Resistance to *Phytophthora cactorum* in Diploid *Fragaria* Species

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Abstract. Sixty accessions/genotypes (entries) of diploid *Fragaria* sp. were tested for susceptibility to *Phytophthora cactorum* in greenhouse tests. Four experiments, each with four to 35 entries, were conducted, and each entry was represented by 36 to 45 plants per experiment. The plants were graded according to the number of weeks of survival during the first 4 weeks and for plants surviving more than the first 4 weeks, scoring was based on amount of necrosis in the crown. Statistical analysis showed no significant difference among the four experiments. A majority of the accessions (48) were categorized as being resistant or moderately resistant to *Phytophthora cactorum*. The disease score for this group varied from 1.06 to 3.09. Five accessions with disease scores ranging from 6.25 to 7.43 were considered highly susceptible. Within *F. vesca*, a highly significant proportion of the total variation in disease scores (57.6%) was attributable to the differences between accessions and, hence, of genetic nature. There was no indication of any *Fragaria* species being more resistant or susceptible than others and no systematic differences resulting from geographic origin.

The genus *Fragaria* in the rose family (Rosaceae) is well known for their edible fruits, and the economically important octoploid *Fragaria ×ananassa* Dutch. produces large red strawberries and is grown all over the world. In 2007, the world production of strawberries was more than 3.8 million t (FAOStat Agricultural Data, <http://www.fao.org>). However, annually, strawberry producers face serious economical losses as a result of the development of diseases caused by pathogens, one of them being the destructive oomycete *Phytophthora cactorum* (Lebert & Cohn) J. Schröt., which causes crown rot.

P. cactorum causes disease in more than 200 plant species, including 150 genera representing 60 plant families, several of them within the rose family (Erwin and Ribeiro, 1996). The pathogen causes fruit rot, root and crown rot, cankers, leaf blights, wilt, and seedling blight (Nienhaus, 1960). *P. cactorum* was first reported as the cause of crown rot of strawberry (*F. ×ananassa*

Dutch.) in 1952 in Germany (Deutschmann, 1954). It has since become an important disease in most European countries and can be a limiting factor to successful strawberry production worldwide (Maas, 1998).

P. cactorum is homothallic and produces oospores in diseased plant tissue, which makes the pathogen able to survive in the soil for many years. There are few means of eradicating it once a field has become infested, and even with fumigation, this pathogen is rarely eliminated (Sneh and McIntosh, 1974; Wilhelm and Paulus, 1980). It is therefore also almost impossible to eliminate all sources of infection in strawberry nurseries (Fennimore et al., 2008). Many of the most commonly grown strawberry cultivars in Europe are susceptible to *P. cactorum* (Eikemo et al., 2003) and this enhances the spreading of the disease and the severity of the disease outbreaks. However, genotypes resistant to crown rot do exist. These include accessions from the octoploid species *Fragaria chiloensis* and *Fragaria virginiana*, species that have been used as sources for other useful traits in strawberry breeding (Hancock et al., 2002).

van de Weg (1997) postulated one single dominant major gene for the resistance to the oomycete *Phytophthora fragaria* var. *fragaria* in strawberry. For resistance to *Phytophthora* root rot caused by *Phytophthora fragaria* var. *rubi* in the closely related diploid red raspberry (*Rubus ideaus*), a two-gene model with dominance has been suggested (Pattison et al., 2007). Previous findings do not support a simple model for *P. cactorum*

resistance in *F. ×ananassa*. Shaw et al. (2006, 2008) indicated an additive, polygenically inherited resistance, and Denoyes-Rothan et al. (2004) found five putative quantitative trait loci for resistance in an experimental *F. ×ananassa* population. Focusing on a simpler system than the octoploid strawberry, e.g., a diploid model system, thus appears attractive to get an understanding of the nature and inheritance of the *Phytophthora* crown rot resistance.

F. vesca has several features that make it attractive as a model species. The plants are easily grown and propagated both through seeds and runners, and they are relatively easy to transform genetically (Oosumi et al., 2006). Moreover, the *F. vesca* genome is only slightly larger than the genome of *Arabidopsis thaliana* (Folta and Davis, 2006), and genetic maps exist for both the diploid (Cipriani et al., 2006; Davis and Yu, 1997; Sargent et al., 2004, 2006) and the octoploid strawberry (Lerceteau-Köhler et al., 2003; Weebadde et al., 2008). Finally, a high degree of macrosynteny and colinearity between diploid and octoploid strawberry exist, and no major chromosomal rearrangements seem to have occurred (Rousseau-Gueutin et al., 2008).

