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Assessment of partial resistance to powdery mildew (*Podosphaera pannosa*) in a tetraploid rose population using a spore-suspension inoculation method

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Abstract

Powdery mildew (*Podosphaera pannosa*) is the most important fungal disease in greenhouse roses and is in practice controlled by fungicides. The creation of novel cultivars with durable resistance to powdery mildew is highly desirable. To understand the inheritance of mildew resistance, a tetraploid rose population with a size of 181 seedlings was obtained by crossing two tetraploid genotypes each having partial resistance. The population and its parents were tested under greenhouse conditions with two well-defined monospore isolates (2 and F1) using artificial inoculation with spore suspensions. Disease score at 11 days post-inoculation, latent period and rate of symptom development were used to describe seedling resistance. The tests for both isolates exhibited a wide and significant variation among genotypes for resistance. The distribution of the genotypic means of the disease scores was continuous and showed a considerable transgression. Statistical analysis, scatter plot of disease scores for the isolates, and correlation analyses indicated that the two isolates differed in pathogenicity. The outcome of the tests showed that the inoculation assay with spore suspensions was a reliable and effective way to screen large numbers of genotypes under greenhouse conditions for genetic and breeding studies. This is the first report on spore-suspension inoculation to be used successfully in rose.

Introduction

Powdery mildew caused by the obligate biotrophic pathogen *Podosphaera pannosa* (syn. *Sphaerotheca pannosa*) is the most important disease of greenhouse roses (Linde and Shishkoff, 2003). It causes severe yield and quality reductions due to the formation of white powdery pustules that appear on the leaves, stems and flowers. Repeated use of chemical fungicides is needed to prevent and control the outbreaks of the disease. As there is an increasing interest in the reduction of the use of chemicals in horticulture worldwide, it is becoming increasingly desirable to create novel cultivars with resistance to powdery mildew. The development of cultivars with improved resistance has been a major breeding challenge for a long time, but successes are scarce. This is due to the lack of highly resistant genetic sources in cultivated roses, a limited knowledge of resistance mechanisms and a large diversity in the pathogen species (Linde and Debener, 2003). There is also a need for more reliable assessment methods for screening.

Evaluations of powdery mildew resistance have been conducted in many rose species, cultivars and hybrids. Genotypes with different degrees of resistance were found and several defence mechanisms of plants against the pathogen have been described. Morphological changes such as the vacuolization of epidermal cells (Temmen et al., 1980), physical barriers such as leaf cuticle thickness (Ferrero et al., 2001) and the formation of papillae in plant cells (Mence and Hildebrandt, 1966) were found to influence fungal penetration. Hypersensitive response (HR) (Conti et al., 1985), simple monogenic control (De Vries and Dubois, 2001), a single dominant gene (Linde and Debener, 2003) and horizontal resistance (Schlosser, 1990; De Vries and Dubois, 2001) confer powdery mildew resistance. It seems that vertical resistance (race-specific, HR or monogenic resistance) is very common in roses. For durable resistance, however, horizontal resistance (race non-specific, partial or polygenic resistance) is desirable. This type of resistance delays the infection, growth and reproduction of powdery mildew and tends to be effective much longer (Temmen et al., 1980; Schlosser, 1990).

The pathogen species shows considerable variation in pathogenicity. The races of the pathogen are traditionally defined by differences in virulence of individual isolates on a so-called differential set of host genotypes. Mence and Hildebrandt (1966) reported two races differing in host range and the production of conidia. Bender and Coyier (1984) identified five races in nine samples from Oregon (USA). Leus et al. (2002, 2003) studied eight isolates collected in Belgium and showed a differential host response, indicating differences in virulence among isolates. Linde and Debener (2003) recently classified eight different races in northern Germany and concluded that the pathogen harbours a high diversity of virulence genes.

