Segregation of powdery mildew (*Podosphaera leucotricha* [Ell. et Ev. /Salm./]) resistance within 54 apple progenies

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ABSTRACT: The occurrence of powdery mildew after heavy spontaneous infections was evaluated on 2,500 apple seedlings of 54 progenies that were derived from crosses made in 1993 and 1994. At the same time, the response to mildew was also assessed on 47 cultivars or selections that were used as parents for the crosses. Scores of the strongest infestation were used for final ranking of every seedling or parent. The highest proportions (33 and 28%) of seedlings with complete resistance to mildew were attained in 2 progenies involving parents transmitting monogenic resistance to the pathogen. A few seedlings with this resistance were also found in other 7 progenies. Seedlings with partial resistance to mildew were distributed in the highest proportions (about 30%) among 7 progenies. In 6 out of these progenies, always one parent was derived from partially resistant selections that were selected in the first generation from the cross Spätblühender Taffetapfel × Court Pendu Plat. A very close relationship was found between mid-scores of parents and mean response to powdery mildew infection in progenies. Seedlings on average were significantly more infested than their parents. Progenies determined to have a columnar growth habit were somewhat less infested than progenies possessing a standard growth pattern only. This study revealed considerable improvement of some donors transmitting partial resistance to powdery mildew.

Keywords: *Podosphaera leucotricha*; apple; mildew; resistance; cultivars; breeding

Powdery mildew is one of the most serious fungal diseases of the apple (*Malus* × *domestica* Borkh.), needing frequent applications of fungicide sprays for its control, and is caused by the fungus *Podosphaera leucotricha* (Ell. et Ev. /Salm./). Complete immunity has not been found within the cultivated apples. It was possible, however, to select some that are very highly resistant and only scarcely produce any infected shoots (ALSTON 1969; BLAŽEK et al. 1979; BLAŽEK 1999). This incomplete resistance is inherited quantitatively, and effects of the parents on the progeny are very significant. Many apple breeding programmes around the world aim at the development of resistant cultivars (VISSER et al. 1974; BLAŽEK, SYROVÁTKO 1991; PITERA, BOGDANOWICZ 1992; KRÜGER 1994; OGNJANOV et al. 1999; NDABAMBI et al. 2000).

Complete resistance (immunity) to powdery mildew was found in wild and ornamental *Malus* species (ALSTON 1983; SCHMIDT 1994), but the use of such species in a breeding programme requires several generations of back-crossing before a high level of fruit quality is attained. Alternatively, levels of partial resistance in cultivated varieties can be introduced in high quality cultivars.

According to BERGENDAL and NYBOM (1966), the cultivars Worcester Pearmain, Golden Delicious and Lord Lambourne were found to be suitable sources of partial resistance. VISSER et al. (1974) found that Antonovka cv., especially in combination with Lord Lambourne, significantly transferred the resistance to mildew to its offspring.

A very important source of mildew resistance seems to be the selection U 211 (Primula open pollinated), which was found to be highly resistant to mildew in field conditions and transmitted the high level of resistance to the majority of its progeny (PITERA, BOGDANOWICZ 1992).

In the Czech Republic it was found that the cultivars Spätblühender Taffetapfel and Böhmischer Jungfernapfel transmitted resistance to its progenies to the largest extent (VONDRÁČEK, KLOUTVOR 1974). Later, on the basis of study of 829 selected seedlings (obtained by an incomplete diallel crossing of eleven commonly grown apple cultivars), 0.3% of the seedlings were classified as resistant and about 5% as partially resistant. The polygenic control of this characteristic with significance for both general and specific combining ability was confirmed. The highest proportion of seedlings with partial resis-tance to mildew was found in the progeny of the cross Starkrimson Delicious and Starkspur Golden Delicious (BLAŽEK, SYROVÁTKO 1991). In the latest study, the highest proportions of seedlings with partial resistance to mildew were found in progenies derived from the cross of Spätblühender Taffetapfel × Court Pendu Plat and in the offspring obtained from Priscilla × Lord Lambourne cross. Other valuable donors of the characteristic proved to be also the cultivars Discovery, Malinové holovouské, Redspur Delicious, Britemac and the selection HL A 28/39,

