

COMPATIBILITY AND INCOMPATIBILITY IN WITLOOF-CHICORY (*CICHORIUM INTYBUS* L.). 2. THE INCOMPATIBILITY SYSTEM

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INDEX WORDS

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SUMMARY

In witloof-chicory fertilization is frequently prevented by the action of an incompatibility mechanism. In two experiments the incompatibility system was investigated. In the IVT phytotron at a constant temperature of 17°C reciprocal crosses were made between unrelated plants followed by diallel crosses between the F1 plants and backcrosses with the parents.

Analyses of the results of the above crosses strongly suggest that in witloof-chicory a one locus sporophytic incompatibility system occurs with different dominance and codominance relationships between S-alleles in pollen and style.

INTRODUCTION

In witloof-chicory (*Cichorium intybus* L.) fertilization is frequently prevented by the action of an incompatibility mechanism. Witloof belongs to the *Compositae*, in many representatives of which a sporophytic incompatibility system occurs (PANDEY, 1960; ARASU, 1968; DE NETTANCOURT, 1977). The presence of the same system in witloof-chicory has been suggested by PÉCAUT (1958, 1962). BANNEROT & FOUILLOUX (1970), however, found some indications for a gametophytic system.

The existing uncertainties, which also have consequences for breeding, made further investigations on the incompatibility system in witloof necessary. Results are presented in this paper.

MATERIALS AND METHODS

To investigate the incompatibility system, two experiments were carried out. The four parents ($P_1 - P_4$) used in these experiments, were single plants of inbred lines (I) derived from the following open pollinated populations:

Experiment 1: $P_1 = I_1$ plant from cv. Dubbelblank,

$P_2 = I_1$ plant from F_2 cv. Vroege Mechelse \times cv. Malina.

Experiment 2: $P_3 = I_2$ plant from cv. Dubbelblank (not derived from P_1),

$P_4 = I_1$ plant from F_2 cv. Vroege Mechelse (cv. Malina \times cv. Vroege Mechelse).

The procedure used in each experiment was as follows:

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the first four weeks of flowering of each plant. Because the frequency of germinated pollen grains gave no clear distinction between compatible and incompatible combinations (EENINK, 1981) and because pollen tube growth in the style could not easily be made visible, the mean number of seeds or rather achenes per flowerhead (usually a mean of four flowerheads) served as the criterion for the (in)compatibility of a cross.

To be certain that all plants from the crosses $P_1 \times P_2$ and $P_3 \times P_4$ were hybrids, flower color was used as a marker. P_1 and P_3 were white flowered whereas P_2 and P_4 were blue with blue dominant (1 gene) over white.

Because of a shortage of flowerheads in F_1 plants in experiment 2 only a part of the crosses between F_1 plants and between F_1 plants and parents could be made.

RESULTS AND DISCUSSION

The crossing results of experiment 1 and 2 are presented in Tables 1 and 4. Analyses will be given separately. On the basis of the mean seed set per cross different incompatibility

