

The inheritance of resistance of some *Brassica oleracea* L. cultivars and lines to downy mildew – *Peronospora parasitica* (Pers.) ex Fr.

Julia HOSER-KRAUZE, Elżbieta ŁAKOWSKA-RYK, Jadwiga ANTOSIK

Department of Genetics and Breeding, Institute of Vegetable Crops, Skierniewice

Abstract. Resistance to downy mildew was tested on resistant cultivars: *Brassica oleracea* PI246077 and PI231210, a broccoli-cauliflower line from Polish selection, susceptible cauliflower lines and their F₁ and F₂ progenies. Infection degree of the inoculated plants was determined at the cotyledon and 4-5 leaf stages. To estimate score plant infection at the 4-5 leaf stage the Williams scale designed for plants inoculated at the cotyledon stage was modified. Resistance to the Polish fungus isolate proved to be a dominant character. At the cotyledon stage depending on the source of resistance, it was determined by four (in the broccoli-cauliflower line) or three (in PI USA) dominant complementary genes, while at the stage of 4-5 leaves – by a single dominant gene (in PI231210), two (in PI246077) or three (in the broccoli-cauliflower line) additive dominant genes.

Key words: broccoli, cauliflower, downy mildew, inheritance, resistance.

Brassica oleracea downy mildew caused by *Peronospora parasitica* is one of the most widespread diseases of cabbage plants in Poland. Most cultivars of head cabbage, and particularly of cauliflower, are susceptible to this pathogene. As a result of tests carried out in the U.S.A. (DICKSON 1989, pers. comm.) and in Poland (HOSER-KRAUZE et al. 1991), several sources of resistance to this pathogene were identified in *B. oleracea* species. Some preliminary experiments showed their resistance to an isolate from Skierniewice as well as to two others derived from the main regions of cabbage plant cultivation in Poland. This research was carried out to determine the mode of inheritance of resistance to the fungus isolate from Skierniewice.

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Correspondence: J. HOSER-KRAUZE, Department of Genetics and Breeding, Institute of Vegetable Crops, Rybickiego 15/17, 96-100 Skierniewice, Poland.

Material and methods

Sources of resistance to downy mildew at the cotyledon stage and at the stage of 4-5 leaves were:

- F_8 inbred line of the hybrid of broccoli resistant at the cotyledon and 4-5 leaf stages and cauliflower resistant only at the stage of 4-5 leaves,
- *B. oleracea* accessions PI246077 and PI231210, resistant both at the cotyledon and 4-5 leaf stages, obtained from the Plant Introduction Station Geneva, N.Y. USA.

These cultivars showed resistance to the fungus population derived from three different regions of Poland (HOSER-KRAUZE et al. 1994) and as well as to two races 1 and 2 found to be generally present in broccoli and cabbage plantings in New York (DICKSON 1989, pers. comm).

Resistant plants from the inbred lines (I_1) of these cultivars were crossed with susceptible cauliflower lines as maternal forms in the greenhouse in 1990. In 1991, F_1 hybrids were inoculated with downy mildew at the cotyledon stage and as well as at the 4-5 leaf stage. From each of the F_1 hybrids some 20 fully resistant plants were self-pollinated to obtain F_2 .

Susceptible and resistant parental lines as well as their F_1 and F_2 hybrids were tested for resistance to downy mildew in the greenhouse in 1992. Plant response to the pathogene was studied under controlled conditions at the cotyledon stage in the first decade of November and at the 4-5 leaf stage – in the last decade of November and in the first decade of December.

Cotyledons and leaves were inoculated through spraying with the fungus conidial suspension at the concentration of 10^5 spores per 1 ml water. The inoculated plants were held in a moist chamber at the 100% relative moisture (RM) and 16°C in darkness for 18 hours. Next, the plants were removed for five days into the greenhouse ($18\text{--}20^\circ\text{C}$). On the sixth day they were placed again at 16°C and 100% RM for 24 hours. On the seventh day they were scored for the disease. The inoculum production as well as inoculation conditions were in accordance with the WILLIAMS (1985) method.

The source of inoculum came from naturally infected leaves of cabbage cultivated in the autumn field growing conditions at the Institute of Vegetable Crops in Skierniewice. As mentioned above, the tested PI cultivars and the broccoli-cauliflower F_8 line, resistant to the isolate from Skierniewice were also resistant to two isolates derived from Central and Southern Poland (HOSER-KRAUZE et al. 1994).