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Table 1. Survey of parents, their mean ratings for mildew and pedigree

Cultivar or selection	Mean incidence of mildew (1–9)*	Parents or pedigree
A 814/9	9.0	Cox Orange × A 467-74 [Golden Delicious × A 142-8 (Jonathan × 3762)]
Akane	5.5	Jonathan × Worcester Pearmain
Angold	5.2	HL A 28/39 (Antonovka o.p.) × Golden Delicious
Discovery	8.1	Worcester Pearmain × Beauty of Bath
East Malling 3762	9.0	*Malus robusta* o.p.
Florina	4.3	Jonathan × PRI 612-1
HL 1 A	6.7	Glockenapfel × Šampion
HL 4 A	5.4	Glockenapfel × Šampion
HL 149	5.6	HL 42 (Golden Spur × Bláhova oranžová) × Prima
HL 166 A	6.1	Clivia × Rubín
HL 166 C	7.8	Clivia × Rubín
HL 196	7.3	D 21-213 (Spartan × M 2439) × Coop 18
HL 209	8.5	A 18/74 (Spätblühender Taffetapfel × Court Pendu Plat) o.p.
HL 278	8.3	HL 1172 (Hagloe Crab × Early Victory) × HL 237 (Starkrimson Delicious × Glockenapfel)
HL 319	7.5	Megumi × Rubín
HL 421	8.3	Golden Spur × Jonalicious
HL 477	8.2	HL I/3 11/11 (Spätblühender Taffetapfel × Court Pendu Plat) × Alkmene
HL 499	8.0	HL A 31/74 (Spätblühender Taffetapfel × Court Pendu Plat) × HL 2 × 57
HL 501	5.9	HL III 12/30 (Jonathan × Ontario) × Rubín
HL 535 A	7.2	James Grieve Compact × HL 938 (Golden Spur × Dukát)
HL 657	6.7	HL 1347 [HL B 14/11 (Spätblühender Taffetapfel × Court Pendu Plat) × Trent] × HL 97 (Bancroft × Starking Delicious)
HL 718	6.9	HL 1347 [HL B 14/11 (Spätblühender Taffetapfel × Court Pendu Plat) × Trent] × HL 97 (Bancroft × Starking Delicious)
HL 801	7.9	HL A 12/74 (Spätblühender Taffetapfel × Court Pendu Plat) × HL 2 × 57
HL 902	5.8	Bláhova oranžová × Priscilla
HL 938	7.7	Golden Spur × Dukát
HL 983	8.4	HL l./3 18/1 (Spätblühender Taffetapfel × Court Pendu Plat) × Rubín
HL 994	7.1	Britemac × Prima
HL 1451	5.8	Cox's Orange × Florina
HL 1636	7.6	HL V.16/50 (Spätblühender Taffetapfel × Court Pendu Plat) × Mantet
HL 1669	5.7	Golden Spur × W 37
HL 1711	6.3	Idared × Discovery
HL 1754	6.5	Golden Spur × W 37
HL 1805	7.4	Fantazja × HL 135 (Lord Lambourne × Spartan)
HL 1816	7.2	Fantazja × HL 135 (Lord Lambourne × Spartan)
HL 1909	6.7	Melrose × Prima
HL 1939	8.2	Starkrimson Delicious × HL 1081 (Golden Delicious × Hopa Crab)
HL 1963	6.4	Fantazja × HL VI 37/45 (James Grieve × Jonathan)
Klára	7.7	Reinette Rouge Etoilée × Hájkova muškátová reneta
Liberty	4.3	PRI 54-12 × Macoun
FAW 3762	9.0	*Malus robusta* o.p.
McIntosh Wijcik	6.0	Mutant of McIntosh
Pinova	5.5	Clivia × Golden Delicious
Red Free	4.1	Raritan × PRI 1018-101
Reglindis	6.5	James Grieve × selection from hybride progeny of Antonovka
Resista	4.9	Prima × NJ 56
Selena	6.5	Britemac × Prima
Šampion	7.5	Golden Delicious × Cox's Orange
Vanda	6.1	Jolana × Lord Lambourne

*LSD = 0.79 (P = 0.05)

which was selected from the progeny of Antonovka obtained after open pollination (BLAŽEK 2000).

