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The inheritance and durability of scab resistance in apple progenies

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***Summary**:* In order to select the appropriate parent cultivars and maintain the durability of resistance, it is important to clarify the mechanisms of inheritance of scab resistance depending on the parents. It has been known that the progeny segregation ratios based on scab-resistance do not depend only on the genotype of the resistance locus but also on the genetical makeup of the donor and recipient parents as well as on the susceptible parent.

The aim of this study has been to demonstrate what factors in the Vf, Vr and VA scab-resistant cultivars – combined with susceptible and resistant parents – affect the inheritance and durability of resistance in seedlings in their first 4 year's growing.four years' growth. After inoculating apple seedlings sown in 2001 with the suspension of *Venturia inaequalis* (Cke.) Wint. in the greenhouse, we studied the segregation ratios of the progenies into reaction classes. Seedlings showing resistance in the greenhouse were also evaluated for scab-resistance after they had been moved to the field and had naturally been infected with the pathogen in 2002 and 2004.

The majority of our results obtained in the greenhouse test, similarlyly to earlier experiences, have not justified monogenic inheritance at the phenotypic level. The effect of susceptible parent cultivars on the segregation ratio of progenies have become apparent again. The high infection rate of seedlings in the field trials, which had previously exhibited varying degrees of resistance in the greenhouse test, has raised concern. Our data has raised further doubts, concerning the durability of Vf resistance in Hungary. It is assumed that the composition of natural field populations of *Venturia inaequalis* in Szigetcsép has changed. The complexity of Vf resistance has been confirmed. The high infection rate in the progenies derived from Vf resistant cultivars draws the attention to the importance of utilizing additional sources of resistance.

***Key words:** Malus x domestica*, inheritance, scab-resistance, cultivar, apple

Introduction

In apple cultivar development, one of the main breeding objectives is to obtain cultivars resistant to pathogens. This is due to the fact that customers require fruits free from chemical residues, and reducing pesticide use to limit toxicological and environmental problems is also inevitable.

In most breeding programmes, the aim is to obtain multiple resistance, but usually the first step of selection is to select for scab-resistance. In order to choose the appropriate parent cultivars and to maintain the durability of resistance, the inheritance of scab-resistance has always been in the focus of attention. However, the mechanisms of the inheritance of resistance, due to the specific plant-pathogen interaction, have not yet been fully elucidated. The characteristics of *Venturia inaequalis* (Cke.) Wint. (the increasing number of its physiological races), the different types of scab-resistance (horizontal, vertical, ontogenetical), the characteristics of genes encoding resistance in different cultivars, and the variable nature of all these elements make the issue rather complex.

The breeding of apples resistant to *Venturia inaequalis* (Cke.) Wint. is a genetically-based strategy for the control of this pathogen (*Crosby* et al. 1992). To obtain resistance, breeders originally reached back to either wild *Malus* species, or looked at old cultivars to select individuals which could be used as resistant parents (*Kellerhals* 1989). *Lespinasse* (1989) as well as *Fischer M.* & *Fischer C.* (1993) described monogenic and polygenic gene sources. In apple breeding, the most often used method is to cross a resistant cultivar (of best quality) with a cultivar of good quality and high yield.

As a result of interspecific origin, apple cultivars have an intricate genetical makeup. It is rather difficult to clarify the rules of the mechanisms of inheritance in the cross-pollinated, heterozygous apple. According to *Lespinasse* (1989), scab-resistance is conferred by 6 dominant genes (Vf, Vr, Vb, Vbj, Vm, VA), which were named after *Malus* taxa.

The majority of today's scab-resistance cultivars carry the Vf gene. This was first thought to be monogenic, but later many researchers pointed out that this type of resistance was conferred by several genes, which accounts for its relative durability (*Biehn* et al. 1966; *Rouselle* et al. 1974; *Lespinasse*

1990. cit. *Kellerhals* 1991). The Vr gene derived from *Malus pumila* provides high resistance. It is most probable that there are 3 dominant and several complementer genes in this locus (*Dayton & Williams* 1968; *Shay* et al. 1953; *Spangelo* et al. 1956). The VA resistance derived from 'Antonovka' is also conferred by several genes.

According to *Gessler* (1992), choosing the appropriate parents, on both the resistant and susceptible sides, can be crucial in optimising the ratio of resistant seedlings. Earlier results (*Lamb & Hamilton*, 1969, *Kellerhals*, 1989, *Kellerhals & Furrer*, 1994, *Fischer*, 1994, *Tóth* et al., 1997) demonstrated that the ratio of resistant seedlings depended not only on the locus genotype of resistance but also on the genetical makeup of the donor and recipient parents. *Rouselle* et al. (1974), *Kellerhals et al.* (1993), *Tóth* et al. (1998), and *Gelvonauski & Gelvonauskiené* (2004) proved that the susceptible parent could significantly affect the segregation ratios of the progenies in respect to resistance.

