Inheritance of resistance to powdery mildew and apple blotch in progenies of scab-resistant apple cultivars

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Breeding for scab (*Venturia inaequalis* Cooke) resistance is the main objective of most apple breeding programs around the world. It is important to combine in new cultivars a higher tolerance to powdery mildew (*Podosphaera leucotricha* Ell. et Ev.) and apple blotch (*Phyllosticta mali* E. et E.) with scab resistance and use them for ecological fruit production.

In our study, for controlled crosses three scab-resistant apple cultivars ('Arbat', 'Florina' and 'Prima') were used as male and eight as female ('Tellissaare', 'Sylvia', Štaris', 'Auksis', 'Aktiubinskoye', 'Discovery', 'Lodi' and 'Quinte') cultivars. In 1995 the seedlings were planted in orchard in four replications. Disease injuries were estimated by using a 0–5 scale: 0 – no injuries on leaves, 5 – more than 75% of leaf area is injured. Significant differences in resistance to scab, powdery mildew and apple blotch were found among the crosses. General combining ability (GCA) and specific combining ability (SCA) were highly significant, except GCA for resistance to apple blotch of testers. The significance of GCA for scab, powdery mildew and apple blotch resistance shows that genetic variability exists for these traits and selection should result in genetic progress, because the mean square for GCA was larger than that calculated for SCA. This means that disease resistance is controlled predominantly by additive gene action. Therefore selection of parents by their phenotype should be effective for development of resistant apple cultivars. The significant SCA estimates indicate that a large number of resistant seedlings from particular crosses should be selected.

Key words: apples, general and specific combining ability, inheritance

INTRODUCTION

Apple scab (*Venturia inaequalis* Cooke) and powdery mildew (*Podosphaera leucotricha* Ell. et Ev.) are the most harmful fungal diseases of apple in Europe and around the world. In Lithuania, apple trees need to be sprayed in nursery with a fungicide for powdery mildew control, because orchard plants usually have no disease symptoms. Apple blotch (*Phyllosticta mali* E. et E.) appears during epiphytoty in some years in Lithuania. Nevertheless, it is important to combine in one genotype resistance or high tolerance to these diseases. Apple breeding programs aimed at obtaining new cultivars with multiple resistance to fungal diseases were initiated in many countries around the world [1–4]. In Germany, *Malus* species were involved in crosses as a source of resistance to scab and powdery mildew to find new donors and get a stable and broad base for resistance [5]. It was reported that the resistance determined by the dominant gene V_f (derived from *M. floribunda* clone 821) was overcome by new races of *V. inaequalis* [6]. Therefore, two or more dominant genes or genes with additive effects should be combined in one cultivar to ensure a higher stability of resistance. There are great differences between cultivars and selections for resistance to apple scab and powdery mildew [7]. Inheritance studies indicate that a polygenic control mode of inheritance exists in progenies of mildew-tolerant apple cultivars [8, 9].

The objective of the current study was to evaluate the resistance to scab, powdery mildew and apple blotch in progenies of scab-resistant cultivars and to determine the mode of inheritance to these fungal diseases in the group of the cultivars studied.

MATERIALS AND METHODS

Apple cultivars were crossed according to the topcross mating design [10] when 8 cultivars ('Tellissaare', 'Sylvia', 'Štaris', 'Auksis', 'Aktiubinskoye', 'Discovery', 'Lodi' and 'Quinte') were used as female and 3 ('Arbat', 'Florina' and 'Prima') as male. Seedlings of 24 crosses were placed in orchard according to a randomised complete-block design with 4 blocks. Disease injuries were estimated by on a 0–5 scale: 0– no injuries on leaves, 5 – more than 75% of leaf area injured. Combining ability was calculated by the method described by Khotyliova [10].

RESULTS AND DISCUSION

The number of resistant apple seedlings in crosses involving 'Arbat' varied from 53.1 to 72.5%, in those involving 'Florina' it reached 51.9–59.5% and in 'Prima' – 51.9–63.4% (Table 1). Approximately half of seedlings in most crosses exhibited susceptible reaction, which shows that the dominant gene determining scab resistance is present in heterozygous condition in the cultivars mentioned above. However, the proportion of resistant seedlings in crosses 'Aktiubinskoye' × 'Arbat', 'Lodi' × 'Arbat', 'Quinte' × 'Prima' was higher than 60%. Lamb and Hamilton [11] and Rousselle et al. [12] reported that the level of resistance determined by the V_f gene increases under the action of genes with additive effects. Both resistant and susceptible parents contribute to their progenies' resistance by transmitting 'minor' genes [11]. Our results are in agreement with results of other researches who showed that scab-resistant apple cultivars carrying V_f gene give a different proportion of resistant seedlings in crosses with susceptible parents [11, 12]. In our case higher percentage (about 7%) of resistant plants was determined in progenies of 'Arbat'.