The octoploid strawberry progenitors *F. virginiana* and *F. chiloensis* are believed to be diploidized allopolyploids, each descending from four diploid ancestors. The ancestry of *F. virginiana* and *F. chiloensis* is not fully known, but the main diploid candidates are *F. vesca*, *F. iinumae*, *F. nubicola*, and *F. orientalis* (Folta and Davis, 2006; Potter et al., 2000). This conserved organization within the *Fragaria* genus supports the use of diploid *Fragaria* as a model system for gaining genetic knowledge that subsequently can be transferred to the more complex and economically important octoploid *F. ×ananassa* (Davis and Yu, 1997; Sargent et al., 2004).

The work presented here is part of a project in which the main goal is to generate basic knowledge about *P. cactorum* resistance in diploid strawberry species. Second, we aim to identify genes and develop genetic markers that can be used as tools in the amelioration of resistant strawberry cultivars or to develop more effective control measures for disease management. Gaining knowledge about the general level of resistance/susceptibility in our model species is a natural first step and the screening of selected genotypes of diverse geographic origin is reported here.

Materials and Methods

Plant material and plant propagation. Accessions of wild strawberry were either collected as runners across Norway or obtained as seeds from East Malling Research (Kent, U.K.) or the National Clonal Germplasm Repository (Corvallis, OR). The accessions come from all over the world with 36 originating from Europe, 14 from Asia, eight from the Americas, and one accession being of unknown origin (Table 1).

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Table 1. *Phytophthora cactorum* disease scores of 60 diploid *Fragaria* accessions tested in four separate greenhouse experiments.

