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Assessment of parental lines, F_1 and F_2 sunflower hybrids to *Septoria* leaf spot infection and some inheritance patterns

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Abstract: The foliar fungal disease *Septoria* leaf spot is economically important for sunflowers. It develops most intensively during the wet and warm season. However, the genetic nature of sunflower resistance to *Septoria* leaf spot is still not clear. The purpose of our work was to identify some inheritance patterns of sunflower resistance to this disease based on the assessment of lines and hybrids of the first and second generations. The studied material was sown in 2020 and 2021 and subsequently grown on a stationary artificial infectious plot enriched with *Septoria helianthi* pathogen. The frequency of infection and the severity of infection of each sample were taken into account. The two-factor variance analysis revealed a significant influence of genotype on the frequency of infection in six sunflower lines and confirmed the effect of individuality of the response of individual genotypes to disease damage. It was shown that about 65 % of the total variation of the trait is due to the genetic nature of the line, and only a little more than 20 % and about 11 % – to the influence of the environment and the "genotype × environment" interaction respectively. Based on disease damage data in 2020 and 2021, the lines were classified as susceptible, moderately susceptible, moderately resistant and resistant. Differentiation of lines according to sensitivity to *Septoria* leaf spot made it possible to obtain hybrids with different manifestations of the trait in their parents. The nature of inheritance of infection frequency in F_1 sunflower hybrids was determined by the degree of dominance. As a result, it was revealed intermediate inheritance, as well as positive and negative overdominance of the trait. The severity of infection by *S. helianthi* pathogen in F_1 hybrids was inherited according to the type of parental form with greater resistance to the disease. F_2 populations were found to inherit infection frequency from the more resistant parent, showing a proportion of infected

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plants similar to that of the more resistant line from a given cross combination. It has been shown that the frequency of infection of the F_2 population with *Septoria* leaf spot can be affected by the severity of infection of F_1 plant with the pathogen *S. helianthi.*

Keywords: frequency of infection; inheritance pattern; lines, F_1 and F_2 hybrids; *Septoria* leaf spot; severity of infection; sunflower.

1 Introduction

Sunflower is the fourth largest oilseed crop in the world, because its cultivation is associated with a relatively short growing season. Sunflower is used in many industries, food and medicine (Fernandez-Luqueno et al. 2014).

The crop is usually grown in warm and temperate semi-arid climate regions of the world from Argentina to France, China, Turkey and Central Africa (Fernandez-Luqueno et al. 2014). In Ukraine, sunflower makes up 70 % of all cultivated oil crops, as it is a strategically important crop in agriculture. Ukraine is one of the main countries of the total world export of sunflower oil. However, the violation of crop rotation in many regions leads to a decrease in soil fertility and the spread of diseases (Polevoy et al. 2013).

Diseases have a negative effect on sunflower cultivation. Diseases are caused by viruses, bacteria and pathogenic fungi. Some diseases are the most damaging, such as leaf spots, including *Septoria* leaf spot (Leite 2014).

Sunflower *Septoria* leaf spot is caused by the fungus *Septoria helianthi*, which is widespread throughout the world. After damage, small spots of irregular shape from yellow to dark brown appear on the plants. The infection from the lower tiers gradually spreads to the upper leaves. Then the spots merge and the leaves wither and dry (Irum 2009). Under the action of the pathogen *S. helianthi*, there is a decrease in the content of chlorophyll in the leaf, a decrease in the yield and the weight of a thousand seeds (Brand et al. 2020; Irum 2009).

One of the more cost-effective methods compared to the use of chemicals in plant protection is the use of tolerant or resistant genotypes. The priority in the fight against *Septoria* leaf spot is genetic resistance, that is, the creation of resistant samples (Leite 2014).

However, the genetic nature of sunflower resistance to *Septoria* leaf spot is practically unknown today. Information about immunity in sunflower samples against the pathogen is quite scarce. Wild sunflower *Helianthus annuus* has only been reported to have genes for resistance to the pathogen (Block 2005). Gulya et al. (2010) also note that wild *Helianthus* species are better sources than cultivated sunflowers of some diseases resistance genes, including *Septoria* leaf spot. Variations in resistance to *Septoria* leaf spot among inbred lines of sunflower were quite briefly noted in their research by Carson and co-authors (1986).