Powdery mildew resistance can be obtained from oligogenic or polygenic sources. Oligogenic resistance is determined by Pl_1 and Pl_2 genes. No such donors were involved in our crosses. The proportion of resistant seedlings of parent cultivars used in the crosses was very different (Table 1). There were 0–12.3% of seedlings resistant to mildew in crosses involving 'Arbat', 0–17.7% in those with 'Florina' and 1.6–14.8% with 'Prima'. Not resistant plants were obtained in crosses 'Quinte' × 'Arbat' and 'Quinte' × 'Florina'. In general, the scab-resistant cultivars Arbat', 'Florina' and 'Prima' are equivalent in transmitting mildew resistance to their progenies. The percentage of resistant seedlings (6.1%) in 'Florina' crosses was a little higher than in crosses of 'Arbat' and 'Prima'. Crosses 'Sylvia' × 'Florina' and 'Discovery' × × 'Florina' differed more distinctly from the rest six crosses of 'Florina', and the percentage of healthy plants was 17.7% and 16.7%, respectively. There were 12.3% of seedlings without disease symptoms in the cross 'Aktiubinskoye' × 'Arbat' and 14.8% in the cross 'Aktiubinskoye' × 'Prima'. Other researchers have revealed a moderate level of resistance within some cultivars [7], and a polygenic control mode of inheritance was indicated [8]. On the average, 15.7% of apple blotch resistant seedlings were in crosses with 'Arbat', 27% in crosses with 'Prima' and 37.5% with 'Florina'. The number of resistant seedlings among the crosses with 'Arbat' varied from 7.0 to 34.3%, with 'Prima' from 14.8 to 52.5% and with 'Florina' from 16.7 to 47.2%. It is evident that both parent cultivars contribute to the resistance level of their progenies.

A histogram of scab, mildew and apple blotch resistance ratings in crosses of 'Arbat', 'Florina' and 'Prima' are presented in Figure. Segregation of seedlings for resistance to mildew in progenies from crosses among scab-resistant and sensitive apple cultivars showed a continuous distribution typical of a polyge-

Table 1. **Number of apple seedlings without disease symptoms in crosses of scab-resistant cultivars, %**

Cross	Number of plants	Scab	Powdery mildew	Apple blotch
Štaris × Arbat	172	65.1	3.5	8.7
Auksis × Arbat	124	62.9	9.7	23.4
Tellissaare × Arbat	181	58.6	4.4	34.3
Aktiubinskoye × Arbat	382	72.5	12.3	24.1
Lodi × Arbat	80	67.5	1.3	7.5
Quinte × Arbat	43	53.5	0.0	7.0
Sylvia × Arbat	156	53.8	9.0	11.5
Discovery × Arbat	49	53.1	3.5	8.7
Average		62.4	5.5	15.7
Štaris × Florina	188	52.1	3.7	43.6
Auksis × Florina	172	52.9	3.5	37.2
Tellissaare × Florina	319	57.4	2.2	43.3
Aktiubinskoye × Florina	163	59.5	1.2	47.2
Lodi × Florina	87	55.2	3.4	23.0
Quinte × Florina	44	59.1	0.0	43.2
Sylvia × Florina	79	51.9	17.7	45.6
Discovery × Florina	12	58.3	16.7	16.7
Average		55.8	6.1	37.5
Štaris × Prima	84	56.0	4.8	22.6
Auksis × Prima	191	53.9	5.2	24.1
Tellissaare × Prima	182	53.8	1.6	20.9
Aktiubinskoye × Prima	108	56.5	14.8	39.8
Lodi × Prima	106	53.8	4.7	18.9
Quinte × Prima	41	63.4	4.9	22.0
Sylvia × Prima	27	51.9	3.7	14.8
Discovery × Prima	118	53.4	5.9	52.5
Average		55.2	5.7	27