5	16	17	18	19	20	21	22	23	24	25	26	27	Overall mean	Parents		
														P_1	P_2	
0	0	0	0	0	0	0	0.3	0	0.3	0	0.2	0	0.1	0.3	3.3±	
0	0	0	0.3	0	0	0.5	1.8	0	1.0	0	0	0	0.3	0	12.0+	
0.5	1.0	0.3	0.2	0.2	0.5	2.3	1.2	1.3	1.0	0.8	0	0	0.9	0.7	17.0+	
0.5	0	0.3	0	0.5	0	0.3	1.5	0	0.5	2.5	0	0	0.4	0	11.4+	
0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	4.0±	
0.3	0	0.5	0.5	0.8	0	1.0	4.3±	2.3	0.9	0	0.5	0	0.7	0	17.0+	
0	0.2	1.5	1.0	4.3±	1.5	1.3	1.7	1.3	3.3±	5.5±	3.0±	1.5	1.7	1.0	10.0+	
0	0.5	1	0.2	0	0	0	0	0	0	0.5	0	0	0.3	0	8.0+	
3.8±	0.3	2.0	1.0	0.3	0	0.8	2.5	0	5.9±	4.0±	0.8	1.0	1.5	2.0	17.0+	
0	0.8	0.3	0	0	0	0.3	0.3	0	0.5	0	0	0	0.3	0	18.0+	
0.3	0.3	0.3	0	0	0	0	0.4	0	0	1.0	0.3	0	0.1	0	8.5+	
2.0	0.5	3.0±	2.0	1.0	2.8	0	4.5±	1.0	4.5±	2.0	0.7	3.5±	1.8	3.0±	17.0+	
0	0	0	0	0	0	0	0.5	0	0	2.0	0	0	0.1	0	5.8±	
0.8	0.1	0.5	0.8	0.5	0	0.3	1.5	2.0	0	3.0±	0	0	0.5	0	10.0+	
0.5	0.3	0.8	0.8	0.9	0	0.1	0.3	0	0.3	0.7	0.3	0.3	0.2	0	6.0±	
0.5	0	0.7	0.3	0	0	0	0	0	0	1.2	0.3	0	0.1	0	17.0+	
3.0±	0	0	2.0	0.7	1.3	0.5	0.5	0.5	1.0	1.3	0.8	1.5	1.0	0.3	8.0+	
0	0	0.3	0.2	0.3	0	0	0.3	0	0	0.3	0	0	0.6	0	6.3+	
0	0	0	0.3	0	0	0	1.3	0.3	0.3	0	0	0	0.1	0	12.0+	
1	0.3	0	1.0	0	0.2	0.5	2.0	0	1.5	1.0	0	0.3	0.6	0.5	10.0+	
1.3	0	0.5	0	0	0.3	0.4	0.3	0.3	1.0	1.8	0	1.3	0.9	1.3	9.3+	
0	0	2.5	0.5	0	0	3.8±	1.0	3.3±	0.8	3.8±	2.5	3.0±	1.1	0.5	18.0+	
0.8	0.3	0	0	0.3	0.3	0	0	×	0	1.0	0	0	0.3	0	15.0+	
0	0	0.8	0	0	0.5	0.3	0.8	0	0.2	0.3	0	0	0.2	0.3	12.0+	
0	0.8	0.5	0	0	1.3	1.5	0.5	1.0	1.0	0.1	0.3	0	0.7	3.5±	14.0+	
1.0	1.0	0.8	0.5	1.0	0.8	0.5	0	0.3	0.3	0.3	0	0	0.5	0.5	6.0±	
0	0	0	0	0	0	0	0	0	0	0.3	0	0.1	0.4	0.3	13.0+	
0.5	0.2	0.6	0.4	0.4	0.3	0.5	1.0	0.5	1.0	1.2	0.4	0.5				
0	0	0	×	0	0	×	0.8	0	0	0	0	0	0	0	14.0+	
15.0+	13.0+	13.0+	0	12.0+	0	6.0±	15.0+	4.5±	17.0+	15.0+	11.0+	16.5+			12.0+	0.2-

phenotypes for the F_1 plants will be suggested. Analyses are hampered by the fact that the compatible and incompatible reaction cannot clearly be distinguished (EENINK, 1979, 1981). Because mean seed production per combination was based on a limited number of four flowerheads, error factors may to some extent positively or negatively influence these means, sometimes resulting in intermediate seed production. Therefore, and on the base of preliminary investigations on seed production, the following somewhat arbitrary distribution of means over three classes was made. A number of seeds below 3 means incompatibility (-), a number of seeds between 3 and 6 can indicate compatibility or incompatibility (\pm) and more than 6 seeds indicates compatibility (+).

Experiment 1. Table 1 shows the mean number of seeds of crosses between 27 F_1 plants, including selfings and of backcrosses between the F_1 plants and their parents. The overall mean seed set per flowerhead varied for the F_1 plants when used as a male and/or as a female parent. Some of these plants had a higher seed production than others. This can also be seen from the results of a combining ability analysis of variance for seed production of the F_1 plants. A significant GCA effect was found and Table 2 shows GCA-values for seed production of the F_1 plants. F_1 plants 25, 12, 22, 9, and 7 had a high GCA value while, for instance, F_1 plants 16 and 5 had a low GCA value. These differences imply that the genetic background for the incompatibility mechanism and/or for seed production differed for the various plants. So modifying genes influence the action of the incompatibility genes and interfere to some extent with the analysis of the crossing results.

The results for seed production of F_1 plants after diallel crossing show that almost all combinations yielded few if any seeds. These combinations are regarded as incompatible (less than 3 seeds per flowerhead, in Table 1 indicated by -).

A small amount of seeds (between 3 and 6 seeds per flowerhead indicated by \pm) was produced if one or both parents showed a rather high value for GCA for seed production. So this seed production probably results from the action of modifier genes, mentioned before, and not from the action of incompatibility genes themselves. Therefore here the \pm combinations are thought to be incompatible.

All crosses between F_1 plants and P_1 were incompatible whereas nearly all crosses between the F_1 plants and P_2 were compatible (indicated by + in Table 1). Few of the $F_1 \times P_2$ crosses produced only a small number of seeds or no seeds at all. To fit the above results in an incompatibility system, many systems with 2-4 different incompatibility genes were compared with the actual results in Table 1 such as:

a) gametophytic systems with 1 or 2 loci;

Table 2. GCA-values for seed production of F_1 plants in diallel crosses in Experiment 1.