Within the framework of the apple breeding programme initiated at the Department of Fruit Science of the Corvinus University of Budapest in the 1990s, following the phytopathological evaluation of plants for scab-resistance, we have been carrying out inheritance studies and assessment. The aim of our present research was to assess in seedlings sown in 2001 how the scab-resistant Vf, Vr and VA cultivars used as parents, and combined with susceptible and resistant parents, affected the segregation of progenies to leaf reaction classes, and the segregation ratio of resistant and susceptible seedlings. First, we studied the inheritance of resistance by parent combinations in 2001, after inoculating the seedlings with the suspension of *Venturia inaequalis* in the greenhouse. In subsequent field trials carried out in 2002 and 2004, we traced the changes in the resistance of seedlings that had previously proved to be resistant in the greenhouse test.

Material and methods

In addition to the resistant 'Prima' (Vf) cultivar that had been previously tested (*Tóth* et al., 1997, *Quang* et al., 1997), out of the scab-resistant cultivars, other Vf resistant cultivars such as 'Retina', 'Renora' and 'Rewena', as well as 'Reka' carrying the Vr gene, and 'Reglindis' with polygenic resistance were included in our tests. To study the effect of susceptible cultivars, 'Idared' and 'Golden Delicious' were used as female parents, combined with scab-resistant cultivars of different genotypes. The Vf resistant 'Liberty' as female parent was combined with 3 scab-resistant pollen parents of different genotypes (Vf, Vr és VA).

After stratification, germinating seeds obtained from the crosses made in 2000 were sown in the greenhouse in January of 2001, and the seedlings at the stage of 2–3 leaves were inoculated with a 2,5–4,0 x 10^5 conidia/ml suspension of *Venturia inaequalis* (Cke.) Wint. After an incubation period of 3 days (18–20 °C, and 90–100% RH), temperature and humidity were kept at 20–22 °C and 70%, respectively. Inoculation, incubation and post-inoculation were repeated after 10–12 days.

After the incubation period was over, symptoms occurring on the leaves of susceptible plants were evaluated by using the 6 class-scale of *Chevalier et al.* (1991), and seedlings belonging to class 4, exhibiting extensive sporulation were regarded as susceptible and were eradicated. Seedlings belonging to reaction classes 0, 2, 3A and 3B, showing resistance in the greenhouse, were moved and planted in the field. The reaction class given to the plant in the greenhouse was marked on each of them, in order to evaluate later the possible changes in resistance by each class. In the field, seedlings were evaluated for their resistance in June and September of 2002 and 2004, after being infected naturally. Plants whose leaves exhibited extensive sporulation were regarded as susceptible, while the rest was considered resistant.

For statistical analysis, chi-squared (homogenity) test was used. When assessing the resistance of the seedlings, they were grouped into resistant or susceptible categories on the basis of the same male or female parent, and were compared by pairs. If the calculated χ^2 value was less than the predicted χ^2value, the two tested distributions were regarded as homogeneous, whereas in other cases it was considered heterogeneous. With this method, it can be determined how the parents affect the inheritance of resistance or susceptibility to scab in the progenies. Hybrids with the same distribution have been marked with the same letter of the alphabet. If the distributions of 2 or 3 progenies derived from the same pollen or female parent are the same, the genotype of this parent is crucial in the inheritance of resistance or susceptibility.

Results

When demonstrating the results, time order is followed. First, the results of the evaluation carried out after the artificial inoculation to make early selections in the greenhouse are shown, followed by the results of the field trials. Finally, conclusions on inheritance are drawn on the basis of the joint data of the two tests.

In 2001, none of the plants in the greenhouse exhibited pin point pits characteristic of the hypersensitive reaction. Subsequently, seedlings were evaluated in the field until 2004, where they were planted in-row spacing used at nurseries and were not treated with chemicals. Results are shown in *Tables 1–3.* and in *Figures 1–3*.

According to the results of the greenhouse test (*Figure 1*), the ratio of the susceptible seedlings belonging to class 4 showed significant variations by progenies. Among the 11 progenies tested, values ranged from 4 to 82%. Nonetheless, apart from 1 progeny ('Idared' x 'Reglindis'), the percentage of seedlings belonging to class 4 did not reach 50%.