Homogeneous inoculation of the pathogen is essential for an accurate screening of genotypes for resistance and race identification in *P. pannosa*. Inoculation methods such as leaf-to-leaf contact, dusting with dry conidial and dispersal of the spores over the test plants with a blower are widely used in breeding and research programmes. These methods, however, often result in deposition of groups of conidia at the inoculation site, implying that these methods give fairly variable results and are not very accurate (Francisco et al., 1988). An improvement of the blowing method using a vacuum-setting tower (Francisco et al., 1988; Linde and Debener, 2003) has made it possible to address this problem but the inoculation method is not adequate for screening large numbers of plants, especially in field and greenhouse tests. The use of spore suspensions in water has been extensively employed for the inoculation of powdery mildew in cucumber (Zijlstra et al., 1995), tomato (Bai et al., 2003) and pepper (Lefebvre et al., 2003), but has never been used in rose since research has shown that water adversely affects the viability and infectivity of the conidia (Yarwood, 1939; Wheeler, 1973). However, Sivapalan (1993) observed that mildew conidia differ in their ability to germinate in water, depending on mildew species and duration of conidial exposure to water.

The objective of this study was to obtain an insight into the genetic variation in powdery mildew resistance in cultivated rose. To this end, we have made a tetraploid population by crossing two genotypes each having partial resistance against powdery mildew. Two well-defined monospore isolates have been used to screen the population for resistance. An assay with a spore-suspension inoculation was tested and proved to be a rapid and reliable quantitative technique suitable for large-scale screening of rose genotypes for mildew resistance in genetic and breeding studies. In this report the results of the greenhouse tests are presented.

Materials and methods

Plant materials and experimental design

A tetraploid (K5) population of 181 individuals was obtained from a cross between two tetraploid rose genotypes, P540 and P867, each being partially resistant to powdery mildew. Cuttings from each of the individuals and the parents were made from mother plants of the same age and rooted in plastic trays with commercial potting soil. A randomised block design with three replications was employed for the experiments. Two-week-old cuttings of uniform growth were selected from each genotype and placed in plastic trays according to the experimental design. More cuttings of the parents were distributed among the plants to be tested as well as at the borders of the plots to

check the uniformity of spore deposition. As a control, about 50 cuttings were randomly selected and kept in a separate greenhouse compartment without inoculation to test whether the source materials were free of mildew.

Inoculation and assessment

Two well-defined monospore isolates, isolate 2 from Ahrensburg, Germany (Linde and Debener, 2003) and isolate F1 from Lesdain, Belgium (Leus et al., 2002), were kindly provided by the authors. The monospore isolates were maintained *in vitro* as described by Linde and Debener (2003). To obtain sufficient inoculum of the isolates, fresh cultures of the pathogen were made 3 weeks before inoculation on clean susceptible plants in a small growth cabinet with conditions set at 22 °C (day)/18 °C (night), ~75% humidity and ~200 μmol m^{-2} s^{-1} light intensity for 16 h.

To test the powdery mildew resistance of the population, separate experiments with isolates 2 and F1 were conducted in March and October 2003, respectively, in temperature-controlled greenhouse compartments at Plant Research International, Wageningen, The Netherlands. Artificial inoculations were performed when the plants had on average four unfolded leaves. For inoculation, a spore suspension with a concentration of 10^3–10^4 conidia ml^{-1} was quickly made by rinsing infected leaves with tap water and immediately sprayed onto the plants in a dose of 60 ml m^{-2}. The temperature in the compartment was increased from 22 °C to ~28 °C prior to spraying and thereafter maintained for about 15 min at 28 °C in order to stimulate the evaporation of water from the inoculum droplets on the leaves. The temperature was then again lowered to 22 °C. Growth conditions in the greenhouses were set at 22 °C (day)/18 °C (night), ~75% humidity and ~200 μmol m^{-2} s^{-1} light intensity for 16 h.