More information about genetic resistance to *Septoria* is available in other crops, primarily wheat. In early studies of the genetic nature of wheat resistance to this disease, genes for immunity or complete resistance to *Septoria tritici* blotch were not detected, and the inheritance of resistance remained unclear (Nelson and Marshall 1990). Later studies of wheat resistance to *S. tritici* blotch in the field showed that the inheritance of resistance can follow dominant, partially dominant, epistatic, recessive, additive and non-additive gene action (Berraies et al. 2014). It was established that the level of resistance of some Iranian wheat genotypes (*Triticum aestivum* L.) to *S. tritici* blotch was under the control of additive and dominant gene effects (Sahbi et al. 2011). According to Chartrain et al. (2005), one line of Portuguese wheat had three specific genes for resistance to the pathogen, as well as good levels of nonspecific partial resistance. Complex genetic control of resistance to *Septoria* is indicated by the results of studies in which highly resistant genotypes of winter wheat were obtained in crossings with two susceptible parents (Wicki et al. 1999). The presence of significant intraspecific variability in sensitivity to *Septoria passerinii* and *Septoria melissae* was also noted in barley (Toubia-Rahme and Steffenson 2004) and *Melissa officinalis* (Kovács et al. 2019), respectively.

At the same time, some researchers point to monogenic control of disease resistance. Thus, studies of the inheritance of resistance in F_2 and F_3 offspring of Agili durum wheat to *S. tritici* blotch showed that resistance in this case is provided by one dominant gene (Sahbi et al. 2011). Kim and co-authors (2004) studied the inheritance of winter wheat resistance to leaf spot caused by the pathogen *Stagonospora nodorum*. They established that resistance in F_1 and F_2 was caused by one dominant gene. However, the phenotypic manifestation of the disease in F_3 did not follow a similar pattern of genetic control.

The purpose of our research was to differentiate a number of sunflower lines according to sensitivity to *Septoria* leaf spot, evaluate hybrids of the first and second generations from crossing lines with different contrast to the disease in the conditions of a stationary artificial infectious plot, and identify some features of inheritance of resistance to the pathogen.

2 Materials and methods

The research was carried out in 2020–2021 on the stationary artificial infectious plot of the Institute of Oilseed Crops of the National Academy of Agricultural Sciences. The stationary infectious plot was organized in the field crop rotation of the Institute of Oilseed Crops in 2005 to evaluate the breeding material of oilseeds for a complex of diseases, including *Septoria* leaf spot. Every year it is enriched with infected plant residues collected in different regions of the Ukraine. The stationary infectious plot of the Institute is located in the northwestern part of the Zaporozhye region of Ukraine.

Septoria leaf spot damage analysis was performed in sunflower breeding lines and their F_1 and F_2 hybrids. F_1 plants were obtained from crossing ZL22A, ZL58A, ZL70A, ZL78A, ZL169A lines (originator – Institute of Oilseed Crops of NAAS) with HA-R7 line (originating from the USA). The HA-R7 line was chosen because in some years it was the best in terms of resistance of *Septoria* leaf spot, including in 2019, when the material was screened for our research (Levitskaya and Lyakh 2022). Each F_2 family was derived from self-pollination of one F_1 plant with varying severity of infection.

The seeds of lines, F_1 and F_2 hybrids were sown by hand in three separate blocks. The seeds of the lines were sown in a block with randomization on single-row plots with 10 rows of holes with a distance between holes of 35 cm, two seeds per hole, in two replications. Hybrid seeds were sown without randomization. The seeds of F_1 samples were sown by hand in plots with 10 rows of holes with a distance between holes of 70 cm, two seeds per hole. The seeds of F_2 samples were sown according to the scheme of the first generation samples with a distance between holes of 35 cm. Plantings were made on April 23, 2020 and April 29, 2021. The plants were assessed on July 8–10, 2020 and July 14–17, 2021.

The weather conditions of 2020–2021 during the sunflower growing season were quite favorable for the development of *Septoria* leaf spot (Table 1).