The groups that can be created on the basis of the female cultivars (separated with dotted line in the Table) make it possible to compare the effect of the pollen parents with

Table 1 Distribution of progenies according to resistant classes after artificial scab-infection in the greenhouse (2001)

Parentage	No. of Seedlings	% in resistance classes						Female*
		0	1	2	3A	3B	4	
Idared x Prima (Vf)	89	15	0	24	26	16	20	a
Idared x Retina (Vf)	133	36	0	26	8	0	29	
Idared x Renora (Vf)	73	11	0	15	10	29	36	
Idared x Reka (Vr)	120	13	0	29	23	18	18	a
Idared x Reglindis (VA)	154	1	0	0	2	15	82	
Golden Delicious x Prima (Vf)	98	4	0	5	21	28	42	b
Golden Delicious x Reka (Vr)	50	20	0	22	16	38	4	
Golden Delicious x Reglindis (VA)	73	0	0	5	14	44	37	b
Liberty (Vf) x Rewena (Vf)	110	6	0	21	29	29	15	c
Liberty (Vf) x Reka (Vr)	120	2	0	15	27	18	39	
Liberty (Vf) x Reglindis (VA)	93	8	0	25	17	32	18	c

Notes:

- *Letters in the column signed by * indicate similar distributions on the basis of x^2 tests in case of the same parents at 95% probability level.*
- *resistant = class 0, 1, 2, 3A and 3B, susceptible = class 4.*

different genotypes on the inheritance of resistance. The distribution by reaction classes of the progenies derived from the susceptible 'Idared' as female parent (*Figure 1*) differed by the male parents, in respect to the different resistance genes (Vf, Vr és VA) as well as within the cultivars with Vf resistance. The data have implied that the interaction between 'Idared' and the five resistant cultivars tested resulted in special combinations.

Regarding the pollen parents carrying the Vf allele, in two-third of the seedlings derived from the cross 'Prima' and 'Retina' the leaves did not exhibit sporulation. Furthermore, among the seedlings derived from the cross 'Idared' x 'Retina', the percentage of symptom-free seedlings belonging to class 0 was outstanding (36%). Among the progeny of the cross 'Idared' x 'Renora', the ratio of susceptible seedlings (class 4) was also 36% , but together with class 3B the rate of seedlings exhibiting sparse sporulation was 65%.

On the leaves of the majority of seedlings derived from the cross 'Idared' x 'Reka' (Vr), symptoms were moderate (2, 3A and 3B), and the percentage of susceptible seedlings was low (18%). In *Figure 1*, data concerning the progenies of the cross 'Idared' x 'Reka' imply a certain version of additive gene effect. Among the progenies of the cross of the polygenic resistant 'Reglindis' and 'Idared' as female parent, the percentage of highly susceptible seedlings belonging to class 4 is strikingly high (82%).

'Golden Delicious' as female parent was crossed with three scab-resistant cultivars of different genotypes. The segregation ratios of the progenies are shown in *Figure 2*. In the 'Golden Delicious' (vfvf) x 'Prima'(Vfvf) hybrid family, the segregation ratios of susceptible and resistant phenotypes differed from the hypothetical ratio of 1:1. The number of resistant seedlings was higher than expected, and this modified the segregation ratio to approx. 2:3. The percentage of the progenies derived from the cross 'Reka' (Vr) x 'Golden Delicious' (vfvf) was similarly low in classes 0, 2 and 3A. However, the ratio of seedlings in class 3B was outstanding, compared to the very low percentage of seedlings belonging to class 4. The histogram demonstrating the segregation of the progenies of the 'Golden Delicious' x 'Reglindis' combination, is rather one-sided as sparse sporulation was detected on the leaves of the majority of seedlings, and the percentage of plants belonging to class 3B and 4 together reached as much as 80%.