In this paper, the segregation of resistance to mildew was studied in apple progenies that were mostly derived from crosses originally designed within a programme of breeding for scab resistance or development of cultivars possessing the columnar growth habit.

MATERIAL AND METHODS

Fifty-four apple progenies segregating for scab resistance or columnar growth habit were chosen for this study. It included in total 2,500 seedlings. Altogether 47 cultivars and selections were used as parents in the crosses. Parents or pedigrees of the cultivars and selections are given in Table 1. The breeding stock was obtained from crosses made in 1993 and 1994. In the subsequent years, seeds were sown and the seedlings were preselected for scab resistance after artificial inoculation at the early stage of their development in a greenhouse. Later on, the seedlings were transplanted and grown in a plastic house with the aim to accelerate their growth rate. Then in August of the second year, buds from the top of every seedling were budded on M 9 rootstocks in an open-field nursery.

Two-year-old nursery trees on M 9 were planted in hybrid orchards at Holovousy at the spacing of 4 × 1 m. Original seedlings (on their own roots) were transplanted to special experimental plots at the denser spacing of 1.5 × 0.3 m. Trees in both plantings were grown without any chemical sprays against fungal diseases, and were left without any training in the first years; but later some pruning was used for controlling the size of trees or to clear access alleys between rows. The differences between susceptible and resistant or tolerant seedlings within the same progeny were tested by analysis of variance.

Evaluations of all seedlings for mildew susceptibility or resistance were done in 2001 and 2002, when the general spontaneous infestation of both plantings was the strongest. Trees on their own roots were 5 to 8 years old at that time, whereas trees on M 9 rootstock were 3 to 6 years old. Assessments were done individually on each seedling in the second half of August using a 1–9 rating scale, with a 9 score for an asymptomatic status and a 1 score for the strongest degree of infestation. On the basis of the assessments, four values (from the two plantings and the two years) were available for each seedling from which the strongest infestation (minimum value of the score) was used for its final ranking.

Parental cultivars or selections were evaluated in another experimental orchard established at Holovousy under a similar pattern (on M 9) several years earlier. There, assessments for mildew incidence were done between 1999–2002, usually on several trees. In these cases, the mean score from the year of maximum infestation was used for the final rank of the genotype.

Differences between progenies in mean infestation and other statistical parameters were tested by analysis of variance.

RESULTS

The mean response of cultivars and selections that were used as parents for the seedlings included in this study, according to their evaluation during recent years at Holovousy, is given in Table 1. These scorings range from 4.1 for the most susceptible cultivar Red Free to 9 for two donors of complete resistance (A 814/9 and FAW 3762). Selections with the highest level of partial resistance were HL 209 and HL 983 with scores 8.5 and 8.4, respectively.

The number of seedlings evaluated in particular progenies fluctuated from 16 (HL 801 × McIntosh Wijcik and HL 983 × HL 196) to 141 (HL 938 × HL 477). The mean score for powdery mildew response of the assessed progenies ranged from 3.58 to 7.1 (Table 2). The mean score for the total number of 2,500 seedlings from all 54 evaluated progenies was equal to 5.58. The values of variability of scoring for progenies ranged from 0.93 to 7.2. Coefficients of variance (CV) were from 1.51% to 10.6%. The highest values of both variability and coefficients of variance were found in progenies with monogenic segregation of complete resistance.

The highest proportions of seedlings with complete resistance to mildew (without any visible symptoms of the infection) segregated only in 2 progenies (Table 2). Both progenies – Florina × A 814/9 and Florina × FAW 3762, involved a parent transmitting monogenic resistance to the pathogen. In these progenies, seedlings segregated into two clearly distinct categories of seedlings – resistant (33 and 28%, respectively) and susceptible. No seedling in these progenies possessed partial resistance. Segregation rates of resistant seedlings in both cases were much smaller than theoretically expected, at 50%. However, the size of the progenies was too small for drawing any conclusions.