It can be seen from the table that the temperature during the growing season of sunflower in both years of research was relevant for this region with continental climate. In general, the average monthly temperature indicators of 2020 and 2021 differed slightly from the multi-year average. As for the amount of precipitation, the years of research turned out to be quite contrasting. So, in June 2020, 73.9 mm of precipitation fell, while at this time in 2021, the amount of precipitation was 177.0 mm, which is three times more than the multi-year figure. The amount of precipitation for the entire growing season of sunflower (May–August) in 2020 was 198.5 mm, which does not exceed the average annual indicators. In 2021, 307.8 mm of precipitation fell during this period, which is significantly higher than the usual annual average. The wettest months were June and July (146.9 and 229 mm of precipitation, respectively), which are quite high humidity indicators for this region.

Therefore, the weather conditions of 2020 and 2021 in the first half of the growing season differed from the average long-term indicators with an increased amount of precipitation, especially in 2021. The air temperature was moderate during the two experimental years and practically did not differ from the long-term indicators. Such weather conditions were exceptionally favorable for the development of foliar fungal diseases.

Table 1: Weather conditions during growing season of sunflower, 2020-2021.

Indicators	**Year**	**Months**			
		V	**VI**	**VII**	**VIII**
Average temperature, t °C	2020	15.8	24.3	25.5	24.3
	2021	17.4	22.0	25.6	25.4
	Average longterm rates	16.0	19.4	22.6	21.2
Rainfall, mm	2020	73.0	73.9	27.6	24.0
	2021	39.8	177.0	52.0	39.0
	Average longterm rates	40.0	62.0	58.0	51.0

The assessment of the damage to the plant by *Septoria* disease was carried out in R 5.2–5.3 stages, by visual inspection of all leaves according to our modified scale: – no lesions on all leaves; ± only the lower leaves are affected (minor lesions); + affected leaves of the lower and middle part of the plant (average lesions); ++ lesion is present on all leaves (severe lesions) (Levitskaya et al. 2022).

Two indicators were taken into account – infection frequency (the susceptibility of the genotype or disease damage) and the severity of its infection (degree of damage). The first indicator was defined as a proportion of affected plants to the total number of plants, in percent. The severity of disease was calculated as a proportion of plants with lower, middle, and upper tier leaves infected to the actual number of plants, in percent.

Statistical processing of the obtained data was carried out using the Microsoft Excel application program package (Kronthaler 2023). To identify significant differences ($p < 0.05$) between the lines in susceptibility to *Septoria* leaf spot, a two-factor analysis of variance (ANOVA) was performed. A paired *t*-test for the means was used to identify differences between certain lines. The strength of the influence of the genotype, environment and their joint action on the manifestation of the analyzed trait was determined by the Plokhinsky method (Lakin 1990).

The percentage error was determined by the formula:

$$s_p = \sqrt{\frac{P \times (100 - P)}{n}},$$

where s_p is the percentage error; P is the percentage of infected plants; n is the total number of analyzed plants (Rokitsky 1973).

The nature of the dominance of infection frequency in the first generation of hybrids was determined by the formula:

$$h_p = \frac{F_1 - MP}{P - MP},$$

where F_1 is the arithmetic mean of the first generation hybrids; MP is the arithmetic mean of the characteristics of two parental forms; P is the arithmetic mean of the parent form with a higher level of the trait (Beil and Atkins 1965).

According to the value of h_p, the nature of inheritance was determined, taking into account that: $h_p = 0$ – absence of dominance; $h_p > +1.0$ – positive overdominance (heterosis); $+0.5 < h_p \leq +1.0$ – positive dominance; $-0.5 \leq h_p \leq +0.5$ – intermediate inheritance; $-1.0 \leq h_p < -0.5$ – negative dominance; $h_p < -1.0$ – negative overdominance (depression).

Dominance coefficients were not determined in the case when the difference between parental forms according to Student's *t*-test was insignificant.

3 Results and discussion

3.1 Evaluation of sunflower lines by *Septoria* leaf spot susceptibility and their differentiation

The conducted two-factor variance analysis of *Septoria* leaf spot damage indicators of six linear sunflower samples during 2020–2021 revealed a significant ($p < 0.05$) influence of genotype, environment, as well as the combined effect of “genotype × environment” on the level of phenotypic manifestation of the infection frequency, and thus statistically confirmed the effect of weather conditions of the year and the individuality of the response of individual genotypes to disease damage. An assessment of the influence of factors on the resulting trait, which was determined using the Plokhinsky method, showed that about 65 % of the total variation of the trait is due to the genetic nature of the line, a little more than 20 % – to the influence of the environment, and only about 11 % – to the “genotype × environment” interaction (Table 2).