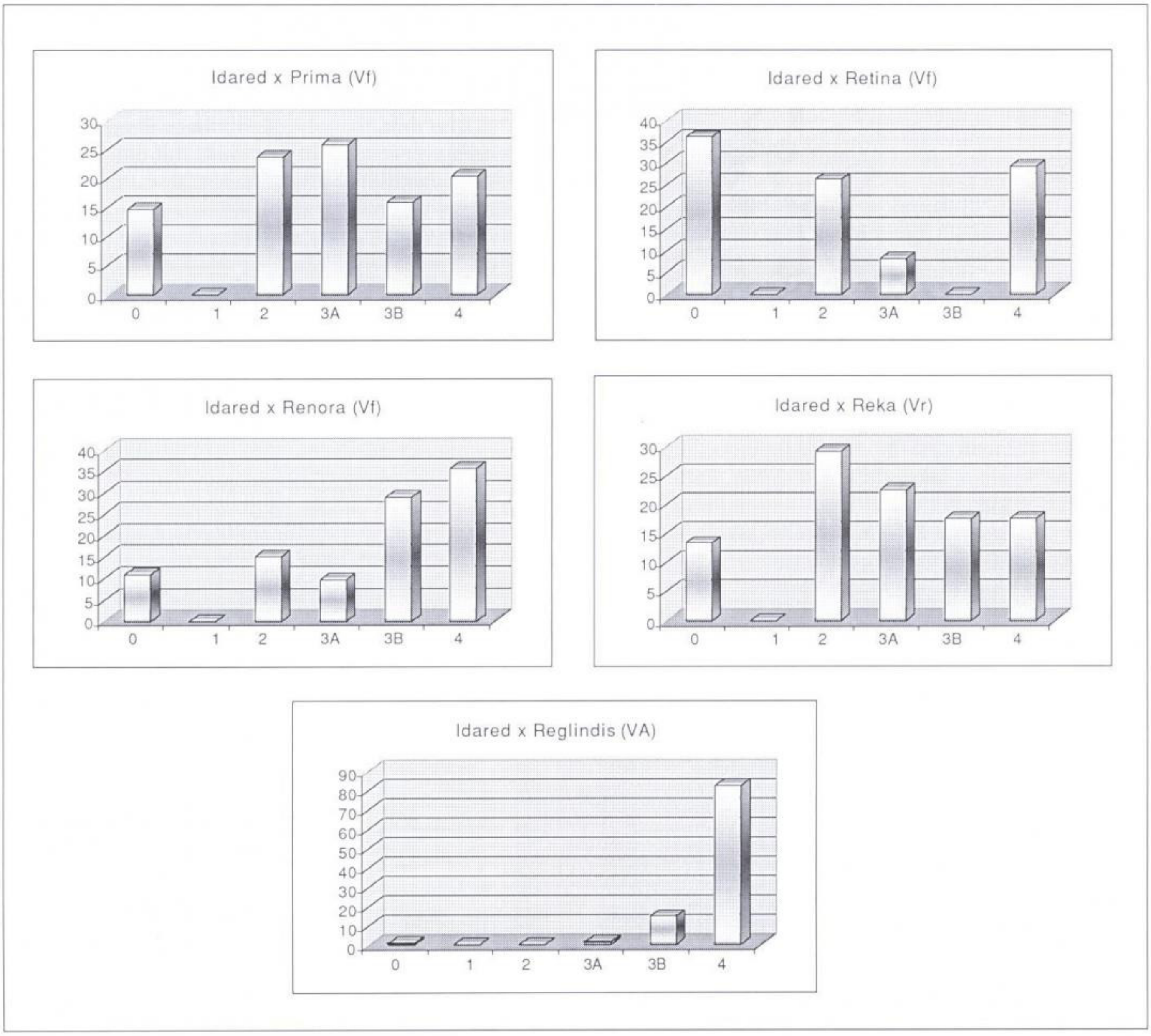
The parents with scab-resistant genotypes were crossed in 3 combinations (*Figure 3.*) After the inoculation in the greenhouse, the segregation ratio in the progenies derived from the cross of 2 resistant, heterozygous (Vfvf) cultivars was 6 resistant: 1 susceptible, instead of the classic ratio of 3 resistant : 1 susceptible. Comparing the ratio of susceptible (class 4) seedlings, it can be concluded that susceptible hybrids occurred by surprisingly higher frequency in the progenies of parents with different types of resistance ('Liberty' (Vf) x 'Reka' (Vr)) than in the progeny derived by

Table 2 Number and rate of susceptible seedlings in the field, which had proved to be resistant in the greenhouse test

Parentage	2001			2002		Altogether	
	No. of Seedlings					evaluated 2004	susceptible
	evaluated	susceptible 2002	susceptible 2004	evaluated	susceptible 2004		%
Idared x Prima (Vf)	44	0	31	.	.	44	70
Idared x Retina (Vf)	87	16	63	22	4	109	61
Idared x Renora (Vf)	38	0	19	19	7	57	46
Idared x Reka (Vr)	67	0	17	8	2	75	25
Idared x Reglindis (VA)	21	0	7	.	.	21	33
Golden Delicious x Prima (Vf)	19	13	19	12	12	31	100
Golden Delicious x Reka (Vr)	40	4	5	18	2	58	12
Golden Delicious x Reglindis (VA)	42	10	41	3	2	45	96
Liberty (Vf) x Rewena (Vf)	82	2	19	.	.	82	23
Liberty (Vf) x Reka (Vr)	51	0	5	30	1	81	7
Liberty (Vf) x Reglindis (VA)	70	2	20	.	.	70	29

Table 3 Number of scab-susceptible seedlings in the field (2004)