F_1 plants	16	5	8	18	1	19	13	11	23	15	20	2	10
GCA value	-0.13	-0.13	-0.10	-0.10	-0.10	-0.10	-0.09	-0.09	-0.04	-0.04	-0.03	-0.03	-0.02
F_1 plants	26	4	24	14	6	21	3	17	25	12	22	9	7
GCA value	0	0	0	0	0.02	0.05	0.05	0.09	0.16	0.17	0.19	0.22	0.24

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Table 3a. Simplified scheme for results of crosses between F_1 plants and between F_1 plants and parents, as shown in Table 1. + = compatible; - = incompatible.

♀ \ ♂	F_1 plants 1-27	P_1	P_2
F_1 plants 1-27	-	-	+
P_1	-	-	+
P_2	+	+	-

Table 3b. S-genotypes of progenies from crosses between parents and F_1 plants with given S-genotypes. + = compatible; - = incompatible.

♀ \ ♂	F_1 plants 1-27 S_1S_2	P_1 S_2S_2	P_2 S_1S_1
F_1 S_1S_2	-	-	+ S_1S_1, S_1S_2
P_1 S_2S_2	-	-	+ S_1S_2
P_2 S_1S_1	+ S_1S_1, S_1S_2	+ S_1S_2	-

b) sporophytic systems with 1, 2 or 3 loci with different dominance and codominance relationships or complementary gene action;

c) combinations of a gametophytic and sporophytic system.

Of all these systems a one locus sporophytic incompatibility system with dominance in pollen and style fitted best. To show this, Table 3a is presented with a simplified scheme for the crossing results of Table 1 based on the following assumptions:

a) All combinations between F_1 plants were incompatible.

b) All combinations between F_1 plants and P_1 were incompatible.

c) All combinations between F_1 plants and P_2 were compatible while the poor or extremely rich seed production in a few $F_1 \times P_2$ combinations resulted from effects of environment or genetic background.

If a one locus sporophytic system is present with the S-genotypes S_2S_2 (P_1), S_1S_1 (P_2) and dominance of S_2 over S_1 ($S_2 > S_1$) in pollen and style, Table 3b results. This hypothesis explains almost all crossing results in Table 1, except for a few combinations which did not yield enough seeds.

Experiment 2. Table 4 shows the mean number of seeds in diallel crosses between 18 F_1 plants including selfings and backcrosses. As only part of the crosses could be made no analysis of variance was carried out to see whether a significant GCA effect for seed production occurred as was found in experiment 1. For the same reason the overall mean seed production per F_1 plant as male or female parent should be regarded with reservation. Nevertheless it seems that the mean seed production of F_1 plants 3, 5, 10 and 13 was higher than that of other plants, which may be due to modifiers of the incompatibility gene effects as was also suggested in the previous experiment.

In this second experiment too the distinction between compatible and incompatible combinations was hindered by poor/intermediate seed production in certain crosses.

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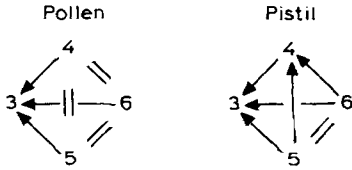


Fig. 1. Assumed relationships between S-alleles in pollen and pistil for experiment 2. 4 → 3 means S₄ dominant to S₃; 5 = 6 means codominance of S₅ and S₆.

Table 5a. Simplified scheme for results of crosses between F₁ plants and between F₁ plants and parents as shown in Table 4, if four incompatibility groups are assumed. + = compatible; - = incompatible.

♀ \ ♂		F ₁ plants 1-18				P ₃	P ₄
		group		group			
		1a	1b	2a	2b		
F ₁ plants 1-18	group 1a	-	-	+	+		
	1b	-	-	+	+		
	group 2a	+	+	-	-		
	2b	+	+	-	-		
P ₃		-	-	-	-	-	+
P ₄		+	-	+	-		-

Table 5b. S-genotypes of progenies from crosses between parental plants and F₁ plants with the given genotypes.

+ = compatible, - = incompatible (found).

⋯ = compatible, -- = incompatible (expected).

For dominance and codominance relationships between S-alleles see text.