The infection degree of the inoculated plants at the cotyledon stage was determined visually according to a 6-grade Williams scale. The infection scale was as follows:

0 – no symptoms,

1 – very few small necrotic spots to small necrosis on the lower surface of the cotyledon, the lack of sporing,

3 – very weak sporing on the upper or lower surface of the cotyledon, frequent necrotic spots, rarely scattered sporing on the upper or lower surface of the cotyledons, necrosis of tissue,

7 – strong to very strong sporing, chiefly on the lower surface, necrosis and chlorosis may occur,

9 – strong sporing on the lower surface of the cotyledon, slight or no necrosis and chlorosis.

The infection symptoms at the 4-5 leaf stage differed from those at the cotyledon stage by the lack of sporing in class 7 and 9. Instead of a strong sporulation, a strong necrosis and chlorosis of leaves was observed in class 7 and a very strong chlorosis to leaf degeneration – in class 9. For that reason plants from classes 0 to 3 at the cotyledon stage were considered resistant. At the stage of 4-5 leaves, individuals from classes 0-1 were described as resistant, while plants from class 3 – as moderately susceptible and those from classes 5 to 9 – as susceptible to very susceptible.

Results

The reaction of F_1 and F_2 hybrids of the broccoli-cauliflower line, PI246077 and PI231210 with susceptible cauliflower lines to *P. parasitica* (Pers.) ex Fr. showed their dominant resistance to this pathogene. To explain the plant segregation ratio of F_2 hybrid of broccoli-cauliflower with cauliflower, a hypothesis was accepted that plant resistance at the cotyledon stage was determined by four pairs of genes and that in the hybrid of PI246077 and PI231210 with cauliflower – by three pairs of genes acting complementarily. Values of the χ^2 test for four gene pairs amounting to 0.00024 ($P = 0.99-0.95$) and for three gene pairs equal to 0.3310 ($P = 0.80-0.50$) and 0.2160 ($P = 0.80-0.50$) (Table 1) proved the agreement between the F_2 plant segregation and theoretical segregation ratios, i.e. 243:13 and 54:10.

Resistance of F_1 plants at the stage of 4-5 leaves as well as predominance of resistant plants in F_2 (Table 2) indicate that this character is dominant. To explain the segregation of the F_2 hybrid of broccoli-cauliflower with cauli-

Table 1. Response of plants at the cotyledon stage to *P. parasitica*

Generation and pedigree	Plant segregation			No. genes pairs	χ^2	P
	observed		expected R : S			
	class 0-3 (R)	class 5-9 (S)				
P ₁ – susceptible lines of cauliflower	0	117				
P ₂ – resistant line of broccoli-cauliflower	66	0				
F ₁ (P ₁ × P ₂)	89	0				
F ₂	679	36	243 : 13	4	0.00024	0.99-0.95
P ₁ – susceptible lines of cauliflower	0	79				
P ₂ – resistant line <i>B. oleracea</i> v. <i>capitata</i> PI 246077	41	6				
F ₁ (P ₁ × P ₂)	57	18				
F ₂	278	56	54 : 10	3	0.331	0.80-0.50
P ₁ – susceptible lines of cauliflower	0	79				
P ₂ – resistant line <i>B. oleracea</i> v. <i>botrytis</i> PI 231210	39	10				
F ₁ (P ₁ × P ₂)	15	0				
F ₂	98	16	54 : 10	3	0.216	0.80-0.50

R – resistant, S – moderately and very susceptible

flower, the theoretical ratio 1:6:15:20:15:6:1 (6, 5, 4, 3, 2, 1 and 0 dominant alleles, respectively) for three dominant of additive action genes was applied. Symptoms of leaf infection were an increasing necrosis and a very weak sporulation of the fungus, which made possible to accurately distinguish only two groups of plants, namely resistant (0-1 classes) and all others as moderately susceptible (class 3) and susceptible (classes 5-9). Thus, a theoretical ratio was compared with an empirical one: 42:22, 42 being a sum of resistant genotypes (1+6+15+20 with 6, 5, 4 and 3 dominant alleles, respectively) and 22 – a sum of the remaining, moderately susceptible and susceptible genotypes (15+6+1 with 2, 1 and 0 resistance alleles, respectively).

The same hypothesis assuming an additive action of dominant genes was adopted to explain segregation of the F₂ hybrid of PI246077 with cauliflower.