Parentage	No. of Seedlings	No. of Susceptible seedlings in field from the groups of				
		0	2	3A	3B	in all
		resistance classes in greenhouse				
Idared x Prima (Vf)	55	7	9	12	3	31
Idared x Retina (Vf)	87	35	20	8	.	63
Idared x Renora (Vf)	38	3	6	3	7	19
Idared x Reka (Vr)	67	4	4	2	7	17
Idared x Reglindis (VA)	21	0	.	0	7	7
Golden Delicious x Prima (Vf)	19	.	.	6	12	18
Golden Delicious x Reka (Vr)	41	0	1	3	1	5
Golden Delicious x Reglindis (VA)	42	.	4	7	30	41
Liberty (Vf) x Rewena (Vf)	82	2	8	6	3	19
Liberty (Vf) x Reka (Vr)	51	0	1	4	0	5
Liberty (Vf) x Reglindis (VA)	70	0	11	4	5	20



Idared x Prima (Vf)

Idared x Retina (Vf)

Idared x Renora (Vf)

Idared x Reka (Vr)

Idared x Reglindis (VA)

Figure 1 Distribution of progenies derived from Idared and different scab resistant parents according to the resistance classes

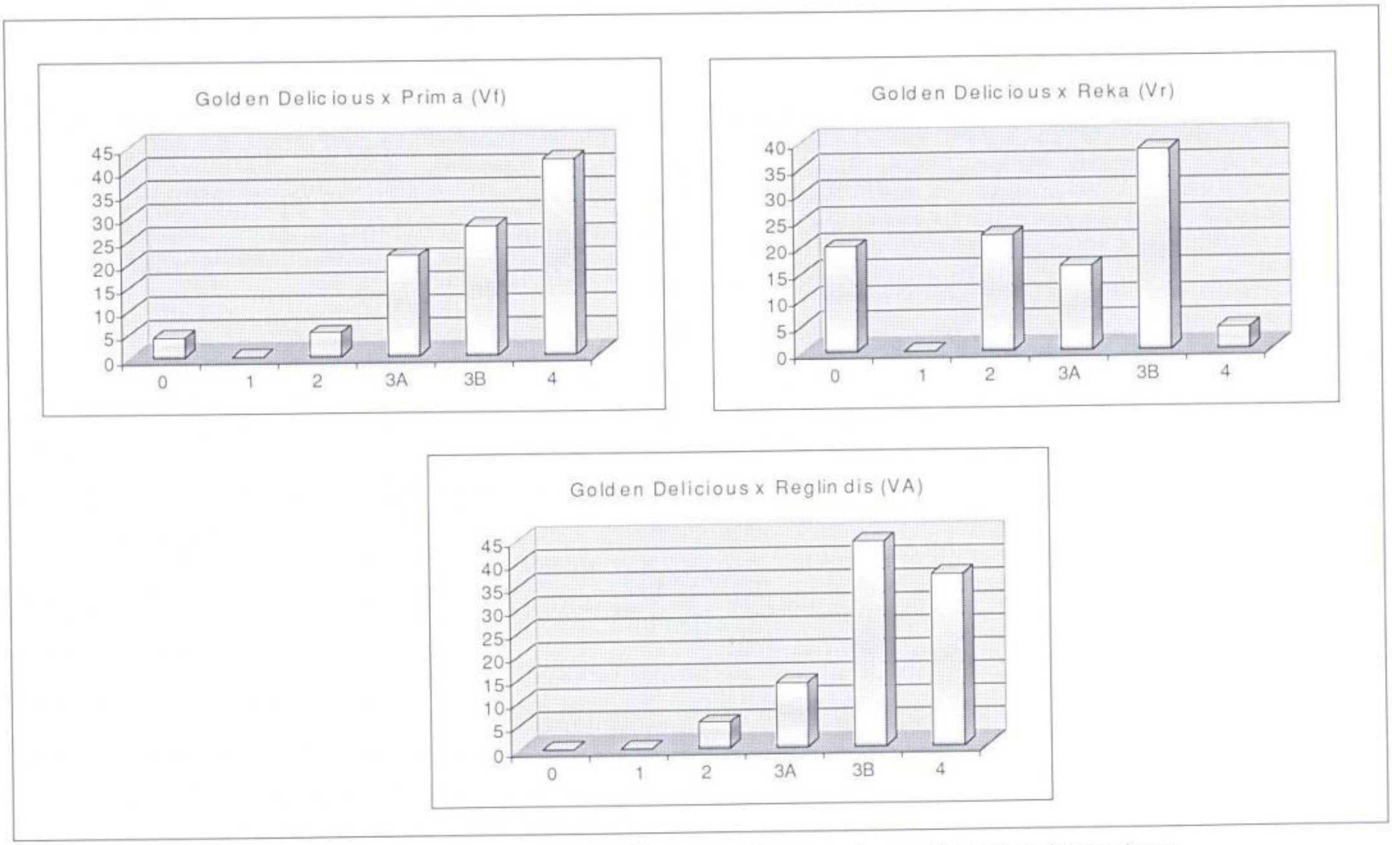


Figure 2 Distribution of progenies derived from Golden Delicious and three scab resistant parents according to the resistance classes