As can be seen from Table 2, the studied six sunflower lines create a series by *Septoria* leaf spot damage: ZL58A, ZL22A, ZL169A, HA-R7, ZL78A, ZL70A, where the ZL58A line is characterized by the highest expression of the symptom, and the ZL70A sample is the lowest. Despite the fact that this order is rather arbitrary due to the variation of the trait by year, it gives a general idea of the material used by us for obtaining hybrids and analyzing inheritance.

Based on *Septoria* infection data in 2020 and 2021, ZL58A and ZL22A were classified as susceptible, HA-R7 as moderately susceptible, ZL169A as moderately resistant, and ZL78A and ZL70A as resistant. The last two lines showed stability in both years of research, differing significantly from all other lines.

A paired *t*-test for the means showed that the HA-R7 line significantly ($p < 0.05$) differed in *Septoria* leaf spot susceptibility from all other five lines in 2020, and from ZL58A, ZL78A and ZL70A in 2021. However, in hybrids with its participation, in some cases, it acted as a more stable parent (ZL22A × HA-R7 and ZL58A × HA-R7), in others – as a less stable component of crossing (ZL70A × HA-R7, ZL78A × HA-R7, ZL169A × HA-R7).

Table 2: Infection frequency with *Septoria helianthi* among sunflower lines on a stationary artificial infectious plot, 2020–2021.

Line	Infected plants, %		Infection response
	2020	2021	
ZL22A	89.2 ± 0.78^{ab}	94.7 ± 1.53^{b}	S
ZL58A	97.9 ± 1.24^{ab}	100^{ab}	S
ZL70A	12.5 ± 0.2^{a}	34.8 ± 7.58^{a}	R
ZL78A	12.9 ± 0.17^{a}	59.0 ± 9.36^{a}	R
ZL169A	21.9 ± 1.79^{ab}	88.6 ± 6.41^{b}	MR
HA-R7	38.2 ± 4.25^{b}	92.1 ± 1.88^{b}	MS

[a] Differences from HA-R7 line are significant at $p < 0.05$; [b] differences from ZL70A and ZL78A lines are significant at $p < 0.05$; S = susceptible, MS = moderately susceptible, R = resistant, and MR = moderately resistant.

3.2 Evaluation of *Septoria* leaf spot damage of sunflower lines and hybrids

Tables 3 and 4 show the data obtained in 2020 and 2021 on the infection frequency and severity of infection of the lines, F_1 hybrids from the crossing of Zaporozhye breeding lines with the HA-R7 line and F_2 hybrids after F_1 self-pollination.

As can be seen from Table 3, the line HA-R7, which acted as the male parent for the hybrids of the first and second generations, had about 40 % of plants affected by the disease. The leaves of the lower (20.2 % of plants) and middle (18.2 % of plants) tiers were mainly affected. No damage to the entire plant was detected. The ZL22A line was much more affected by *Septoria* leaf spot than the HA-R7 line (89.2 % of affected plants). The majority (58.5 %) of the plants had symptoms of the disease on

Table 3: Assessment of *Septoria* leaf spot infection in the parental lines, F_1 and F_2 sunflower hybrids, 2020.

Genotype	Severity of infection in F_1 plant	Number of plants	Severity of infection, %				Infected plants, %
			−	±	+	++	
		Parental lines					
ZL22A			10.8	1.5	58.5	29.2	89.2
ZL58A			2.1	6.5	45.7	45.7	97.9
ZL70A			87.5	12.5	–	–	12.5
ZL78A			87.1	12.9	–	–	12.9
ZL169A			78.1	15.6	6.3	–	21.9
HA-R7			61.8	20.0	18.2	–	38.2
		F_1 hybrids					
ZL22A × HA-R7		52	44.2	48.1	5.8	1.9	55.8
ZL58A × HA-R7		26	19.2	57.7	19.2	3.9	80.8
ZL70A × HA-R7		77	79.8	19.5	–	1.3	20.8
ZL78A × HA-R7		20	60.0	35.0	5.0	–	40.0
ZL169A × HA-R7		37	83.8	16.2	–	–	16.2
		F_2 hybrids					
ZL58A × HA-R7	−	163	76.7	6.7	12.9	3.7	23.3
ZL58A × HA-R7	−	184	75.0	10.9	13.6	0.5	25.0
ZL58A × HA-R7	+	21	61.9	28.6	9.5	–	38.1
ZL58A × HA-R7	+	33	69.7	24.2	6.1	–	30.3
ZL70A × HA-R7	−	160	86.2	10.6	3.1	–	13.8
ZL78A × HA-R7	−	167	86.2	9.6	4.2	–	13.8