A 0–6 disease score was used to describe the development of the symptoms. The basis for the score is the percentage of total area of the four inoculated leaves covered with mycelium. The scores given were 0: no symptoms; 1: very small necrotic lesions with <1% leaf area covered with mycelium; 2: 1–5% leaf area with mycelium; 3: 6–20% leaf area with mycelium; 4: 21–40% leaf area with mycelium; 5: 41–60% leaf area with mycelium and 6: >60% leaf area with mycelium. Evaluation was conducted daily from the first day when symptoms became visible (~5 days after inoculation) until the moment that almost all susceptible plants were heavily infected (~15 days after inoculation).

For further data analysis and interpretation, the two partial resistance component traits, i.e. latent period (LP) and rate of symptom development (RSD), were calculated from the time course of disease scores of individual plants during the first 11 days post-inoculation (dpi). The LP is defined as the number of days from inoculation to the day of the first visual appearance of sporulation. The RSD indicates the ratio of the disease score at 11 dpi and the time interval (in days) from the appearance of the first visible symptom to 11 dpi (i.e. 11-LP).

Statistical analysis

For the traits of disease score at 11 dpi, latent period and rate of symptom development, separate variance analyses were performed with GenStat® (Payne et al., 2002) using (1) the two separate data sets of the tests with individual isolates and (2) combined data of the tests. In the latter, genotypes and isolates were treated as fixed factors. Broad-sense heritability for each trait was calculated by $h^2 = \sigma_g^2/(\sigma_g^2 + \sigma_e^2/r)$ for the separate tests with individual isolates, where, $\sigma_g{}^2$ represents the genetic variance, $\sigma_e{}^2$ the residual variance and r the number of replications.

To describe genetic differences in response to the isolates, two contrasting subsets of genotypes denoted as R and S were composed based on the disease scores selected at 11 dpi. Subset R included the 30 most resistant genotypes and the contrasting subset S the 30 most highly infected ones. The size of the two subsets was arbitrary. The disease scores of the selected genotypes at each evaluation time point were then used to calculate the average scores of the classes. Disease progress curves of the contrasting classes for each isolate were plotted against evaluation time points.

Results

Applicability of the inoculation and assessment protocols

To tackle the common problems of artificial inoculation of plants, such as even spore distribution

among the plants to be tested and the laboriousness of inoculating hundreds of plants simultaneously, we adapted an inoculation assay based on spore suspensions of powdery mildew that has not been described before in rose. The assay was successfully used in the two resistance tests, giving sufficient and evenly distributed infections. In contrast, the non-inoculated cuttings kept in an adjacent compartment did not show infection, indicating that the cuttings used in the tests were free from mildew at the start of the experiments.

The first symptoms of powdery mildew on cuttings of probably susceptable genotypes became visible at 5 dpi. From this moment all plants were scored daily for about 10 days. At the end of the scoring period (14 dpi) almost all plants showing early sporulation were heavily infected (scoring rating >4). The frequency distributions of the mean disease scores of genotypes at the various monitoring times were continuous and changed from negatively skewed to more or less normal, to positively skewed for both tests (data not shown). At 10–11 dpi, the distribution of the disease scores was approximately normal (Figure 1, a1 and a2). Variance analysis of the scores at this time point showed the largest genetic variation among genotypes and a normal distribution of residuals (data not shown).

Variation among rose genotypes

Disease score

Significant genetic differences for disease scores at 11 dpi were found among the genotypes in both isolate tests (data not shown). The analysis of the combined data from both tests collected at 11 dpi