crossing one of the two susceptible cultivars ('Idared' or 'Golden Delicious') with Vf resistant parents (*Figure 1 and 2*). Seedlings derived from the cross 'Liberty' x 'Reglindis' showed a normal distribution by classes, and the percentage of susceptible seedlings with extensive sporulation was low.

The results of the evaluation of seedlings in the field trial in 2002 and 2004, which had proved to be resistant in the greenhouse test in 2001, are shown in *Table 2*.

On the basis of the results of several experiments, *MacHardy* (1996) argues that seedlings exhibiting symptoms characteristic of the reaction classes 0, 1, 2, 3A and 3B in the greenhouse become symptom-free in the field. Our results shown in *Table 2* do not support *MacHardy*'s statement. Seedlings exhibiting resistance in the greenhouse became seriously infected in the field. In 2002, the rate of infection was low, but in 2004 some of the progenies became totally infected. The rate of infection in the field was particularly high in hybrids obtained from the combination of 'Prima' and 'Retina', both of which carry the Vf gene, as well as from the crosses between 'Reglindis' with polygenic resistance and cultivars with susceptible genotypes. As opposed to this, in the progenies of 'Reka' (Vr) and in those obtained from the combination of hybrids with resistant genotypes (Vf x Vf, Vf x Vr, Vf x VA), sporulation was detected on the leaves of only a few seedlings.

The infection rate of seedlings previously grouped into different reaction classes in the greenhouse was evaluated in the field in 2004, and results are shown in *Table 3*. The standard deviation of the data does not allow us to draw general, clear conclusions, but two facts should be highlighted. First, seedlings obtained from the cross 'Golden Delicious' x 'Reglindis', which – due to sparse sporulation on their leaves – were grouped into class 3B in the greenhouse evaluation, were undoubtedly susceptible in the field. Second, on the basis of the desirable segregation ratio within the group of the seedlings derived from the cross 'Idared' x 'Retina' (*Figure 1.*) and the results of the natural field infection, it can be stated that in the greenhouse genotype only partially controlled phenotypic appearance, as the majority of seedlings which were symptom-free in the greenhouse, became infected in the field.

Some of the results (*Figure 4*) obtained by combining the data of the greenhouse test with those of the field trial, are notable, in that the infection rate of seedlings derived from certain susceptible x resistant combinations reached as much as 100%. This particularly applies to the progenies of pollen parents with Vf and VA resistance. Out of the crosses between resistant genotypes, the segregation ratio in the progenies of 'Liberty' (Vfvf) x 'Rewena' (Vfvf) was the classic 3 resistant: 1 susceptible.

Discussion

Parts of the afore-mentioned results have confirmed previous experiences and hypotheses, whereas others render new ones possible. Out of the resistant genotypes used in our tests, the Vf gene of 'Prima' and 'Liberty' was obtained from *Malus floribunda* 821, that of 'Retina', 'Renora' and

