Impact of Foliar Fungi on Dogroses

Effekten av bladsvampsjukdomar hos nyponrosor

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Master’s thesis

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Abstract

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Roses are not only popular ornamentals, but some of the wild species also supply us with food, cosmetics and even medicine. Wild roses of the section *Caninae*, commonly known as dogroses, are often used for their fruits but may also harbour resistance genes that can be used for breeding healthier ornamentals. However, due to the special so-called *Canina*-meiosis, inheritance is mainly matroclinal with a comparatively small paternal contribution. Therefore, it is important to know how resistance genes are transmitted to the progeny. Different foliar fungi damage roses, most important are blackspot (*Marssonina rosae*) and powdery mildew (*Sphaerotheca pannosa*). Furthermore, rust (*Phragmidium* spec.) is known to infect roses, and a leafspot-disease called *Sphaceloma rosarum* has recently become more serious.

Two fields with dogroses, one with plants obtained by open pollination in wild populations, and one with plants obtained from intra- and interspecific crosses, were evaluated for blackspot, powdery mildew, rust and leafspots in the autumn of 2005. The data was statistically analysed with Systat 5.2. Additionally, microscopic investigations were conducted to gather more knowledge about the appearance of the diseases on the dogrose species.

Interestingly, no symptoms of powdery mildew were found in either field, although the fungus infected wild roses of a different section in a field close by. The investigated dogrose plants had previously been damaged by powdery mildew, suggesting that the presently achieved tolerance is due to plant age or exterior influences. Surprisingly few symptoms of blackspot were found and they differed considerably from those found on ornamental cultivars, indicating a lower susceptibility. Most important in 2005 was rust, followed by leafspot symptoms. The latter were found to be caused not only by *Sphaceloma rosarum*, but also by *Septoria rosae*, a fungus never before noticed at Balsgård. The two leafspot diseases produce similar-looking spots that may vary somewhat depending on the host species, and can be properly discriminated only in a microscope.

The rose species vary in their disease susceptibility but there was no evidence of really high levels of resistance. Amount of disease symptoms was mainly matroclinally inherited, but a contribution of the pollen parent was also found. Plants with *Rosa rubiginosa* as seed parent appear to be the most promising candidates for plant breeding since they performed best for rust and leafspots, and might even be resistant to *Septoria*-leafspot.

Sammanfattning

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Rosor är inte bara omtyckta som prydnadsväxter, några av de vilda arterna förser oss även med mat, kosmetika och till och med medicin. Vildrosor av sektionen *Caninae*, allmänt kända som nyponrosor, används ofta för sina frukter, men kan också innehålla resistensgener som kan utnyttjas för att framställa friskare prydnadsrosor. På grund av den särskilda så kallade *Canina*-meiosen är nedärvningen huvudsakligen maternell med ett jämförelsevis litet bidrag från fadern. Därför är det viktigt att veta hur resistensgener förs vidare till avkommorna. Olika bladsvampar som skadar rosor förekommer, vanliga är svartfläcksjuka (*Marssonina rosae*) och mjöldagg (*Sphaerotheca pannosa*). Dessutom är rost (*Phragmidium* spec.) känd för att infektera rosor och en bladfläcksjukdom orsakad av *Sphaceloma rosarum* har blivit alltmer vanligt förekommande.

Två fält med rosor, varav ett med plantor som härstammar från fri avblomning, och ett med plantor från mellan- och inomartskorsningar, utvärderades för svartfläcksjuka, mjöldagg, rost och bladfläckar under hösten 2005. Erhållna data analyserades med Systat 5.2. Dessutom undersöktes symptomen i mikroskop för att öka kunskapen om sjukdomarnas utseende på nyponrosarter.

Intressant var att inga symptom av mjöldagg hittades på något av fälten, trots att svampen infekterade vildrosor av en annan sektion på ett fält i närheten. De undersökta nyponplantorna hade angripits av mjöldagg tidigare år, därför ligger det nära till hands att tro att den förvärvade toleransen beror på plantornas ålder eller på yttre påverkan. Överraskande få symptom av svartfläcksjuka hittades och dessa var påfallande olika de symptom som hittades på prydnadsrossorter, vilket pekar på mindre mottaglighet hos nyponrosorna. Störst skada 2005 orsakades av rost, därefter följde bladfläckssymptom. De sistnämnda visade sig vara orsakade inte bara av *Sphaceloma rosarum*, utan också av *Septoria rosae*, en svamp som inte tidigare observerats på Balsgård. De två bladfläcksjukdomarna framkallar liknande fläckar som kan variera beroende på typ av värdväxt, och kan bara skiljas ordentligt under mikroskop.

Rosarterna varierade i sin sjukdomsmottaglighet, men det fanns inga indikationer på verkligt höga nivåer av resistens. Graden av sjukdomssymptom visade huvudsakligen matroklin nedärvning, men bidrag från pollenföräldern hittades också. Plantor med *Rosa rubiginosa* som fröförälder tycks vara de mest lovande för växtförädling eftersom de var minst mottagliga för rost och bladfläckar och kanske även är resistenta mot *Septoria*-bladfläckar.