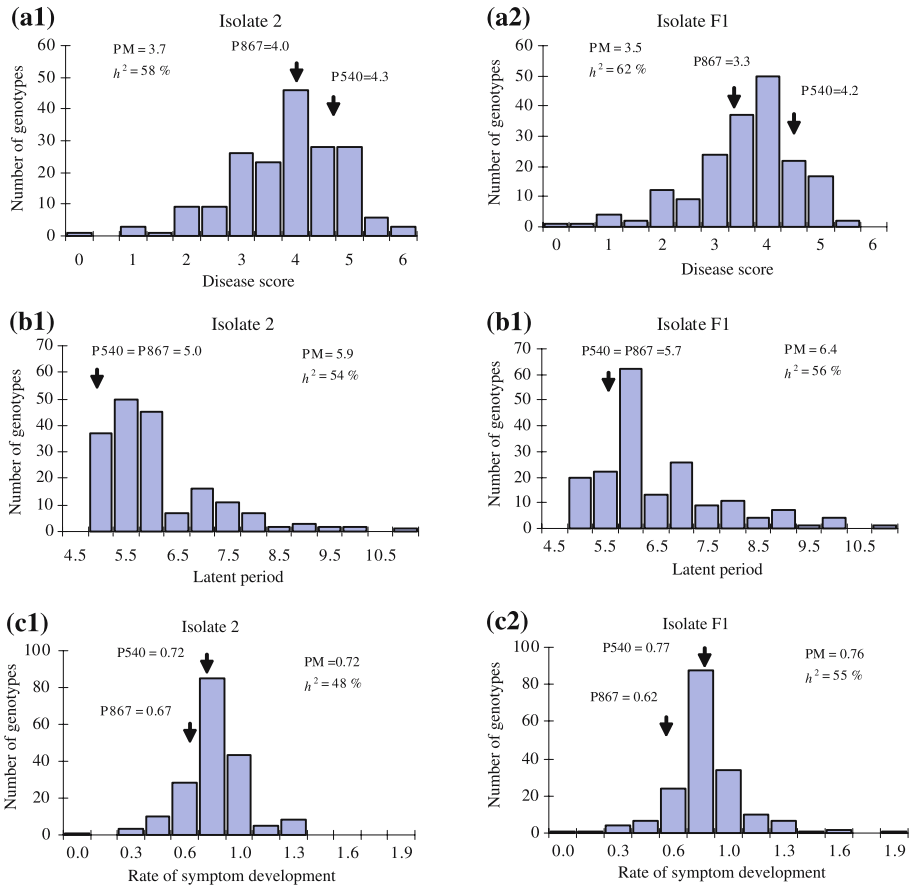

Figure 1. Frequency distributions of powdery mildew disease scores at 11 dpi (a), latent period (b) and rate of symptom development (c) of the rose population after inoculation with isolates 2 and F1. The means of parents P540 and P867, population mean (PM) and broad-sense heritability (h^2) are presented.

showed highly significant genotypic variation ($P < 0.001$) for resistance (Table 1).

The population showed a continuous normal distribution for the mean disease scores of the seedlings at 11 dpi in both resistance tests (Figure 1, a1 and a2). A transgressive segregation of the resistance was observed. The two parents showed partial resistance to both isolates 2 and F1. Parent P867 appeared to be more resistant than parent P540 (Figure 1, a1 and a2), however, a significant difference between the parents was found only with isolate F1.

Comparing the tests with two isolates, differences in the ranges of variation and distributions of the disease scores existed although the population means were similar. The population mean with isolate 2 was smaller than the parental means, whereas that with isolate F1 was in between the parental ones (Table 1). The estimates of broad-sense heritabilities of the disease score were high to both isolates, being 57% for isolate 2 and 62% for isolate F1 (Figure 1, a1 and a2).

Latent period

Significant ($P < 0.001$) genetic differences for the duration of the latent periods were observed in the tests with individual isolates (data not shown) as well as in the combined data (Table 1). The frequency distributions for the duration of latent periods for the two different isolates are illustrated in Figure 1 (b1 and b2). With both isolates, a majority of genotypes had a latent period of about 6 days. A wide range in latent period, i.e. 5–11 days for both isolates, was found among seedlings. The two parents had the same latent period to a specific isolate but differed with different isolates, i.e. both parents had a latent period of 5.0 days in the test with isolate 2 and 5.7 days with isolate F1. The estimates of the heritabilities for latent period were 54% for isolate 2 and 56% for isolate F1.