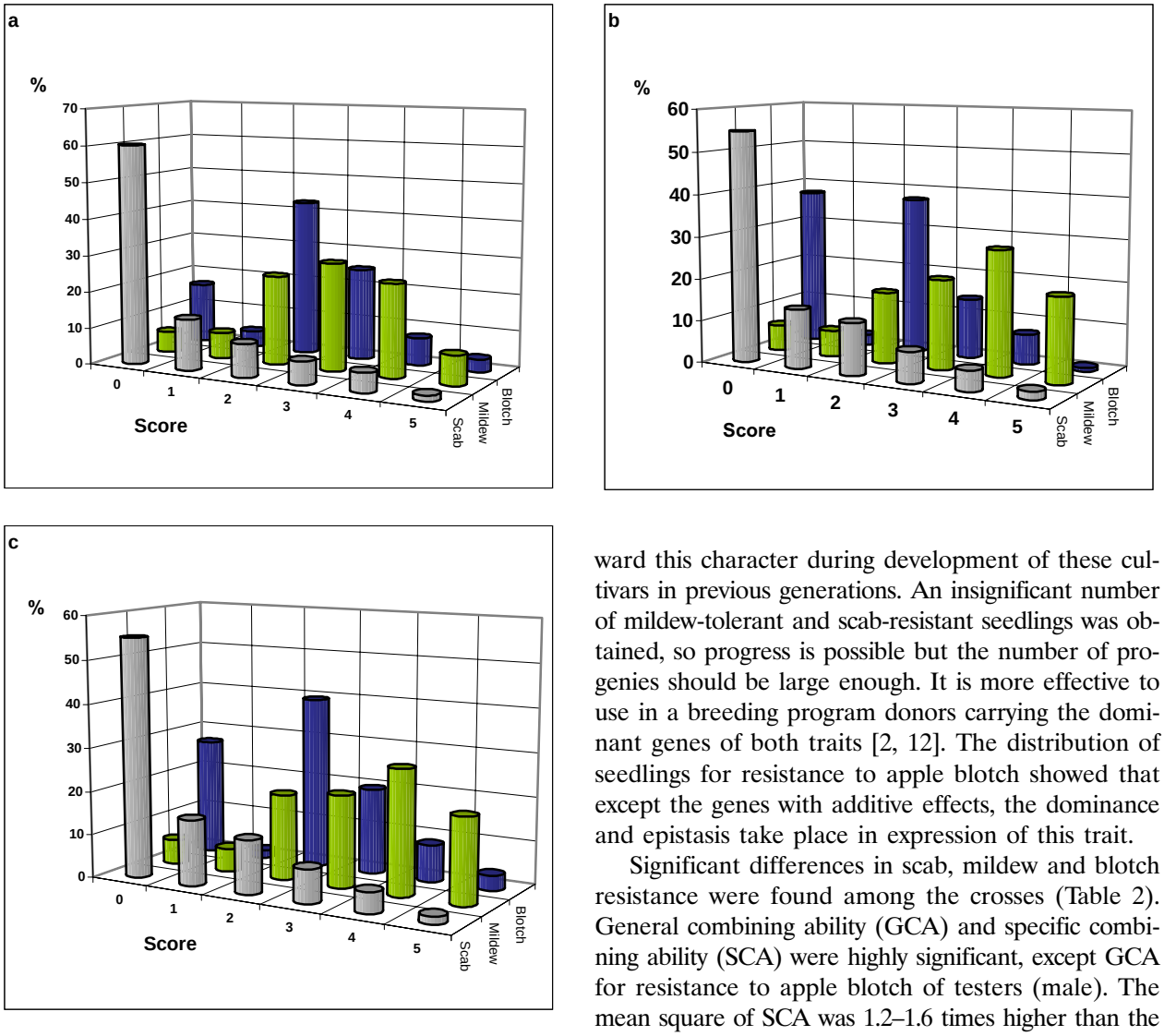

Figure. Frequency of apple seedlings with different resistance to scab, mildew and apple blotch in progenies involving: a – 'Arbat', b – 'Florina' and c – 'Prima'

nic control of the trait. The results presented in this paper showed susceptibility to mildew in the progenies of scab-resistant donors such as 'Arbat', 'Florina' and 'Prima'. It is the result of selection law pressure toward this character during development of these cultivars in previous generations. An insignificant number of mildew-tolerant and scab-resistant seedlings was obtained, so progress is possible but the number of progenies should be large enough. It is more effective to use in a breeding program donors carrying the dominant genes of both traits [2, 12]. The distribution of seedlings for resistance to apple blotch showed that except the genes with additive effects, the dominance and epistasis take place in expression of this trait.

Significant differences in scab, mildew and blotch resistance were found among the crosses (Table 2). General combining ability (GCA) and specific combining ability (SCA) were highly significant, except GCA for resistance to apple blotch of testers (male). The mean square of SCA was 1.2–1.6 times higher than the GCA mean square for scab resistance. This difference can be explained by the fact that in crosses as male parents (testers) were involved apple cultivars carrying the dominant gene. The variance due to GCA for mildew and apple blotch resistance was more important than the variance due to SCA, except GCA variance for male. The GCA mean squares were 1.6–2.4 times higher than those calculated for SCA for mildew resistance and 4 times for apple blotch (female). The

Table 2. **Analysis of variance for scab, mildew and apple blotch resistance**

Source	Scab			Mildew			Apple blotch		
	df	MS	F	df	MS	F	df	MS	F
Crosses	23	15.16	6.42**	23	1.13	11.13**	23	0.15	5.57**
GCA (female)	7	14.13	5.98**	7	1.37	13.49**	7	0.32	11.97**
GCA (male)	2	10.01	4.24*	2	2.07	20.42**	2	0.08	0.29
SCA	14	16.42	6.95**	14	0.87	8.62**	14	0.08	3.13**
Error	69	2.36		69	0.10		69	0.03	

*,** F value is significant, P ≤ 0.05 and 0.01, respectively.

results suggest that the effects of genetic factors controlling mildew and apple blotch resistance are predominantly additive. Therefore selection of parents by their phenotype should be effective for development of resistant apple cultivars. The significant SCA estimates indicate that a large number of resistant seedlings from particular crosses should be selected.