A few seedlings with complete resistance to mildew segregated in other 7 progenies, but except for one of them it was always only one individual seedling more or less close to the higher proportions of other seedlings with partial resistance to the disease.

Seedlings with partial resistance to mildew segregated in the highest proportions (about 30%) in the following 7 progenies: HL 209 × HL 1805, HL 209 × HL 1916, HL 421 × HL 938, HL 499 × McIntosh Wijcik, HL 938 × HL 477, HL 938 × HL 994 and HL 983 × HL 938. In six out of these progenies, always one parent was derived from partially resistant selections that were selected in the first generation from the cross Spätblühender Taffetapfel × Court Pendu Plat (VONDRÁČEK, KLOUTVOR 1974), and the second parent was derived from Lord Lambourne or Golden Spur. The same level of potential mildew resistance was transmitted also from HL 421 (Golden Spur × Jonalicious).

In another 13 progenies, seedlings with partial resistance to mildew segregated in rates between 10 to 24%. The majority of parents involved in these progenies was the same or similar to the previous group. As other donors, there were Discovery, HL 278 (Early Victory and

Table 2. Characteristics and parameters of evaluated progenies

Code	Female parent	Male parent	No. of seedlings	Mean score of parents	Mean score of seedlings*	Variability	CV (%)	Completely resistant seedlings (%)	Partially resistant seedlings (%)
1	Akane	Šampion	41	6.5	5.58	1.61	3.55	0	2.4
2	Discovery	Florina	30	6.2	4.96	3.43	6.81	0	10.0
3	Discovery	Reglindis	24	7.3	6.04	1.79	4.52	0	12.5
4	Discovery	Vanda	31	7.1	6.22	1.27	3.25	0	16.1
5	Florina	A 814/9	29	6.6	5.34	6.22	8.67	27.6	0
6	Florina	FAW 3762	21	6.6	5.52	7.20	10.60	33.3	0
7	HL 1 A	Vanda	126	6.4	5.08	2.63	2.84	0	1.6
8	HL 1 A	HL 938	23	7.2	6.01	0.96	3.40	0	4.3
9	HL 4 A	Angold	39	5.3	4.48	2.35	5.47	0	0
10	HL 4 A	Resista	105	5.2	4.36	1.43	2.67	0	0
11	HL 149	HL 1805	54	6.8	5.81	1.22	2.59	0	1.9
12	HL 166 A	HL 938	46	6.9	5.78	2.47	4.01	0	8.7
13	HL196	HL 1754	30	6.9	5.83	0.87	2.92	0	3.3
14	HL 209	HL 1805	56	8.0	6.78	1.56	2.46	1.9	32.1
15	HL 209	HL 1816	41	7.8	6.85	1.34	2.64	2.4	34.4
16	HL 278	HL 1805	21	7.8	6.66	0.98	3.25	0	23.8
17	HL 319	HL 1816	28	7.4	6.14	1.76	4.09	0	14.3
18	HL 319	McIntosh Wijcik	23	6.8	6.04	1.17	3.73	0	4.3
19	HL 421	HL 938	19	8.0	7.10	1.46	3.90	10.5	31.6
20	HL 499	McIntosh Wijcik	25	7.0	6.40	2.24	4.68	4	28.0
21	HL 499	HL 535 A	25	7.6	6.68	1.18	3.25	0	24.0
22	HL 501	Resista	23	5.4	4.04	2.82	8.67	0	0
23	HL 535 A	HL 4 A	31	6.3	5.61	2.69	5.25	0	0
24	HL 535 A	HL 477	23	7.7	6.78	1.39	3.62	4.3	21.7
25	HL 657	HL 1711	29	6.5	5.55	1.07	3.47	0	0
26	HL 657	HL 1963	30	6.6	5.73	0.93	3.07	0	0
27	HL 657	HL1816	111	7.0	5.84	1.62	2.07	0	10.8
28	HL 718	HL 1963	29	6.6	5.48	1.28	3.84	0	0
29	HL 801	HL1816	25	7.6	6.24	1.06	3.30	0	12.0
30	HL 801	McIntosh Wijcik	16	7.0	6.31	1.09	4.13	0	12.5
31	HL 902	HL 1711	82	6.0	5.03	2.03	3.13	0	3.7
32	HL 938	HL 477	141	8.0	6.70	1.44	1.51	0.7	29.1