Table 4: Assessment of *Septoria* leaf spot infection in the parental lines, F_1 and F_2 sunflower hybrids, 2021.

Genotype	Severity of infection in F_1 plant	Number of plants	Severity of infection %				Infected plants,%
			−	±	+	++	
Parental lines							
ZL22A			2.5	10.0	37.5	50.0	97.5
ZL58A			–	–	29.8	70.2	100.0
ZL70A			65.2	17.4	17.4	–	34.8
ZL78A			50.0	36.8	13.2	–	50.0
ZL169A			11.4	71.4	17.2	–	88.6
HA-R7			7.9	58.8	33.3	–	92.1
F_1 hybrids							
ZL22A × HA-R7		12	8.3	58.4	33.3	–	91.7
ZL70A × HA-R7		20	40.0	55.0	5.0	–	60.0
F_2 hybrids							
ZL22A × HA-R7	−	144	74.3	13.9	8.3	3.5	25.7
ZL22A × HA-R7	+	106	33.0	23.6	8.5	34.9	**67.0**
ZL22A × HA-R7	+	116	15.5	28.5	36.2	19.8	**84.5**
ZL58A × HA-R7	−	131	39.7	26.7	19.8	13.8	60.3
ZL58A × HA-R7	−	60	51.7	13.3	25.0	10.0	48.3
ZL58A × HA-R7	−	93	12.9	19.3	31.2	36.6	87.1
ZL58A × HA-R7	−	114	12.3	11.4	40.4	35.9	87.7
ZL58A × HA-R7	+	103	11.7	13.6	25.2	49.5	88.3
ZL58A × HA-R7	+	133	14.3	28.6	42.1	15.0	85.7
ZL58A × HA-R7	+	59	40.7	15.3	23.7	20.3	59.3
ZL58A × HA-R7	+	82	28.0	22.0	29.3	20.7	72.0
ZL58A × HA-R7	+	121	–	12.4	28.9	58.7	100
ZL70A × HA-R7	−	85	42.4	38.8	16.5	2.4	57.6
ZL70A × HA-R7	−	90	47.8	35.6	15.5	1.1	52.2
ZL70A × HA-R7	+	97	29.9	35.0	32.0	3.1	70.1
ZL70A × HA-R7	+	100	59.0	32.0	9.0	–	41.0
ZL78A × HA-R7	−	74	37.8	28.4	23.0	10.8	62.2
ZL78A × HA-R7	−	103	46.6	27.2	17.5	8.7	53.4
ZL78A × HA-R7	±	89	46.1	13.5	21.3	19.1	53.9
ZL78A × HA-R7	±	114	18.4	24.6	35.1	21.9	**81.6**
ZL169A × HA-R7	−	83	48.2	37.3	14.5	–	51.8
ZL169A × HA-R7	−	115	52.2	34.8	11.3	1.7	47.8
ZL169A × HA-R7	±	70	40.0	15.7	41.4	2.9	60.0
ZL169A × HA-R7	±	99	55.6	34.3	10.1	–	44.4

Bold indicates a significant excess in infection frequency over F_2 families from uninfected F_1 plants within one crossing combination.

the leaves of the lower and middle tiers, and about 30 % of the plants – on the leaves of the entire plant. Only 1.5 % of plants had minor damage. The F_1 hybrid of the ZL22A × HA-R7 combination was affected by the disease less than the ZL22A line, but more than the HA-R7 line. Most of the hybrid plants (48.1 %) had minor damage, that is, they were characterized by damage to the leaves of only the lower layer. There were quite a few plants with more severe damage.