Table 2. Response of plants at the 4-5 leaf stage to *P. parasitica*

Generation and pedigree	Plant segregation			No. genes pairs	χ^2	P
	observed		expected R : S			
	class 0-1 (R)	class 3-9 (S)				
P ₁ – susceptible lines of cauliflower	0	194				
P ₂ – resistant line of broccoli-cauliflower	57	6				
F ₁ (P ₁ × P ₂)	62	18				
F ₂	387	188	42 : 22	3	0.716	0.50-0.20
P ₁ – susceptible lines of cauliflower	0	73				
P ₂ – resistant line <i>B. oleracea</i> v. <i>capitata</i> PI 246077	35	8				
F ₁ (P ₁ × P ₂)	60	2				
F ₂	282	124	11 : 5	2	0.0935	0.80-0.50
P ₁ – susceptible lines of cauliflower	0	75				
P ₂ – resistant line <i>B. oleracea</i> v. <i>botrytis</i> PI 231210	30	10				
F ₁ (P ₁ × P ₂)	10	0				
F ₂	64	18	3 : 1	1	0.407	0.80-0.50

R – resistant, S – moderately and very susceptible

A theoretical segregation ratio for two pairs of genes was 1:4:6:1 (with 4, 3, 2, 1 and 0 dominant alleles, respectively). It was possible to express the above theoretical ratio as 11:5 showing a relationship between the sum of resistant genotypes (1+4+6 with 4, 3 and 2 resistance alleles), and the sum of moderately susceptible and susceptible genotypes (4+1 with 1 and 0 resistance alleles). The value of $\chi^2 = 0.7160$ (P = 0.50-0.20) for the segregation ratio 42:11 for three gene pairs as well as $\chi^2 = 0.0935$ (P = 0.80-0.50) for the segregation ratio 11:5 for two gene pairs (Table 2) confirmed a high degree of similarity between empirical data and theoretical ratios.

The segregation ratio 3:1 of F₂ hybrid of PI231210 with cauliflower ($\chi^2 = 0.407$, P = 0.80-0.50) indicated a monogenic inheritance of resistance.

Discussion

The response of F₁ and F₂ to the isolate of *P. parasitica* from Skierniewice indicated the existence of different genes determining resistance at the cotyledon and 4-5 leaf stages of plant development. This is in accordance with the previously obtained results (HOSER-KRAUZE et al. 1987).

Plant resistance at the cotyledon stage, statistically interpreted by the χ^2 test, was found to be governed by three or four dominant complementary genes. The introductions from the PI collection (USA) had three genes and the broccoli-cauliflower line of the Polish selection had 4 genes controlling their resistance to the pathogene. According to NATTI et al. (1967), resistance to the two races of *P. parasitica* was determined by two dominant independent genes. Although the ratio 3:1 indicated the action of a single gene, there were also plants among resistant individuals with a lower degree of resistance, which suggested the occurrence of some other genetic factors.

Resistance of plants at the 4-5 leaf stage was interpreted by the action of additive dominant genes. The number of genes depended on the source of resistance. Three gene pairs were responsible for resistance of the broccoli-cauliflower line, two gene pairs were responsible for resistance of PI246077 and a single dominant gene determined resistance of PI231210. The research on broccoli at the stage of more than 8 leaves, carried out by DICKSON and PETZODT (1993) confirmed that resistance may be determined by a single dominant gene as reported by NATTI et al. (1967). However, the continuous variation in the degree of resistance observed by them they explained by the action of modifying genes. Moreover, DICKSON and PETZODT (1993) noticed a supplementary effect of the plant age on resistance expression: out of 49 broccoli lines inoculated at the stage of 7 or more leaves, 40 lines were found to be resistant, while the same lines tested at the seedling stage appeared to be susceptible to the same fungus culture.

Thus it seems reasonable to introduce resistance to *P. parasitica* into susceptible lines from different sources to cumulate resistance genes. Inoculation should be done at the cotyledon and 4-5 leaf stages, and after selecting resistant plants – again at the stage of mature plants (with 7 or more leaves).

The results of this research confirm suggestions of the mentioned researchers, that there are more than only a single dominant gene of resistance, as well as a report by MOSS et al. (1988) explaining the inheritance of resistance in the local cv. Palermo Green by a model of action of two or three main genes.

Conclusions

The response of F₁ and F₂ to the isolate from Skierniewice indicated that resistance to *P. parasitica* is a dominant character, governed by different genes at the cotyledon stage than those at the stage of 4-5 leaves. At the cotyledon stage resistance was determined by three or four complementary dominant genes, depending on the source of resistance. At the stage of 4-5 leaves resistance was determined by a single dominant gene or 2-3 dominant additive genes, depending on the source of resistance. When introducing resistance genes into susceptible lines, several sources of resistance should be used to cumulate resistance genes.

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