Rate of symptom development

The rate of symptom development is a measure of the speed at which an epidemic develops. The genetic differences for rate of symptom development were also found to be significant ($P < 0.001$) in the tests with isolates 2 and F1 (data not shown) as well as within combined data of the tests (Table 1). The frequency distributions of the rate of symptom development of the genotypes are presented in Figure 1 with both isolates. The heritability estimates for rate of symptom development were 48% for isolate 2 and 55% for isolate F1 (Figure 1, c1 and c2).

Relationship of the isolates

A scatter distribution of the mean disease scores at 11 dpi with isolates 2 and F1 is plotted in Figure 2. No strong relationship was found between the two isolates. The coefficient of correlation between the disease scores for the two isolates was low ($r = 0.19$, Figure 2). A weak relationship was also

Table 1. Combined ANOVA for resistance tests on rose with powdery mildew isolates 2 and F1

Source of variation	DF	SS	MS	*F*
Disease score				
Genotypes (G)	182	677.46	3.72	3.36***
Isolates (I)	1	15.49	15.49	13.98***
G×I	179 (3)	370.30	2.07	1.87***
Residual	702 (28)	777.69	1.11	
Latent period				
Genotypes	182	859.62	4.92	2.51***
Isolates	1	42.76	42.76	21.77***
G×I	179 (3)	583.69	3.26	1.66***
Residual	704 (26)	1382.88	1.96	
Rate of symptom development				
Genotypes	182	23.08	0.13	1.45***
Isolates	1	0.19	0.19	2.13***
G×I	179 (3)	26.07	0.15	1.67***
Residual	704 (26)	61.49	0.09	

The traits analysed are disease score at 11 days post-inoculation (dpi), latent period and rate of symptom development. The numbers of missing data are in brackets in the 'DF' column. *** indicates $P < 0.001$.

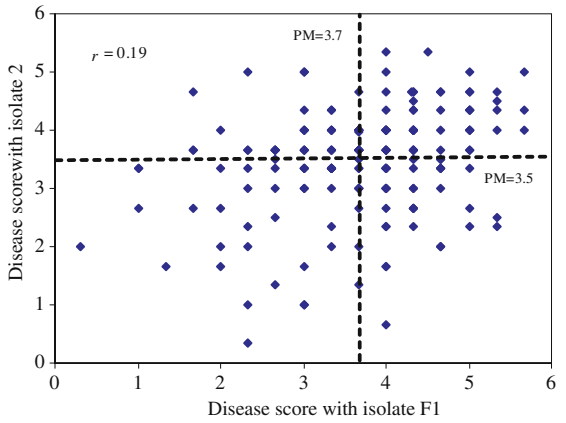

Figure 2. Scatter plot describing the mean powdery mildew disease scores at 11 dpi with isolates 2 and F1. The coefficient of correlation (r) between the disease scores for the two isolates is presented.

found for latent period (r = 0.21) and rate of symptom development (r = 0.16). The variance analyses of combined data sets for the three traits showed that the two isolates differed somewhat in pathogenicity (Table 1).

Interaction between rose genotype and isolate

The interaction of rose genotype and pathogen isolate was highly significant for all traits (Table 1). This interaction for disease scores at 11 dpi is illustrated in Figure 2. Some genotypes responded more to isolate 2, some responded more to isolate F1 and others had a similar response to both isolates. In Figure 3, the disease progress for two contrasting classes of resistance to each isolate is presented. A clear difference in disease development was found between the classes for both isolates. As expected, the resistant class showed a relatively slow increase of the mean disease scores with time and the susceptible a fast increase. The largest difference between classes was found at 10–11 dpi for both resistance tests. After that time point the disease score of the resistant class also increased quickly. Compared to isolate F1, isolate 2 showed a quicker progress after 11 dpi.