Accession ^z	Accession received as	Species/subspecies	Country of origin	Disease scores				Least square means disease scores and the corresponding SES
				Expt. 1	Expt. 2	Expt. 3	Expt. 4	
CFRA1363	Seed	vesca	Bolivia		1.07	1.07		1.06 ± 0.64
Bukammen	Runners	vesca	Norway	1.20	1.13	1.07	1.20	1.15 ± 0.45
CFRA1603	Seed	vesca/vesca	Bulgaria		1.07	1.27		1.16 ± 0.64
CFRA573	Seed	vesca/vesca	NA		1.20			1.22 ± 0.92
CFRA564	Seed	vesca/vesca	Russia		1.27	1.27		1.26 ± 0.64
CFRA1780	Seed	vesca	Ukraine		1.33	1.20		1.26 ± 0.64
CFRA1848	Seed	vesca	Japan		1.27			1.26 ± 0.64
ÅS	Runners	vesca	Norway	1.40		1.20		1.29 ± 0.65
CFRA1024	Seed	vesca	Sweden		1.27			1.29 ± 0.92
CFRA1825	Seed	nilgerrensis	China (Yunnan)		1.33	1.33		1.33 ± 0.64
ÅS 2	Runners	vesca	Norway	1.53	1.20			1.38 ± 0.65
CFRA980	Seed	vesca	Kazakhstan		1.27	1.53		1.39 ± 0.64
CFRA197	Seed	vesca	Hawaii ^y	1.27			1.53	1.41 ± 0.64
CFRA1025	Seed	vesca	Sweden		1.20	1.67		1.43 ± 0.64
Haugstøl	Runners	vesca	Norway	1.67		1.33	1.40	1.46 ± 0.52
CFRA502	Seed	vesca/bracteata	USA (New Mexico)		1.53			1.55 ± 0.92
CFRA522	Seed	nubicola	Pakistan		1.53			1.55 ± 0.92
GRYTØY 2	Runners	vesca	Norway	1.53				1.55 ± 0.92
HARDANGER 2	Runners	vesca	Norway	1.53				1.55 ± 0.92
KOPPAREN	Runners	vesca	Norway	1.53				1.55 ± 0.92
CFRA1309	Seed	vesca	Italy		1.53			1.56 ± 0.92
CFRA1610	Seed	nilgerrensis	China (Hubei)		1.53			1.56 ± 0.92
Haugstøl 2	Runners	vesca	Norway	1.53		1.60		1.56 ± 0.65
CFRA1364	Seed	vesca	Italy		1.60			1.62 ± 0.92
ALTA	Runners	vesca	Norway	1.60	1.67			1.65 ± 0.65
ÅS 3	Runners	vesca	Norway	1.67				1.68 ± 0.92
FDP405	Seed	nilgerrensis	China (Guizhou)	1.80	1.53			1.68 ± 0.65
RÅDAL	Runners	vesca	Norway	1.67				1.68 ± 0.92
GRYTØY	Runners	vesca	Norway	1.73				1.75 ± 0.92
GRYTØY 3	Runners	vesca	Norway	1.80				1.81 ± 0.92
NAMSOS	Runners	vesca	Norway	1.87				1.88 ± 0.92
CFRA1861	Seed	nipponica	Japan		1.93			1.95 ± 0.92
CFRA1001	Seed	vesca	Ecuador		1.93			1.96 ± 0.92
ALTA 2	Runners	vesca	Norway	2.00				2.01 ± 0.92
CFRA612	Seed	vesca/vesca	Sweden		2.07			2.09 ± 0.92
NAMSOS 3	Runners	vesca	Norway	2.13				2.15 ± 0.92
CFRA562	Seed	vesca/vesca	Russia		1.13	3.33		2.23 ± 0.64
FDP701	Seed	pentaphylla	China	2.27				2.28 ± 0.92
VASSBYGDA	Runners	vesca	Norway	2.27				2.28 ± 0.92
ALTA 3	Runners	vesca	Norway	2.40				2.41 ± 0.92
HARDANGER	Runners	vesca	Norway	2.47				2.48 ± 0.92
FDP301	Seed	bucharica	Pakistan	2.73				2.75 ± 0.92
NAMSOS 2	Runners	vesca	Norway	3.07		2.47		2.76 ± 0.65
HARDANGER 3	Runners	vesca	Norway	3.60		2.13		2.86 ± 0.65
CFRA1855	Seed	iinumae	Japan		2.93			2.95 ± 0.92
Ljøen	Runners	vesca	Norway	3.70		2.27		2.96 ± 0.65
CFRA1850	Seed	iinumae	Japan		3.07			3.09 ± 0.92
CFRA1856	Seed	iinumae	Japan		3.07			3.09 ± 0.92
CFRA1866	Seed	nipponica	Japan		3.47			3.49 ± 0.92
CFRA479	Seed	vesca/vesca	Germany	3.54				3.56 ± 0.92
FDP818	Seed	vesca/californica	USA (California)	3.87				3.94 ± 0.92
CFRA565	Seed	vesca/vesca	Russia		4.00			4.02 ± 0.92
CFRA1869	Seed	nipponica	Japan		3.67	5.00		4.33 ± 0.64
CFRA1428	Seed	vesca	Bolivia		5.80	3.07		4.43 ± 0.62
FDP 815 (I3)	Seed	vesca/vesca	Germany	2.60	5.13	7.73		5.15 ± 0.52
CFRA175	Seed	vesca/crinita	USA (Oregon)		5.80	6.73		6.25 ± 0.64
Haugstøl 3	Runners	vesca	Norway	5.80		7.53		6.65 ± 0.65
CFRA1218	Seed	vesca	Europe ^x		6.07	8.00		7.02 ± 0.64
FDP821	Seed	vesca/americana	USA (South Dakota)	7.00	7.40	7.73	7.20	7.33 ± 0.44
CFRA424	Seed	vesca/bracteata	USA (Oregon)		6.87	8.00		7.43 ± 0.64

^zAll accessions with the CFRA prefix were obtained from the National Clonal Germplasm Repository, Corvallis, OR. Accessions with the FDP prefix were obtained from East Malling Research, East Malling, U.K.

^yThis accession is believed not to be indigenous to Hawaii.

^xEuropean country unknown.

NA = not available.

The 60 accessions of diploid *Fragaria* sp. belong to the species *F. vesca* (48, including different subspecies), *F. nilgerrensis* (three), *F. iinumae* (three), *F. nipponica* (three), *F. bucharica* (one), *F. nubicola* (one), and *F. pentaphylla* (one). Seed was germinated in

mist chambers. All accessions were propagated as runner plants for use in the resistance test experiments. One representative plant, originating from either seed or runners, was used as a source for all the runner plants. Propagation was done in a greenhouse with

16 h day/20 °C and 8 h night/14 °C. After multiplication and establishment, the plants were grown for an additional 1 to 2 weeks before pathogen inoculation. Artificial light was provided by high-pressure sodium lamps (SON/T, 120 µE·s⁻¹·m⁻²) in periods with less

than 16 h of natural light. Before inoculation, the plants were subjectively graded for size relative to each other using a 1 to 3 scale.