Among the lines, ZL58A had the most disease damage. Thus, 97.9 % of the plants of this line were affected by *Septoria* leaf spot. One half of these plants had mid-layer leaves affected, while the other half had the entire plant affected. There were only 6.5 % of plants with a minor degree of damage. The F_1 hybrid ZL58A × HA-R7 was characterized by severe disease damage (80.8 % of affected plants), but was more resistant than ZL58A by this indicator. Significant differences from the maternal line were observed in terms of the degree of damage. Most of the affected hybrid plants had symptoms of the disease only on the leaves of the lower tier (57.7 % of plants). There were very few plants with severe damage (3.9 %).

One of the least affected maternal lines was the ZL70A line. There were only 12.5 % of affected plants. The degree of damage to the plants was insignificant, that is, only the leaves of the lower tier were affected. The F_1 hybrid ZL70A × HA-R7 had 20.8 % of plants affected by *Septoria* leaf spot. Almost all affected plants showed symptoms of the disease mainly on the leaves of the lower tier, as did the parent line ZL70A of this hybrid.

Line ZL78A, like the previous line ZL70A, was the least affected by the disease. It was also similar to the ZL70A line in terms of quantitative and qualitative indicators of damage. There were about 13 % of diseased plants, and all of them had lesions only on the lower leaves. The F_1 hybrid ZL78A × HA-R7 had 40.0 % of plants affected by the disease. According to the degree of damage, almost all of them (35 %) were characterized by minor damage, as was the ZL78A line.

Line ZL169A in 2020 was quite resistant to *Septoria* leaf spot and had about 80 % of healthy plants. Only slightly more than 20 % of the plants were affected by the disease, of which 15.6 % had minor lesions, and 6.3 % of the plants had symptoms of the disease on the lower and middle layers of the leaves. The F_1 hybrid of the ZL169A × HA-R7 combination was close to the maternal line of the hybrid in terms of damage and had 83.8 % healthy plants. 16.2 % of plants were affected by *Septoria* leaf spot. All of them had a slight degree of damage, characteristic of the ZL169A line.

Table 4 shows that compared to 2020, in 2021 both lines and hybrids of the first and second generations were much more affected by *Septoria* leaf spot. The HA-R7 line in 2021 had more than 90 % of affected plants and was almost indistinguishable from the most susceptible to *Septoria* leaf spot lines – ZL22A and ZL58A. However, the majority of HA-R7 plants (58.8 %) had lesions on the lower leaves, and a third of the affected plants had lesions on the leaves of the lower and middle tiers. Line ZL22A was one of the highly susceptible to the disease, as in 2020. 97.5 % of the plants were affected by the pathogen, of which 10.0 % of the plants had minor damage, 37.5 % had moderate damage, and 50.0 % of the plants had severe damage.

The ZL58A line was the most affected by *Septoria* leaf spot, as in 2020. She had 100 % affected plants. According to the severity of infection, more than 70 % of the plants of this line had damage to the entire plant. The ZL70A line was the least affected among the lines, although it had a higher percentage of diseased plants in 2021 (34.8 % vs. 12.5 % in 2020) compared to the previous year. Affected plants had a slight and medium degree of damage, i.e. they had symptoms of the disease on the leaves of the lower and middle layers. In 2021, the ZL78A line had 50.0 % affected plants. The severity of infection in 36.8 % of diseased plants was insignificant, and in 13.2 % – average. Line ZL169A had 88.6 % of plants affected by *Septoria* leaf spot, although in the previous year there were only 21.9 %. According to the degree of damage, the largest number of diseased plants (71.4 %) had symptoms of the disease on the leaves of the lower tier, and 17.2 % of the affected plants had medium damage.

The F_1 hybrid of the ZL22A × HA-R7 combination, as well as both parent lines of the hybrid, had a rather strong disease lesion – 91.7 %. However, the severity of infection of the hybrid practically did not differ from the parent line HA-R7. Most of the plants (58.4 %) had minor damage, and 33.3 % had moderate damage. The F_1 hybrid ZL70A × HA-R7 had 60.0 % of plants affected by *Septoria* leaf spot, and the severity of infection varied from slight (55.0 % of plants) to moderate (5.0 % of plants).

3.3 Inheritance of susceptibility to *Septoria* leaf spot in F_1 and F_2 sunflower hybrids

The nature of inheritance of *Septoria* leaf spot damage in the first generation of sunflower hybrids was determined by the degree of dominance (Table 5).