Negative GCA effects mean that a parent cultivar transmits disease resistance to their progenies (Table 3). The highest GCA effects among the female cultivars were shown by 'Štaris' (–1.00) and 'Lodi' (1.07). The GCA effects of 'Auksis' and 'Discovery' were somewhat lower (–0.74 and –0.66, respectively). Among male cultivars distinguished 'Arbat' and 'Florina', they showed the strongest negative GCA effects (–0.32). The high negative GCA effect for mildew resistance of 'Auksis' (–3.77), 'Discovery' (–2.77), 'Sylvia' (–2.52) and 'Lodi' (–1.77) indicates that these parents contribute to mildew resistance in their progenies. 'Arbat' and 'Prima' showed the strongest GCA effects among male cultivars. The GCA effects were the strongest for female cultivars 'Sylvia' and 'Quinte' (–1.69 and –1.27). Male cultivars did not differ from each other. 'Sylvia' and 'Discovery' showed negative GCA effects on all three diseases. The latter two cultivars and 'Arbat' could be involved into the apple breeding program as parents to improve the resistance and obtain the individuals with complex resistance to scab, mildew and apple blotch.

Received
20 October 2002

Table 3. **General combining ability effects $(g)_i$ of apple cultivars on scab, mildew and apple blotch resistance**

Parent	g_i		
	Scab	Mildew	Apple blotch
Female			
Tellissaare	0.84	6.15	0.23
Sylvia	–0.32	–2.52	–1.69
Shtaris	–1.00	1.48	–0.35
Auksis	–0.74	–3.77	3.56
Aktiubinskoye	1.43	0.31	–0.19
Discovery	–0.66	–2.77	–0.85
Lodi	–1.07	–1.77	0.56
Quinte	1.51	2.90	–1.27
Male			
Arbat	–0.32	–1.44	–0.07
Florina	–0.32	2.94	–0.10
Prima	0.64	–1.50	0.18
LSD, female	0.83*	1.71**	0.88**
male	0.44*	0.92**	0.47

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RAUPLĖMS ATSPARIŲ OBELŲ VEISLIŲ PALIKUONIŲ ATSPARUMO MILTLIGEI IR FILOSTIKTOZEI PAVELDĖJIMAS

S a n t r a u k a

Vienas pagrindinių obelų selekcijos tikslų yra atsparumas rauplėms (*Venturia inaequalis* Cooke). Svarbu išvesti veisles, kurios būtų atsparios miltligei (*Podosphaera leucotricha* Ell. et Ev.), filostiktozei (*Phyllosticta mali* E. et E.) bei rauplėms.

Kontroliuojamų kryžminimų topkrosinėje schemoje trys veislės ('Arbat', 'Florina' ir 'Prima') naudotos kaip tėvinės (testeriai) ir aštuonios – kaip motininės ('Tellissaare', 'Sylvia', Štaris', 'Auksis', 'Aktiubinskoje', 'Discovery', 'Lodi' ir 'Quinte'). 1995 m. sėjinukai pasodinti selekciniame sode. Jų pažeidimas ligomis įvertintas pagal penkių balų skalę: 0 – lapai sveiki, 5 – pažeista daugiau nei 75% lapo paviršiaus. Pagal atsparumą ligoms tarp kombinacijų nustatyti patikimi skirtumai. Gauti patikimi bendrosios ir specifinės kombinacinės galios (BKG ir SKG) skirtumai visiems požymiams, išskyrus testerių BKG atsparumą filostiktozei. Atsparumo rauplėms BKG vidutiniai kvadratai buvo mažesni už SKG vidutinius kvadratus, nes testeriai turėjo atsparumą determinuojančius dominantinius genus. Atsparumo miltligei ir filostiktozei BKG didesni vidutiniai kvadratai už SKG vidutinius kvadratus rodo, kad atsparumas dažniausiai determinuotas genų su adityviniais efektais. Tėvų parinkimas pagal fenotipą turėtų būti efektyvus, o patikimos SKG reikšmės rodo, kad įvairiai kryžminant galima gauti didelį kiekį atsparių augalų.