Table 2. to be continued

Code	Female parent	Male parent	No. of seedlings	Mean score of parents	Mean score of seedlings*	Variability	CV (%)	Completely resistant seedlings (%)	Partially resistant seedlings (%)
33	HL 938	HL 994	67	7.4	6.41	2.18	2.81	0	28.4
34	HL 938	Resista	41	6.3	5.09	3.60	5.81	0	4.9
35	HL 983	HL 196	16	7.8	6.68	0.83	3.42	0	18.8
36	HL 983	HL 938	35	8.0	6.97	0.82	2.21	2.9	28.6
37	HL 1451	HL 1816	31	6.5	5.16	1.04	3.54	0	0
38	HL 1636	McIntosh Wijcik	66	6.8	6.23	1.18	2.14	0	7.6
39	HL 1669	HL 196	23	6.5	5.34	1.44	4.67	0	0
40	HL 1669	HL 1909	26	6.2	4.92	2.99	6.89	0	3.8
41	HL 1754	HL 1909	29	6.6	5.69	1.59	4.12	0	3.4
42	HL 1754	Resista	27	5.7	4.62	2.82	6.99	0	0
43	HL 1939	HL 1816	24	7.7	6.46	1.25	3.53	0	16.7
44	Klára	McIntosh Wijcik	35	6.8	6.20	1.36	3.18	0	11.4
45	Liberty	HL166 C	50	6.0	5.08	1.11	2.94	0	0
46	McIntosh Wijcik	Selena	40	6.4	5.62	1.68	3.65	0	5.0
47	Red Free	Pinova	31	4.8	3.68	1.70	6.37	0	0
48	Resista	HL 166 A	47	5.5	4.43	1.82	4.44	0	2.1
49	Resista	HL 938	103	6.3	5.44	2.34	2.77	0	7.8
50	Resista	HL 1711	118	5.6	4.84	1.71	2.49	0	0
51	Resista	HL 1754	94	5.7	4.67	2.30	3.35	0	0
52	Resista	HL 1816	129	6.1	5.16	2.15	2.50	0	0
53	Selena	HL 1711	29	6.4	5.14	2.25	5.43	0	3.4
54	Selena	HL 1805	62	7.0	5.68	1.99	3.16	0	4.8
Total			2,500	6.71	5.58	2.49	0.57	0.92	8.48

*LSD = 0.57 (P = 0.05)

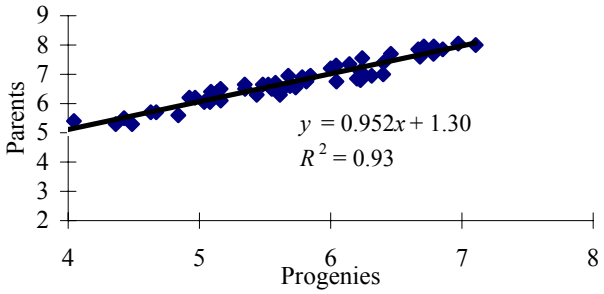

Fig. 1. Regression of mean scores of progenies on mean scores of parents

Starkrimson Delicious), HL 1939 (Starkrimson Delicious and Hopa Crab) and Klára.

In 17 progenies, seedlings with partial resistance to mildew segregated in rates up to 10%. In most cases there were combinations of donors of mildew resistance with medium susceptible or susceptible parents. No segregation of either resistant or partially resistant seedlings was observed in the remaining 15 progenies whose parentage mostly involved medium susceptible or susceptible parents.