The degrees of dominance obtained in 2020 based on the results of the analysis of the F_1 hybrids in most cases revealed intermediate inheritance, as well as positive and negative overdominance of the trait “infection frequency”. For the F_1 hybrid ZL70A × HA-R7, the indicator of the degree of dominance did not change in 2021, demonstrating the intermediate inheritance of the investigated trait.

The analysis of the F_1 hybrids and their parental components carried out in 2020 proved that the hybrids inherited the severity of infection characteristic of a more resistant line from this crossbreeding combination (Table 3). In F_1 hybrids ZL22A × HA-R7 and ZL58A × HA-R7, the HA-R7 line was more stable. Affected plants of these hybrids showed symptoms of the disease mainly on the leaves of the lower and

Table 5: The degree of dominance of *Septoria* leaf spot symptoms in the first generation of sunflower hybrids.

Genotype of F_1 hybrid	Degree of dominance	Type of inheritance
2020		
ZL22A × HA-R7	−0.31	Intermediate inheritance
ZL58A × HA-R7	0.43	Intermediate inheritance
ZL70A × HA-R7	−0.35	Intermediate inheritance
ZL78A × HA-R7	1.14	Positive overdominance
ZL169A × HA-R7	−1.7	Negative overdominance
2021		
ZL70A × HA-R7	−0.12	Intermediate inheritance

middle tiers, just like the HA-R7 line, in contrast to lines ZL22A and ZL58A, in which symptoms of the disease were observed on the leaves of the middle tier or the entire plant. In three other hybrids of the first generation (ZL70A × HA-R7, ZL78A × HA-R7 and ZL169A × HA-R7), the HA-R7 line was less resistant to the maternal components of the hybrids. The symptoms of the disease in the specified hybrids were observed mainly on the leaves of the lower layer, as well as in the lines more resistant to HA-R7 – ZL70A, ZL78A and ZL169A. A similar pattern can be observed in 2021 when analyzing F_1 hybrids of ZL22A × HA-R7 and ZL70A × HA-R7 crossing combinations (Table 4).

Analyzing the resistance to *Septoria* leaf spot of F_2 families, it is possible to identify the pattern of inheritance of the trait “infection frequency” according to the type of a more resistant parent. Thus, in populations F_2 of crossing combinations ZL70A × HA-R7 and ZL78A × HA-R7 under the conditions of a stationary artificial infectious plot of 2020, there were about 14 % of infected plants, while resistant parents showed about 13 % of diseased plants (ZL70A and ZL78A), respectively, and unstable parent −38 % (HA-R7). In F_2 populations, combinations of crossing ZL58A × HA-R7 plants with symptoms of the disease ranged from 23.3 to 38.1 %, while the more resistant parent from this pair of HA-R7 showed 38 % of the affected plants, and the non-resistant ZL58A – about 100 % (Table 3). A similar pattern can be traced in 2021, despite the fact that the disease damage of all analyzed plant material was significantly higher than in 2020 (Table 4).

When assessing the F_2 populations in 2020, the presence of *Septoria* blight on the F_1 hybrid plant was taken into account, as a result of self-pollination of which this population of F_2 hybrids was obtained. As can be seen from Table 3, the F_2 populations of the ZL58A × HA-R7 combination, obtained from F_1 plants not affected by

Septoria leaf spot, included about 75 % of plants free from infection. In turn, F_2 populations from self-pollination of F_1 hybrids with disease symptoms on the whole plant had from 61.9 to 69.7 % of healthy plants. The small volume of the last two plant populations F_2 combination ZL58A × HA-R7 is due to poor seed germination, which was only 10.5–16.5 %. Plants of the second generation of crossing combinations ZL70A × HA-R7 and ZL78A × HA-R7 were obtained only from F_1 plants not affected by *Septoria* leaf spot. The F_2 hybrids of these combinations were found to be more resistant than the F_2 populations of the ZL58A × HA-R7 combination, showing more than 86 % of plants free of *S. helianthi* pathogen at all.