Discussion

A tetraploid population of rose was evaluated successfully for resistance to two different monospore isolates of powdery mildew. The novel inoculation method with a spore suspension gave consistent results with both isolates. The satisfactory results were largely due to the even distribution of the spores and the easy applicability of the method. The homogeneous distribution of the spores is essential for the evaluation of plant diseases having a quantitative inheritance. It is a key factor for genetic studies to measure the contribution of minor genes for resistance (Lindhout, 2002; Linde and Debener, 2003). This is the first report on the use of spore suspension inoculation of powdery mildew in rose. Prior to the current experiments, a pilot study was carried out with the *in vitro* bioassay according to Linde and Debener (2003). This assay makes use of detached leaves

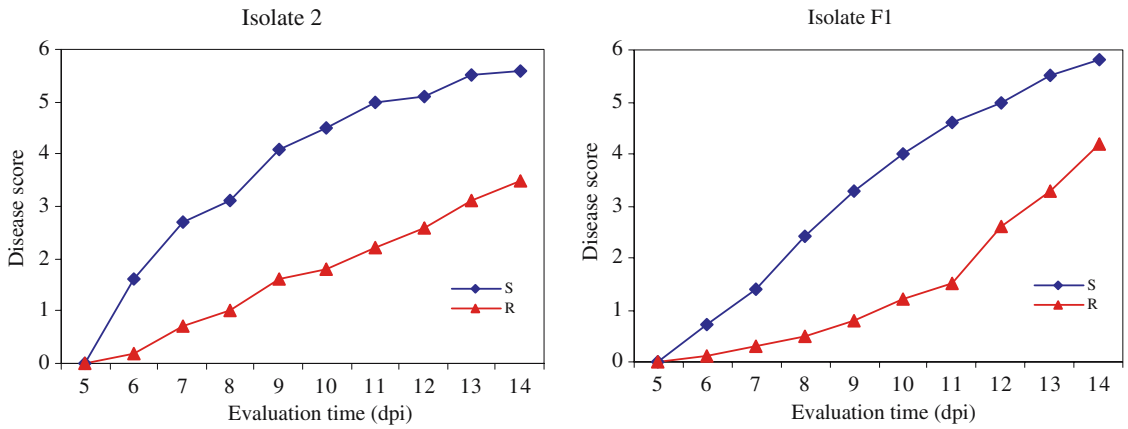

Figure 3. Time courses of the disease in two classes of rose genotypes contrasting for resistance to powdery mildew. At each evaluation time point, mean disease scores for the 30 most resistant (R) and the 30 most susceptible (S) individuals chosen from the population at 11 dpi were used.

placed on water agar that are inoculated with dry spores using a vacuum-setting tower. Using this assay we encountered many problems such as uneven distribution of the spores and infections with unwanted fungi like *Botrytis* during the incubation period, which negatively affected the repeatability and reliability of the assay. In addition, this type of laboratory assay would be very laborious and time-consuming when the size of the population to be evaluated in this study (183 genotypes $\times$ 3 replications $\times$ 2 mildew isolates) is taken into account.

The inoculation method with spore suspensions is based on the methods for powdery mildew inoculation used in cucumber (Zijlstra et al., 1995), tomato (Bai et al., 2003) and pepper (Lefebvre et al., 2003). Water appears to have a negative effect on the germination and viability of mildew conidia (Yarwood, 1939; Wheeler, 1973). An extensive study of the effects of water on the germination of conidia from a variety of mildew species conducted by Sivapalan (1993), however, indicated that short-time storage of conidia in water will not dramatically affect their ability to infect leaves. Our findings are in agreement with his observations. It is essential that the spore suspension is prepared quickly. Furthermore, a temperature-controlled greenhouse compartment or climate room in which the temperature can be shifted quickly from 22 °C to about 28 °C is a necessity to evaporate the water from the fine droplets of inoculum after dispersion on plant leaves as quickly as possible. This inoculation assay is suitable for resistance screening of large sets of genotypes under growth conditions similar to those found in commercial greenhouses.

