-2, V-5, V-10, V-13, V-19, V-23, V-25, V-92) were cloned and the ears of the same clones were pollinated by interline hybrids and F_1 (SS plant × SF line) hybrids. In each cross pollen from only one hybrid plant has been used. The plants in the progenies from these crosses were selfed in standard pergamine bags and segregations for self-fertility have been analyzed.

Table 1. The origin of self-fertile inbred lines

Line	Inbred generation	Original form (variety)
2	I(12)	Monstrous branched ear
3	I(12)	The same
4	I(7)	Steel
5	I(30)	Steel (from Muntzing)
6	I(31)	Steel
7	I(7)	Vijatka
8	> I(6)	Petkus

The identification of the genotype of a self-fertile line for Sf alleles

The determination of the number of S loci which contain an Sf allele in a self-fertile line. According to Lundqvist (1958), self-fertile rye forms have inactive (*Sf*) alleles of at least one of the S-loci. Hybrids obtained from crosses between SS plant and an SF line contain a self-fertility allele (*Sf*) in one (*S1f/S1n*) or in two (*S1f/S1n S2f/S2n*) S loci, where *Sf* is a mutant allele and *Sn* is any active allele of an S-locus. When SS plants are pollinated by such hybrids we might expect half of offspring plants to carry an *Sf* allele and half of them not to carry an *Sf* allele if the self-fertile line carried an *Sf* allele at only one S locus. On the other hand, we might expect 3/4 of the offspring plants to carry an *Sf* allele in at least one of S loci and 1/4 of plants not to carry any *Sf* allele in cases where the original self-fertile line had *Sf* alleles at two S loci.

Thus, if segregation in progenies from an SS plant × F_1 (SS plant × SF line) cross is 1SF:1SS then the line studied must carry an *Sf* allele at only one S locus whereas if segregation is 3SF:1SS then the self-fertile line carries *Sf* alleles at two S loci.

The test of Sf mutations from different lines on their allelism. If two self-fertile lines carry at least one *Sf* mutation in the same S locus, for example in the *S1* locus, then their interline hybrid possesses a genotype *S1f/S1f*, where *S1f* is a mutant allele of the *S1* gene. When such an interline hybrid is crossed with a self-sterile plant, all the offspring must carry the *S1f* allele and therefore have to be self-fertile.

If self-fertile lines contain *Sf* alleles at different S loci, for example one line carries a *S1f* allele and the other a *S2f* allele, then the genotype of their interline hybrid is *S1f/S1n S2f/S2m* (where *Sn*, *Sm* are any active alleles of S loci). In the progeny from the cross of this hybrid with a self-sterile plant we must expect 1/4 of offspring plants not to carry any *Sf* allele and 3/4 of offspring plants to carry either *S1f* or *S2f* or else both of the *S1f* and *S2f* alleles; in other words, a segregation of 1SS:3SF is expected.

Similarly, a segregation ratio of 1SS:7SF is expected in the progeny of such a type of a cross if one line carries *Sf* alleles at two different S loci and the other an *Sf* allele at a third S locus.

Results

Self-fertility levels of plants and hybrids involved in the studied crosses

The self-fertility levels of all plants and hybrids involved in crosses have been examined. All eight Volkhova's clones were self-sterile. Their self-fertility values ranged from 0 to 3 per cent. By contrast, all the interline hybrids and F_1 (SS plant × SF line) hybrids were self-fertile. They set more than 49% seeds after self-pollination. This shows that self-fertility is inherited as a dominant character.

The number of S loci containing an Sf allele in a self-fertile line

The distributions of seed set values after self-pollination in progenies from the crosses of SS plants with F_1 (SS plant × SF line) hybrids make it evident that the offspring plants from every cross may be divided into two groups. In the first, the majority of plants have seed set values of less than 5%, in the second all plants show more than 10% seed set after self-pollination. There are very few plants with a 5–10% seed set. This permits us to consider 10% seed set as a boundary between self-fertility and self-sterility so that segregations for self-fertility in progenies from these crosses can be identified (Table 2).

The χ^2 test values clearly demonstrate that the segregations fit well to a ratio of 1SF:1SS in progenies from every cross and we can therefore conclude that each of the lines studied carries an *Sf* allele at only one S locus.