Preparation of inoculum, inoculation, and disease scoring. One isolate (Bioforsk isolate ID number 10300) of *P. cactorum*, originally isolated from the rhizome of a field-grown strawberry plant in Norway, was used in all experiments. Previous tests of aggressiveness revealed no differences between *P. cactorum* isolates (Eikemo, 1998). In agreement with this, amplified fragment length polymorphism displayed a very low level of molecular variation within the crown rot pathotype of *P. cactorum* isolates from all over the world (Eikemo et al., 2004). Zoospore suspensions of *P. cactorum* were prepared as described previously (Eikemo et al., 2000). Plants were gently wounded in the rhizome with a scalpel and inoculated with 2 mL of the zoospore suspension (1×10^5 spores/mL) added onto the crown and lower parts of the plant with a pipette. This method of inoculation was chosen because previous experience has shown that inoculation of plug plants without wounding can lead to poor disease development (Eikemo et al., 2000). The plants were watered 1 to 2 h before inoculation to ensure that the soil was wet and postinoculation watered only on the pot trays, not directly onto the soil.

Disease was scored on a scale from 1 to 8 (Eikemo et al., 2000; Simpson et al., 1994). The plants that died during the first, second, third, or fourth week after inoculation were given the scores 8, 7, 6, or 5, respectively. After 4 weeks, the remaining plants were bisected longitudinally and scored 1 to 4 based on the degree of necrosis in the crown: 1 = no symptoms, 2 = a few brown/dark speckles, 3 = small patches of necrosis, and 4 = more than 50% of the crown necrotic.

Experimental setup and statistical analysis. Four similar experiments were conducted, each with a varying number of accessions being tested. In the first experiment, 31 genotypes were tested, and in the second, 29 additional genotypes as well as six of the extremes (susceptible and resistant) from the first experiments. In Expts. 3 and 4, 24 and four of the extreme genotypes, respectively, were tested again. Each experiment consisted of three replicates, each replicate with 12 to 15 plants, and all experiments were organized in a completely randomized block design. Control plants (wounded and inoculated with water) were included in all experiments. To get within-experiment means, the data from each experiment were analyzed using analysis of variance in which the replicates were considered random and the accessions fixed. When all the experiments were analyzed together, the effect of experiment was also considered random. The statistical model used for the overall analysis was

$$y_{ijkl} = \mu + \text{exp}_i + \text{rep}_j(\text{exp}_i) + \text{Gen}_k + (\text{Gen} \times \text{exp})_{ik} + e_{ijkl}$$

where

y_{ijkl} is the disease score on a single plant;
 μ is the grand mean;
 exp is the random effect of experiment i ;
 $i = 1$ to 4;
 rep is the random effect of replicate; $j = 1$ to 3;
 Gen is the fixed or random effect of accession k ; $k = 1$ to 60; and
 e is the error on the l^{th} plant; $l = 1$ to 12 (or 15).

Disease score least square means were estimated from the mixed effects model in which the accessions were considered fixed and the experiments and replications were considered random. For the estimation of the variance components, a completely random effects model was used. The significance of the random effects was tested using the likelihood ratio (Self and Liang, 1987). Finally, the covariate (i.e., plant size) was included. All computations were done using Proc Mixed® in SAS® (SAS, 1999).

Results and Discussion

There are only a few reports on resistance to *P. cactorum* in wild strawberry species. Harrison et al. (1998) tested wild octoploid strawberry (*F. virginiana* and *F. chiloensis*) for resistance to crown rot, and Parikka (1998) included some wild diploid *Fragaria* genotypes among a wide selection of cultivated strawberry (*F. ×ananassa*) cultivars. Results from both these studies indicated that there is variation in resistance to *P. cactorum* among wild strawberries and, consequently, it should be possible to find genotypes with extreme qualities in a larger collection of accessions. The results from the present study show that diploid *Fragaria* species vary significantly ($P < 0.0001$) in their expression of *P. cactorum* resistance. The most resistant genotypes had an average score of 1.06 (only a few plants showing symptoms after 4 weeks) and the most susceptible a score of 7.43 (all plants dead within 2 weeks). None of the control plants showed symptoms of crown rot in any of the experiments. The combined statistical analysis showed that the variance component resulting from different experiments was not significant and neither was the effect of replication within experiments. However, the accessions responded somewhat differently to the pathogen in the different experiments resulting in a different grade or rank of the cultivars between experiments, revealed as significant a genotype $\times$ experiment interaction ($P < 0.0001$). The effect of plant size on disease score was not significant and hence not included in the analysis. The accession means from each experiment and the overall least square means and their corresponding SES are given in Table 1.