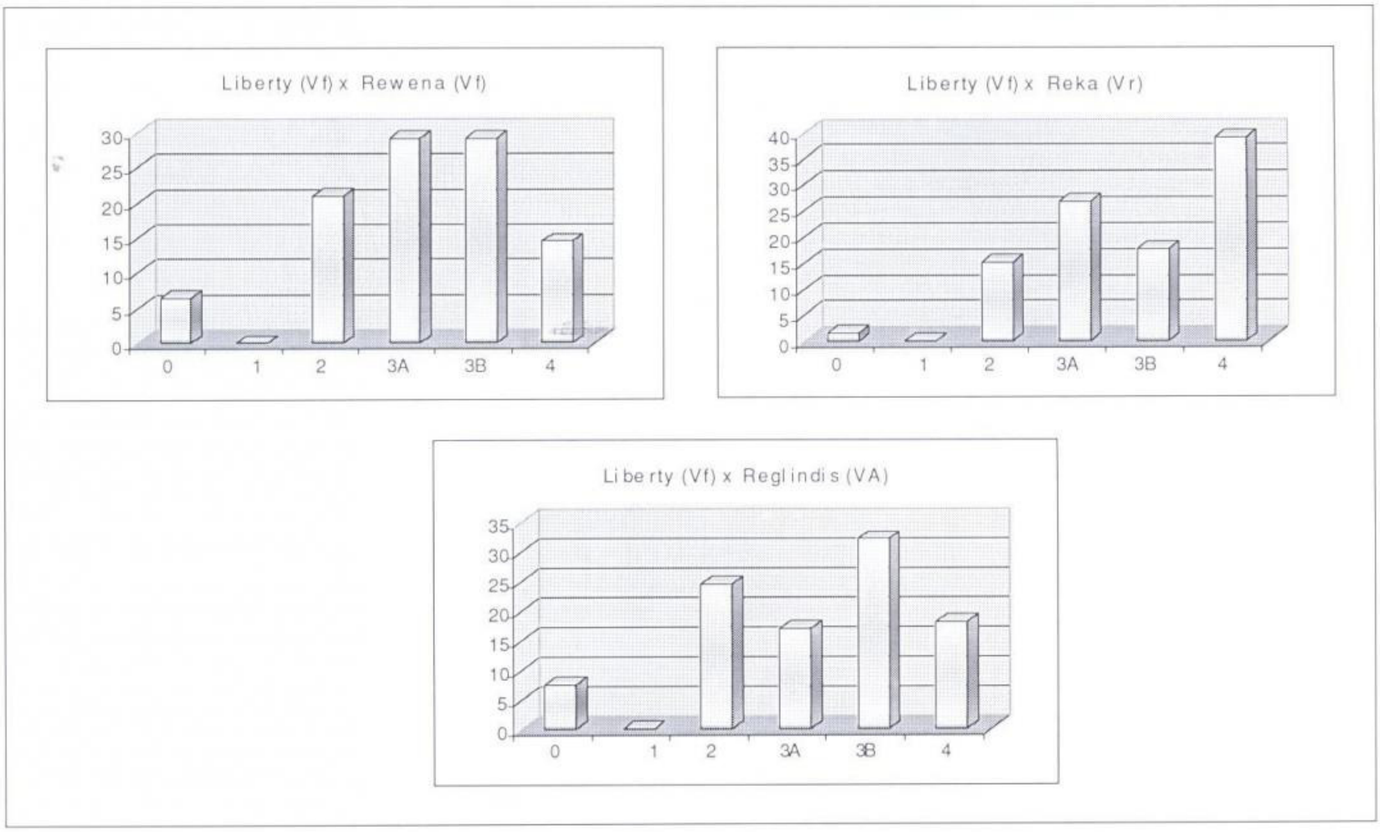


Figure 3 Distribution of progenies derived from crosses Liberty by Vf, Vr and VA genotypes according to the resistance classes

'Rewena' from *Malus floribunda* selected at the Institute for Fruit Breeding in Dresden-Pillnitz, 'Reglindis' with VA from 'Stein Antonovka', and 'Reka' with Vr from *Malus pumila*. 'Reglindis' and 'Reka' were selected from the third generation of the original gene source, whereas the other tested cultivars were selected from the fourth generation (*Lamb* et al., 1979, *Fischer*, 1994, *Dayton* et al., 1970).

Our results of the greenhouse test, similarly to those obtained previously by other researchers (e.g. *Lamb* & *Hamilton*, 1969), have not proved monogenic resistance at the phenotypic level, as the rate of infected plants in the progenies of Vf genotypes was well below 50%. Our earlier results (*Tóth* et al., 1997, *Quang* et al., 1997) and the results presented in this paper indicate – similarly to those of *Kellerhals et al.* (1993) – that the susceptible parents affected the segregation ratios of the progenies too.

None of the hybrids in the greenhouse exhibited pin point pits characteristic of hypersensitive reaction. This could be down to the inoculum, as according to *MacHardy* (1996), the occurance of such symptoms highly depends on the composition of the inoculum. In other explanations, *Malus floribunda* 821 contains two complementer Vf genes: the Vf gene which is responsible for class 2 and 3a reaction types in the greenhouse, and the Vfh gene responsible for class 0 and 1 reaction types. There are cultivars which carry only the Vf gene, therefore in their progenies it is often difficult to

Table 4 Segregation of progenies for resistance to apple scab – the joint effect of the greenhouse inoculation and the natural scab infection (2001, 2004)