	F ₁ plants 1-18: ♂				P ₃	P ₄
	group		group			
	1a	1b	2a	2b		
	S ₃ S ₅	S ₄ S ₅	S ₃ S ₆	S ₄ S ₆	S ₅ S ₆	S ₃ S ₄
F ₁ plants 1-18: ♀						
group 1a			S ₃ S ₃ + S ₃ S ₆	S ₃ S ₄ + S ₃ S ₆	--	⋯
S ₃ S ₅	-	-	S ₃ S ₅ + S ₃ S ₆	S ₄ S ₅ + S ₅ S ₆	--	⋯
group 1b			S ₃ S ₄ + S ₄ S ₆	S ₄ S ₄ + S ₄ S ₆	--	⋯
S ₄ S ₅	-	-	S ₃ S ₅ + S ₃ S ₆	S ₄ S ₅ + S ₅ S ₆	--	⋯
group 2a	S ₃ S ₃ + S ₃ S ₅	S ₃ S ₄ + S ₃ S ₅	-	-	--	⋯
S ₃ S ₆	S ₃ S ₆ + S ₃ S ₆	S ₄ S ₆ + S ₅ S ₆	-	-	--	⋯
group 2b	S ₃ S ₄ + S ₄ S ₅	S ₄ S ₄ + S ₄ S ₅	-	-	--	⋯
S ₄ S ₆	S ₃ S ₆ + S ₅ S ₆	S ₄ S ₆ + S ₅ S ₆	-	-	--	⋯
P ₃ S ₅ S ₆	-	-	-	-	-	S ₃ S ₅ + S ₄ S ₅ S ₃ S ₆ + S ₄ S ₆
P ₄ S ₃ S ₄	S ₃ S ₃ + S ₃ S ₅ S ₃ S ₄ + S ₄ S ₅	-	S ₃ S ₃ + S ₃ S ₆ S ₃ S ₄ + S ₄ S ₆	-	⋯	-

The same categories as in experiment 1 were used ($-$, \pm , $+$).

On the basis of compatible and incompatible combinations of the diallel crosses of the F_1 plants, two incompatibility phenotypes seem to occur.

Phenotype 1: F_1 plants 1, 2, 4, 6, 7, 11, 12, 14, 15, 16, 17 and 18.

Phenotype 2: F_1 plants 3, 5, 8, 9, 10, 13.

All crosses within a phenotypical group appear incompatible while crosses between F_1 plants of different groups appear compatible. On the basis of their (in)compatibility reaction with both parents (P_3 and P_4) within each phenotypical group two subgroups (a and b) can be distinguished:

a) Crosses between F_1 plants and P_3 are incompatible and between F_1 plants and P_4 are compatible.

b) Crosses between F_1 plants and P_3 and P_4 are incompatible.

The F_1 plants can thus be distributed over four incompatibility phenotypes:

group 1a: 2, 12;

group 1b: 1, 4, 6, 7, 11, 14, 15, 16, 17, 18;

group 2a: 5, 9, 13;

group 2b: 3, 8, 10.

The above distinction leads to a simplified scheme for the crossing results of experiment 2 and is shown in Table 5a. These results fit into the one locus sporophytic incompatibility model if the following assumptions are made:

1) In the parents four different S-alleles are present (S_5S_6 in P_3 and S_3S_4 in P_4);

2) Different relationships occur between the S-alleles, which are indicated in Fig. 1.

The S_3S_4 and S_5S_6 incompatibility genotypes of the parents result in four S-genotypes of the F_1 plants which are shown in Table 5b including the progenies from sib – and backcrossing. Although unfortunately certain crosses are missing, especially backcrosses between F_1 plants as a female parent and P_3 and P_4 as a male parent, Tables 3, 5a and 5b agree well, which illustrates that a one locus sporophytic system may again explain the (in)compatibility reaction of the parents and the F_1 .

CONCLUSIONS

Results of analyses of experiments 1 and 2 strongly suggest that in witloof-chicory a one locus sporophytic incompatibility system occurs with different dominance and codominance relationships between S-alleles in pollen and style. Nothing can be said about the total number of S-alleles present in the different witloof populations. P_1 and P_3 with S_2 , S_5 and S_6 originate from the same basic population (cv. Dubbelblank) and so the suggested S_2 may be identical with S_5 or S_6 . P_2 and P_4 also have similar ancestors (cvs. Vroege Mechelse and Malina), so maybe S_1 equals S_3 or S_4 . This means that in the four parents used here at least four different S-alleles will be present.

This one locus sporophytic system in witloof-chicory might offer possibilities for the production of F_1 hybrid varieties which until now have been produced on the basis of more or less self-compatible inbred lines (BANNEROT & DE CONINCK, 1970; EENINK, 1979). However if severely self-incompatible plants are used, methods should be available to induce self-fertilization in these plants. None of the pollination methods investigated so far has given positive results (EENINK, unpublished).

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