Figure 1 shows the distribution of the least square means of the tested accessions across the four experiments. From this distribution, we cannot postulate anything concerning the nature of the *Phytophthora* resistance.

Despite the seemingly continuous distribution, the possibility of major genes being involved cannot be excluded because the noise in our data is large both the unexplained residual variance and the variance from the accession $\times$ experiment interaction. Using the *F. vesca* subset of our data in a variance component analysis, 57.6% of the total variance was attributable to differences between accessions, whereas 13.8% was the result of the accession $\times$ experiment interaction. Hence, a majority of the observed variation was genetically regulated. In an exploratory experiment like the present one, however, it is not possible to suggest any genetic mechanism for this regulation.

We are unable to postulate any differences between the most resistant accession CFRA1363, with an average score of 1.06, and the accession CFRA1856, which has an average of 3.09. The difference between CFRA1363 and CFRA1866 with disease score 3.49 is, however, significant ($P = 0.0367$), indicating that accessions with disease scores 3.49 and higher belong to a different group as far as susceptibility concerns. On the susceptible side of the distribution, we could not find any significant differences among the five most susceptible genotypes—CFRA175, Haugastøl 3, CFRA1218, FDP821, and CFRA424—leaving them as a putative distinct group. In conclusion, a majority of the accessions (48) were categorized as being resistant or moderately resistant to *Phytophthora cactorum*. The disease score for this group varied from 1.06 to 3.09. Five accessions with disease scores ranging from 6.25 to 7.43 were considered highly susceptible. A majority of the accessions (48) were categorized as being resistant or moderately resistant to *Phytophthora cactorum*. The disease score for this group varied from 1.06 to 3.09. Five accessions with disease scores ranging from 6.25 to 7.43 were considered highly susceptible.

There was no indication of any *Fragaria* species being more resistant or susceptible than others and no systematic differences resulting from geographic origin. The majority of accessions (48 of 60) tested were *F. vesca*, and among these, the disease scores varied from 1.06 to 7.43. A maximum of three accessions was tested from the other *Fragaria* species; hence, no conclusion could be made about the general resistance level in these species. In general, the distribution of resistance to *P. cactorum* in diploid *Fragaria* is comparable to results found in *F. ×ananassa*, in which the disease score ranged from 1.15 to 6.44 using the same method of disease scoring but a slightly different method of inoculation (Eikemo et al., 2003). The present results also showed that wild *F. vesca* accessions collected from the same location may have very different levels of resistance. The three Norwegian accessions named Haugastøl 1, 2, and 3 were collected in the same area within only 2- to 3-km distance. Two of the accessions were quite resistant (1.46 and 1.56), whereas the third, Haugastøl 3, was very susceptible (6.65). All three

Fig. 1. The distribution of disease scores in diploid *Fragaria* ssp. artificially infected with zoospores from *Phytophthora cactorum* strain 10300. Disease was scored on a scale from 5 to 8 during 4 weeks based on when the plants died or 1 to 4 based on degree of necrosis in the rhizome of the surviving plants 4 weeks after inoculation. The accessions were obtained from National Clonal Germplasm Repository, OR (CFRA), East Malling Research, U.K. (FDP), or collected in the wild in Norway.

Haugastøl accessions were tested in two or three experiments. Our own unpublished microsatellite analysis has confirmed the divergence of Haugastøl 3 compared with the other two Haugastøl accessions. One explanation for these differences is that different accessions have been imported by humans and subsequently naturalized. Hence, the three Haugastøl accessions may have quite different origins. Multiple collections within the other sites (mainly from the Norwegian collection) showed more similar degrees of resistance.

In conclusion, we report here the results from testing of diploid *Fragaria* accessions for resistance to *Phytophthora cactorum* in a greenhouse. Both resistant and susceptible accessions have been identified. This information is necessary for gaining basic knowledge about the *P. cactorum* resistance mechanism in the *F. vesca* model system and for the identification for resistance genes and genetic markers to such genes. It is believed that such knowledge eventually will lead to the advancement in the development of *F. xananassa* cultivars. Moreover, recent research has confirmed that there is a high degree of similarity between more distantly related genera of the Rosaceae family (Shulaev et al., 2008; Vilanova et al., 2008). This indicates that information from the *F. vesca* model

system is also relevant to other economically important crops like apple or pear.

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