Conclusions from this study have to be limited to the current experimental population and the isolates used. The present population showed not only a considerable quantitative variation for resistance to each of the isolates, separately, but also a striking difference in response to the two isolates which indicates the presence of differences in the pathogenicity between the two isolates. The transgressive segregation observed for resistance to each of the isolates indicates that each parent is heterozygous for one or more resistance genes (Falak et al., 1999). In earlier resistance studies in rose a major dominant gene (*Rpp1*) for race-specific resistance to powdery mildew has been identified (Linde and Debener, 2003; Linde et al., 2004). However, it is quite likely that rose as well as other species may have several additional genes contributing to the overall resistance against this pathogen. For example, both qualitative and quantitative resistances to powdery mildew have been found in species such as barley (Jorgensen, 1994; Williams, 2003), wheat (Mingeot et al., 2002), tomato (Bai, 2004) and *Arabidopsis thaliana* (Schiff et al., 2001). Therefore, studies including other resistant rose genotypes are needed to get a more complete picture of the inheritance of powdery mildew resistance in cultivated roses.

The largest differences in resistance among genotypes were found at about 11 dpi, which was indicated by genetic analysis as well as by the disease progress for different classes of resistance. This time point is preceded by a 5–6 day latent period, which is in line with 5 days for other genotypes at optimal conditions (Frinking and Verweij, 1989; Xu, 1999) and a 6 day period with mild symptom development. The symptoms increased dramatically after 11 dpi when a second infection cycle became evident. Therefore, the resistance differences among plant genotypes became less pronounced as infection pressure increased.

Variance analyses, disease progress curves and correlation analyses indicated that the two isolates are most likely to be different in pathogenicity. It is obvious, as shown in Figure 3, that different host ranges existed between isolates or, in another words, race-specific responses occurred among plant genotypes. The large diversity of responses of the genotypes, the significant genetic variation and the relatively high heritability of resistance found in the present population may facilitate the selection of highly resistant genotypes. It is to be hoped that a QTL analysis in which isolate-specific and non isolate-specific QTLs for resistance can be identified will shed more light on the genetics of resistance as well as on the differential responses. In addition, such a QTL analysis will facilitate pyramiding of resistance genes from both parents, preferably effective against both isolates as well as others.

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References

Bai Y, Huang CC, Van der Hulst R, Meijer-Dekens F, Bonnema G and Lindhout P (2003) QTLs for tomato powdery mildew resistance (*Oidium lycopersici*) in *Lycopersicon parviflorum* G1.1601 co-localize with two qualitative powdery mildew resistance genes. Molecular Plant–Microbe Interactions 16: 169–176.

Bai Y (2004) The genetics and mechanisms of resistance to tomato powdery mildew (*Oidium lycopersici*) in *Lycopersicon* species. PhD thesis, Wageningen University, Wageningen, The Netherlands.

Bender CL and Coyier DL (1984) Isolation and identification of races of *Sphaerotheca pannosa* var. *rosae*. Phytopathology 73: 100–103.

Conti GG, Bassi M, Maffi D and Bonecchi R (1985) Host–parasite relationship in a susceptible and a resistant rose cultivar inoculated with *Sphaerotheca pannosa*. I. Fungal growth, mechanical barriers and hypersensitive response. Phytopathology 113: 71–80.

De Vries DP and Dubois LAM (2001) Developments in breeding for horizontal and vertical fungus resistance in roses. Acta Horticulturae 552: 103–112.

Falak I, Falk DE, Tinker NA and Mather DE (1999) Resistance to powdery mildew in a doubled haploid barley population and its association with marker loci. Euphytica 107: 185–192.

Ferrero F, Cadour-Marvaldi P, Jacob Y, Coudret A, Sallanon H and Urban L (2001) Evaluation of the resistance to powdery mildew, *Sphaerotheca pannosa* var. *rosae*, of rose-tree species and hybrids. Acta Horticulturae 547: 379–381.

Francisco JB, Reifschneider FJB and Boiteux LS (1988) A vacuum-operating setting tower for inoculation of powdery mildew fungi. The American Phytopathology Society 78: 1463–1465.

Frinking HD and Verweij R (1989) Colonization of rose by *Sphaerotheca pannosa* (Wallr.) Lev. var. *rosae* Wor. Netherlands Journal of Plant Pathology 95: 63–72.