The mean infestation of all progenies included in this study was equal to 5.58, whereas the mean value of all the parents was only 6.71. This difference shows that seedlings, on average, were more susceptible than their parents. The difference in the mean infestation of parents and their progenies was, however, significantly lower (about 0.4) in the case of the progenies in which seedlings with columnar growth habit were segregated. In these progenies, usually more seedlings with partial resistance to mildew segregated than it could be expected.

A very close relationship was found between the mid-scores of parents and the mean response to powdery mildew infection in progenies (Fig. 1). This is a good indicator of a simple quantitative pattern of inheritance of the character, and also estimates rather a high level of its heritability.

DISCUSSION

Donors of monogenetically based resistance to powdery mildew A 814/9 and FAW 3762 proved to be a valuable source in this breeding programme. However, the fruit quality of their seedlings is not of sufficiently good quality yet to be accepted as new cultivars. Probably more than one generation of backcrossing to top quality cultivars will be necessary before this drawback is removed. The main advantage of these donors is that resistant offspring can be obtained by their crossing with a very susceptible cultivar, which can hardly be used as a parent of partial resistance.

This study also revealed considerable improvement in donors transmitting partial resistance to powdery mildew. The improvement consists in an increase in the proportions of seedlings with resistance and also in some improvement of their fruit quality. Especially promising, in this respect, are the selections HL 209, HL 499 and HL 477, which were selected in the second generation using genotypes selected among the progeny of the cross Spätblühender Taffetapfel × Court Pendu Plat. This material, moreover, segregates for scab resistance according to a polygenic pattern. There is a potential for greater use for the next crossing for HL 421 (Golden Spur × Jonalicious) that also segregates for columnar growth habit.

In several progenies included in this study seedlings segregated and part of them possessed both scab resistance based on the Vf gene and partial resistance to mildew. This complex resistance was also reported in the previous paper (BLAŽEK 2000). While seedlings with scab resistance are quite easy to be pre-selected in very early stages of their development, the selection for partial powdery mildew resistance requires considerably much more time. Some ways of making amendments of the hitherto procedures, in this respect, are outlined in another paper (BLAŽEK 2004).

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Vyštěpování odolnosti proti padlí jabloňovému (*Podosphaera leucotricha* [Ell. et Ev. /Salm./]) u 54 potomstev jabloní

ABSTRAKT: Výskyt padlí jabloňového byl hodnocen po silných spontánních infekcích u 2 500 semenáčků jabloní celkem z 54 potomstev, která byla získána křížením provedeným v letech 1993 a 1994. Napadení padlím bylo zároveň hodnoceno u 47 odrůd a vybraných hybridů, které byly použity jako rodiče pro tato křížení. Pro charakteristiku každého semenáče nebo rodiče byly použity vždy nejvyšší hodnoty napadení, které byly zjištěny během celého hodnocení. Nejvyšší podíly (33 a 28 %) semenáčů zcela rezistentních vůči padlí vyštěpily ve dvou potomstvech zahrnujících rodiče přenášející monogenně podmíněnou odolnost proti této chorobě. Několik rezistentních semenáčů vyštěpilo v dalších sedmi potomstvech. Semenáče s částečnou odolností vůči padlí vyštěpovaly ve větší míře (kolem 30 %) také v sedmi potomstvech. Z nich šest potomstev pocházelo z křížení, kde vždy jeden z rodičů byl nositelem částečné odolnosti přenesené z vybraných hybridů první generace křížení hybridní kombinace odrůd Hedvábné pozdékvěté a Krátkostopka královská. Velmi těsná závislost byla zjištěna mezi hodnotou charakterizující stupeň napadení rodičů s průměrem této hodnoty u potomstev. Semenáče však byly v průměru významně silněji napadeny než jejich rodiče. Poněkud méně však byla napadávána potomstva, ve kterých vyštěpovaly semenáče se sloupcovým charakterem růstu stromů. Z celkového pohledu práce dokumentuje významné zlepšení u některých donorů přenášejících částečnou odolnost vůči padlí jabloňovému.

Klíčová slova: *Podosphaera leucotricha*; jabloň; padlí jabloňové; odolnost; odrůdy; šlechtění

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