In 2021, F_2 populations of all five crossing combinations were evaluated for resistance to *Septoria* leaf spot (Table 4). Within each combination, both progeny of healthy F_1 hybrid plants and F_1 plants with disease symptoms were presented. Comparing three F_2 populations of the ZL22A × HA-R7 cross combination with each other, it can be seen that the population obtained from the self-pollination of the F_1 hybrid plant without symptoms of the disease significantly exceeded the two other populations in resistance to *Septoria*, which were the offspring of the F_1 hybrid plants with severe damage to the entire plant. Within the ZL58A × HA-R7 combination, F_2 families varied significantly in disease incidence both in the group of progeny from healthy F_1 plants and infected ones. However, the range of variation in the first case was 48.3–87.7 %, and among F_2 families from F_1-affected plants it was 59.3–100 %. In the ZL70A × HA-R7 cross combination, families were also found to have significantly more *Septoria* leaf spot damage when they were obtained from F_1 infected plants.

It should be noted that the nature of the manifestation of the quantitative trait in hybrids is determined by the ratio of recessive and dominant alleles and the features of the interaction of genes in parental forms, as well as the specificity of the reaction of the hybrid genotype to the factors of the growth environment. The degrees of dominance obtained from the analysis of the first generation of hybrids revealed intermediate inheritance of the “infection frequency” trait in three out of five hybrids. Overdominance effects were also observed. The significant dependence of the degree of dominance of *Septoria* leaf spot damage on the combination of crossings indicates that genes with an additive effect play an important role in the control of the trait in some lines, while overdominance effects are observed in others. Resistance to *Septoria* foliar disease due to additive and dominant gene effects was previously observed in wheat (Bastam et al. 2010; Simon et al. 2004; Zhang et al. 2001).

In our earlier studies on limited material and under the conditions of 2019, which specifically affected the manifestation of *Septoria* leaf spot in sunflower hybrids, we assumed the presence of cytoplasmic effects and the dominance of sensitivity in the genetic control of this disease (Levitskaya and Lyakh 2022). But subsequent and more extensive research formed our opinion that most F1 hybrids were characterized by intermediate inheritance of the trait “infection frequency”, and the severity of infection by the pathogen was inherited according to the type of parental form with greater resistance.

As already noted in our work, sometimes the offspring of F_1 hybrid plants infected with the pathogen *S. helianti* were characterized by a higher infection frequency compared to the offspring of healthy F_1 plants. This fact testifies in favor of the fact that the infection could be transmitted with seeds, which led to a higher proportion of diseased plants in F_2. With respect to sunflower, there is still a discussion about the transmission of this infection by seeds. However, the possibility of spreading *Septoria* disease with seeds has been convincingly shown in other crops (Majumder et al. 2013; Tok and Kurt 2019).

4 Conclusions

In terms of *Septoria* leaf spot damage, the studied sunflower lines of Zaporizhzhya breeding and the HA-R7 line of USA origin create a series of ZL58A, ZL22A, ZL169A, HA-R7, ZL78A, ZL70A, where the ZL58A line is characterized by the highest trait value, and the ZL70A sample is the lowest. Based on *Septoria* infection data in 2020 and 2021, ZL58A and ZL22A were classified as susceptible, HA-R7 as moderately susceptible, ZL169A as moderately resistant, and ZL78A and ZL70A as resistant.

According to the results of the two-factor variance analysis of *Septoria* leaf spot damage indicators of six linear sunflower samples, a significant ($P < 0.05$) influence of genotype, environment and the interaction “genotype × environment” on the level of phenotypic manifestation of the trait “infection frequency” was revealed. It was shown that about 65 % of the total variation of the trait is due to the genetic nature of the line, slightly more than 20 % – to the influence of the environment, and about 11 % – to the “genotype × environment” interaction.

The analysis of the first generation hybrids obtained from the crossing of the Zaporizhzhya breeding lines with the HA-R7 line, in most cases, revealed intermediate inheritance, as well as positive and negative overdominance of the “susceptibility to *Septoria* leaf spot” trait. This indicates that the genetic control of *Septoria* leaf spot damage is carried out by an additive-dominant system of genes.

It was established that in F_1 sunflower hybrids, the severity of infection by *S. helianthi* pathogen was inherited according to the type of parental form with greater resistance to the disease.

F_2 populations inherited *Septoria* leaf spot resistance from the more resistant parent, showing a proportion of infected plants close to the more resistant line from this cross combination. It was found that the number of plants affected by *Septoria* leaf spot in the F_2 population can be affected by the presence or absence of pathogen infection in the F_1 hybrid plant.

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