Parentage	No. of seedlings	Susceptible (db)			Susceptible (%)	Resistant (%)	Female*	Male*
		in greenhouse	in field	in both				
Idared x Prima (Vf)	73	18	31	49	67	33	a	a
Idared x Retina (Vf)	126	39	63	102	95	5	b	
Idared x Renora (Vf)	64	26	19	44	69	31	a, b	
Idared x Reka (Vr)	88	21	17	38	43	57		
Idared x Reglindis (VA)	148	127	7	134	91	9		
Golden Delicious x Prima (Vf)	60	41	19	60	100	0	c	
Golden Delicious x Reka (Vr)	43	2	5	7	16	84		
Golden Delicious x Reglindis (VA)	69	27	41	68	99	1	c	
Liberty (Vf) x Rewena (Vf)	98	16	19	35	36	64	d	a
Liberty (Vf) x Reka (Vr)	98	47	5	52	53	47	e	
Liberty (Vf) x Reglindis (VA)	87	17	20	37	42	58	d, e	

*Notes: – Letters in the column signed by * indicate similar distributions on the basis of x^2 tests in case of the same parents at 95% probability level.*

identify class 1 reaction type (*Parisi* et al., 1996 cit. *Lateur* et al., 1998; *Bénaouf & Parisi L.*, 2000).

The high infection rate of seedlings in the field trials, seedlings which had previously shown varying degrees of resistance in the greenhouse test, has raised concern, as in 2004 – especially in certain populations – extensive sporulation was observed on the leaves of the majority of seedlings. This could be partly down to the weather conditions which resulted in a long infection period in Szigetcsép in the first part of 2004. Based on the results gained in ecological production systems by *Holb* (2000ab, 2002), it has been assumed that the long infection period resulted in a high amount of inocula and high infection pressure in the dense seedling stock.

Our data raise further doubts (*Krüger*, 1988 & *Parisi* et al., 1993) concerning the durability of Vf resistance. Our earlier results (*Tóth* et al., 1998), and those of *Pauwels & Keulemans* (2000) have already proved the field infection of seedlings regarded as resistant, belonging to classes 0, 1, 2 and 3A in the greenhouse. However, the high rate of seedlings exhibiting sporulation in our tests discussed here is somewhat extraordinary and new. Based on our present knowledge, two explanations could be given for this.

According to *Sierotzki et al.* (1994), the variability of natural field inoculum is probably much higher than that of the inoculum used in the greenhouse. The presence of different races at a time can cause higher infection pressure. Therefore, it is assumed that the composition of natural populations of *Venturia inaequalis* in Szigetcsép has changed over the last few years.

The other explanation is of genetical nature. In the opinion of *MacHardy* (1996), reaction classes from 1 to 3B justify the possible presence of modifying and minor genes besides the Vf gene. The significant sporulation of seedlings tested by us could mean that (some of) these modifying and small genes did not get activated in them. Thus, in the absence of the modifying genes promoting the manifestation of scab-resistance, the Vf gene could not block the reproduction of *Venturia inaequalis*. This justifies the hypothesis of *Lespinasse* (1989) concerning the „eroding" of genes linked to the main gene in the Vf locus. However, as it is well known, the fully linked genes act as one, that is they do not segregate during meiosis. Thus, it is feasible that the afore-mentioned genes are only partially linked with Vf, and their „dose" is related to the specific combination of given genotypes. This coincides with the opinions of *Pauwels & Keulemans* (2000), according to which the Vf resistance is a complex resistance which can be divided into different levels.

Nevertheless, the high infection rate in progenies derived from cultivars with Vf resistance has drawn the attention to the importance of widening the range of gene sources responsible for resistance. According to *Lespinasse* (1994) and *Kellerhalls & Furrer* (1994), this could be reached by combining different resistance genes in one genome (pyramidal) and by including additional sources of resistance.

Based on our results, 'Reglindis' (VA) – compared to other cultivars with polygenic resistance – was less effective in inheriting scab-resistance. It is suggested that the VA gene as parent should not be used in combinations with susceptible cultivars against Hungarian populations of the pathogen. On the other hand, on the basis of the results concerning the cross of 'Liberty' x 'Reglindis', the combination of polygenic and Vf resistance is still recommended for the future to obtain durable resistance.

Based on the high level of field resistance of the Vr resistant 'Reka' and its positive effect on the inheritance of resistance, as well as on the results of *Donati* et al. (2002) concerning the progenies of 'Realka' (Vr), and on the segregation ratios in the progenies of the cross 'Ariwa' (Vf) x 'Regia' (Vr) made by *Kellerhals* et al. (2004), the following can be concluded: combining Vr resistance with Vf resistance could be a possible solution for durable resistance. Based on the results of *Kellerhals et al.* (2004) on inheritance, and on those of marker analysis made by *Boudichevskaia et al.* (2004), it can be stated that in the afore-mentioned two cultivars, Vr resistance is not encoded by the same alleles, and 'Reka' is recommended instead of 'Regia' for the inheritance of Vr resistance.

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