The test of the allelism of Sf mutations from different lines

The distributions of seed set values in the progenies from the crosses of SS plants with interline hybrids show that crosses in which interline hybrids 8 × 7, 8 × 6, 8 × 5, 7 × 6, 6 × 5 and 2 × 3 participated gave only self-fertile offspring plants (all of them with higher than 10% seed set after self-pollination). In the progenies of other crosses both self-sterile and self-fertile plants were present (Table 3).

Because each of the self-fertile lines studied carries an *Sf* allele at only one S locus, we may conclude that lines 5, 6, 7 and 8 carry *Sf* alleles of the same S locus. This is also the case for lines 2 and 3. But these two groups of lines have *Sf* alleles of different S loci because

Table 2. The self-fertility segregations in the offspring from the crosses of SS plants with F_1 (SS plant × SF line) hybrids

SF line	Number of plants		χ^2	
	Self-sterile	Self-fertile	1:1	1:3
2	22	30	1.23	8.31*
3	21	32	2.28	6.04*
4	32	23	1.47	32.29*
5	21	18	0.23	17.30*
6	18	18	0.0	12.00*
7	29	28	0.02	20.53*
8	25	25	0.0	16.67*

* $P < 0.05$

Table 3. The self-fertility segregations in the progenies from the crosses of SS plants with interline hybrids

Interline hybrids	Number of plants		χ^2 1:3
	Self-sterile	Self-fertile	
8 × 7	0	70	23.33*
8 × 6	0	65	21.67*
8 × 5	0	71	23.67*
7 × 6	0	66	22.00*
6 × 5	0	59	19.67*
2 × 3	0	65	21.67*
4 × 2	17	32	2.45
4 × 3	13	45	0.21
5 × 4	16	42	0.21
6 × 4	37	126	0.46
7 × 4	24	71	0.01
8 × 4	13	56	1.39
5 × 2	19	40	1.63
5 × 3	16	34	1.31
6 × 3	12	21	2.27
7 × 2	12	39	0.06
7 × 3	21	47	1.25

* $P < 0.01$

corresponding interline hybrids (5 × 2, 5 × 3, 6 × 3 etc.) give segregations of 1SS:3SF after the cross with self-sterile plants. For the same reason line 4 has an *Sf* mutation which is different from the *Sf* mutation of lines 5, 6, 7, 8 and from the *Sf* mutation of lines 2 and 3. These results are in good agreement with our data concerning the linkage of the three identified S loci with the isozyme markers of chromosomes 1R (*S1f* in lines 5 and 8) 2R (*S2f* in line 4) and 5R (*S5f* in lines 2 and 3) (Fam Thanh Fuong et al. 1993).

Thus we can determine the genotypes of the lines studied for their S genes: lines 5, 6, 7 and 8 are *S1f/S1f S2n/S2n S5m/S5m*, line 4 is *S1n/S1n S2f/S2f S5m/S5m*, and lines 2 and 3 are *S1n/S1n S2m/S2m S5f/S5f* (The designation *Sn*, Sm means the presence of active incompatibility alleles).

Discussion

The methods used in this study permit us to distinguish the different genotypes of the investigated self-fertile lines in terms of their *Sf* alleles. The procedure for estimating the number of S loci containing an *Sf* allele in a given line is significant for further differentiating self-fertile lines into groups according to their *Sf* alleles, especially in cases where some of the self-fertile lines carry *Sf* alleles at several S loci.

The ratio of self-sterile and self-fertile plants seems to be in a good agreement with expected values. Therefore, the 10% seed set value appears to be a genuine natural boundary between self-fertility and self-sterility. A similar conclusion was made by Lundqvist (1956, 1958) although he emphasized the arbitrary nature of this boundary.

The identification of three different S loci in rye made on the basis of a genetic analysis of the inheritance of self-fertility is in complete agreement with our results obtained by studying the linkage between S loci and isozyme markers (Fam Thanh Fuong et al. 1993). Lundqvist (1958) showed that self-fertility mutations may be found in *S* or *Z* genes of rye. Subsequently (Lundqvist 1968) he did not exclude the possibility of the existence of other S genes besides *S* and *Z*. All self-sterile plants and self-fertile lines in his studies originated from Steel rye and in this material segregation had been observed for only two loci, *S* and *Z*. In our study lines 4, 5 and 6 also originate from Steel rye and the mutant alleles *S1f* and *S2f* may be identical to Lundqvist's *Sf* and *Zf*.

We do not exclude the presence of more than three loci controlling self-incompatibility in rye. By including self-fertile lines from new sources in further studies it will probably be possible to observe segregation for new S loci.

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