Jorgensen JH (1994) Genetics of powdery mildew resistance in barley. Critical Reviews in Plant Sciences 13: 97–119.

Lefebvre V, Daubeze AM, Van der Voort RJ, Peleman J, Bardin M and Palloix A (2003) QTLs for resistance to powdery mildew in pepper under natural and artificial infections. Theoretical and Applied Genetics 107: 661–666.

Leus L, Huylenbroeck and Van Bockstaele E (2002) Powdery mildew on roses: Pathotype screening. Acta Horticulturae 572: 91–95.

Leus L, Van Huylenbroeck, Van Bockstaele E and Hofte M (2003) Bioassays for resistance screening in commercial rose breeding. Acta Horticulturae 612: 39–45.

Linde M and Debener T (2003) Isolation and identification of eight races of powdery mildew of roses (*Podosphaera pannosa*) (Wallr.:Fr.) de Bary and the genetic analysis of the resistance gene *Rpp1*. Theoretical and Applied Genetics 107: 256–262.

Linde M and Shishkoff N (2003) Powdery mildew. In: Roberts A, Debener T and Gudin S (eds.) Encyclopedia of Rose Sciences (pp 158–165) Elsevier Science, Oxford.

Linde M, Mattiesch L and Debener T (2004) *Rpp1*, a dominant gene providing race-specific resistance to rose powdery mildew (*Podosphaera pannosa*): Molecular mapping, SCAR development and confirmation of disease resistance data. Theoretical and Applied Genetics 109: 1261–1266.

Lindhout P (2002) The perspectives of polygenic resistance in breeding for durable disease resistance. Euphytica 124: 217–226.

Mence M and Hildebrandt AC (1966) Resistance to powdery mildew in rose. Annals of Applied Biology 58: 309–320.

Mingeot D, Chantret N, Baret PV, Dekeyser A, Bouphatem N, Sourdille P, Doussinault G and Jacquemin JM (2002) Mapping QTL involved in adult plant resistance to powdery mildew in the winter wheat line RE714 in two susceptible genetic backgrounds. Plant Breeding 121: 33–140.

Payne R, Murray D, Harding S, Baird D, Soutar D and Lane P (2002) GenStat® for Windows™ (6th Edition) Introduction, VSN International, Oxford.

Schiff CL, Wilson IW and Somerville SC (2001) Polygenic powdery mildew disease resistance in *Arabidopsis thaliana*: Quantitative trait analysis of the accession Warschau-1. Plant Pathology 50: 690–701.

Schlosser E (1990) Horizontal resistance of some plant species to powdery mildew. Mededelingen Faculteit Landbouw Rijksuniversiteit Gent 55: 203–206.

Sivapalan A (1993) Effects of water on germination of powdery mildew conidia. Mycological Research 97: 71–76.

Temmen KH, Gruppe W and Schlosser E (1980) Investigation on the resistance of plants to powdery mildew. V. Basis for horizontal resistance of *Rosa* against *Sphaerotheca pannosa*. Mededelingen Faculteit Landbouw Rijksuniversiteit Gent 45: 153–158.

Wheeler BEJ (1973) Research on rose powdery mildew at Imperial College. Journal of the Royal Horticultural Society 15: 225–230.

Willams KJ (2003) The molecular genetics of disease resistance in barley. Australian Journal of Agricultural Research 54: 1065–1079.

Xu X-M (1999) Effects of temperature on the latent period of the rose powdery mildew pathogen, *Sphaerotheca pannosa*. Plant Pathology 48: 662–667.

Yarwood CE (1939) Control of powdery mildews with a water spray. Phytopathology 29: 282–284.

Zijlstra S, Jansen RC and Groot SP (1995) The relationship between powdery mildew (*Sphaerotheca fuliginea*) resistance and leaf chlorosis sensitivity in cucumber (*Cucumis sativus*) studied in single seed decent lines. Euphytica 81: 193–198.