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. Schrö., 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*) 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 fragariae* var. *fragariae* in strawberry. For resistance to *Phytophthora* root rot caused by *Phytophthora fragariae* var. *rubri* in the closely related diploid red raspberry (*Rubus idaeus*), 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, polygenetically 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 (Ososumi 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 macro-synteny 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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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

| Accession² | 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 |                                                        |
| CFRA1365   | Seed vesca           | Bolivia            | 1.07              | 1.07    | 1.06 ± 0.64                                             |
| Bukammen   | Runners vesca        | Norway             | 1.20              | 1.13    | 1.07 ± 0.64                                             |
| CFRA1603   | Seed vesca/vesca     | Bulgaria           | 1.07              | 1.27    | 1.16 ± 0.64                                             |
| CFRA573    | Seed vesca/vesca     | NA                 | 1.20              | 1.07    | 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              | 1.27    | 1.26 ± 0.64                                             |
| AS         | Runners vesca        | Norway             | 1.40              | 1.20    | 1.29 ± 0.65                                             |
| CFRA1024   | Seed vesca           | Sweden             | 1.27              | 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           | Hawaii²            | 1.27              | 1.53    | 1.41 ± 0.64                                             |
| HAUGASTØL | Runners vesca        | Norway             | 1.67              | 1.33    | 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                                             |
| GRYTOY 2   | Runners vesca        | Norway             | 1.53              |         | 1.55 ± 0.92                                             |
| HARDANGER  | 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                                             |
| HAUGASTØL | Runners vesca        | Norway             | 1.53              | 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 ± 0.92                                             |
| RÅDAL      | Runners vesca        | Norway             | 1.67              |         | 1.68 ± 0.92                                             |
| GRYTOY     | Runners vesca        | Norway             | 1.73              |         | 1.75 ± 0.92                                             |
| GRYTOY 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                                             |
| ALT 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             | 2.27              | 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  | Runners vesca        | Norway             | 3.60              | 2.13    | 2.86 ± 0.65                                             |
| CFRA1855   | Seed iinumae         | Japan              | 3.93              |         | 2.95 ± 0.92                                             |
| Ljøen      | Runners vesca        | Norway             | 3.70              | 2.27    | 2.96 ± 0.92                                             |
| 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            | 5.37              | 7.73    | 5.15 ± 0.52                                             |
| CFRA175    | Seed vesca/bracteata | USA (Oregon)       | 5.80              | 6.73    | 6.25 ± 0.64                                             |
| Haugastol  | Runners vesca        | Norway             | 5.80              | 7.53    | 6.65 ± 0.65                                             |
| CFRA1218   | Seed vesca           | Europe²            | 6.07              | 8.00    | 7.02 ± 0.64                                             |
| FDP821     | Seed vesca/americanica | USA (South Dakota) | 7.00              | 7.37    | 7.20 ± 0.44                                             |
| CFRA424    | Seed vesca/bracteata | USA (Oregon)       | 6.87              | 8.00    | 7.43 ± 0.64                                             |

²All 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.

²This accession is believed not to be indigenous to Hawaii.

²European country unknown.

NA = not available.
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 (Bioforsks 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 et al., 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;
- \(\mu\) is the grand mean;
- \(\text{exp}\) is the random effect of experiment \(i\);
- \(j = 1\) to 4;
- \(\text{rep}\) is the random effect of replicate; \(j = 1\) to 3;
- \(\text{Gen}\) 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. xananaussa_) 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 × 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 s.e.s 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 × 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 × 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 CFRA1356, with an average score of 1.06, and the accession CFRA1856, which has an average of 3.09. The difference between CFRA1356 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. xananaussa_, 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...
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. ×ananassa cultivars and in offspring from crosses between cultivars differing in susceptibility to the disease. Ann. Appl. Biol. 142:83–89.

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