Zusammenfassung

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Rosen sind nicht nur beliebte Zierpflanzen, einige der wilden Arten liefern auch Nahrungsmittel, Kosmetika und sogar Medikamente. Wildrosen der Sektion *Caninae*, allgemein bekannt als Hundsrosen, werden häufig wegen der Früchte verwendet, könnten aber auch Träger von Resistenzgenen sein, die zur Züchtung gesünderer Zierrosen nützlich sein können. Aufgrund einer besonderen, sogenannten *Canina*-Meiose ist die Vererbung jedoch überwiegend matroklin mit vergleichsweise geringem väterlichen Beitrag. Deshalb ist es wichtig zu wissen, wie Resistenzgene an die Nachkommen weitergegeben werden. Verschiedene Blattpilze verursachen Schäden an Rosen, am problematischsten sind Sternrußtau (*Marssonina rosae*) und Mehltau (*Sphaerotheca pannosa*). Außerdem ist Rost (*Phragmidium* spec.) ein bekanntes Pathogen an Rosen, und eine Blattfleckkrankheit namens *Sphaceloma rosarum* fällt seit einiger Zeit zunehmend auf.

Im Herbst 2005 wurden zwei Felder mit Hundsrosen hinsichtlich Sternrußtau, Mehltau, Rost und Blattflecken bewertet, dabei standen auf einem der Felder Pflanzen, die von offener Bestäubung in Wildbeständen herrühren, auf dem anderen solche, die von intra- und interspezifischen Kreuzungen stammen. Die Daten wurden mit Systat 5.2 statistisch analysiert. Zusätzlich wurden mikroskopische Untersuchungen durchgeführt, um mehr Wissen über das Erscheinungsbild der Krankheiten auf den Hundsrosenarten zu sammeln.

Interessanterweise wurden in keinem der beiden Felder Symptome von Mehltau gefunden, während der Pilz Wildrosen einer anderen Sektion in einem nahe gelegenem Feld befallen hatte. Die untersuchten Hundsrosen waren früher von Mehltau beschädigt worden, was eine kürzlich erworbene Toleranz nahe legt, die durch das Pflanzenalter oder äußere Einflüsse bedingt ist. Für Sternrußtau wurden überraschend wenige Symptome gefunden, und diese unterschieden sich beträchtlich von denen an Zierrosen-Sorten, was auf eine niedrigere Anfälligkeit hindeutet. Von größter Bedeutung im Jahr 2005 war Rost, danach folgten die Blattfleck-Symptome. Bei letzteren stellte sich heraus, daß sie nicht nur von *Sphaceloma rosarum* verursacht wurden, sondern auch von *Septoria rosae*, einem Pilz der bis dato nicht in Balsgård aufgefallen war. Beide Blattfleckerkrankungen verursachten ähnlich aussehende Flecken, die je nach Wirtsart leicht variierten und nur mit einem Mikroskop zuverlässig unterschieden werden können.

Die Rosenarten schwanken hinsichtlich der Anfälligkeit für Krankheiten, aber es gab keinen Hinweis für einen wirklich hohen Grad an Resistenz. Das Ausmaß der Symptome wurde hauptsächlich matroklin vererbt, aber ein Beitrag des Pollenelters wurde auch festgestellt. Pflanzen mit *Rosa rubiginosa* als Samenelter scheinen vielversprechend für die Züchtung zu sein, da sie bezüglich von Rost und der Blattflecken am besten abgeschnitten haben und möglicherweise sogar gegen *Septoria*-Blattflecken resistent sind.

Contents

Introduction

When roses are mentioned, most people think of one of the most popular ornamentals world-wide, a cut-flower for many occasions as well as a garden plant in all possible shapes and sizes. But roses have much more going for them than just pretty flowers. There is essential rose oil and rose water (Friedrich & Schuricht, 1985). Jam and tea can be produced both from petals and fruit, and even the seeds are useful because of their valuable fatty oil (Çinar & Çolakoğlu, 2005; Çinar & Dayısoylu, 2005). The cultivation of roses goes far back in history, especially in the Orient where they were grown for their beauty and the production of rose oil. From there, cultivation spread to Egypt, Greece and the Roman empire, and in about 1200 a.C. the rose was known in all of Europe, where it was seen as an ornamental as well as a medicinal plant (Friedrich & Schuricht, 1985). Collection of rosehips as wild fruit has a long tradition in northern Europe. A dessert soup that used to be a main source of vitamin C in Scandinavian winters is still very popular in Sweden (Uggla & Martinsson, 2005; Werlemark & Nybom, 2005). In Turkey, there are even projects to establish completely new products like rosehip yoghurt and rosehip ice cream (Duman et al., 2005; Dayısoylu et al., 2005).

The high contents of C-vitamins in rosehips are well known, carotenoids in high amounts are interesting for health as well as for pigments, and Gao et al. (2000) found phenolics to contribute considerably to high antioxidant activities. Antioxidant nutrients are considered to be important for the protection against reactive oxygen (ROS) and nitrogen (RNS) species. Furthermore, Winther et al. (1999) found anti-inflammatory properties of rosehips harvested from the so-called dogrose species, thus providing a new drug against osteoarthritis (Rein et al., 2004). This healing effect was also confirmed by a Norwegian research group (Warholm et al., 2003). In Germany, three youths won a price at the young researchers competition ”Jugend forscht” for their discovery that rosehip tea shows
antiviral activity (Anonymous, http://www.merck.de/servlet/PB/menu/1420520/index.html, accessed 13-Feb-2006).

The list of benefits is long and may prompt the development of new cultivars with different characters due to different, highly specialized end products. Today, production of rosehip soup, tea or drugs in central and northern Europe is based mainly on wild-collected material imported from Chile or eastern Europe. Availability as well as outer and inner quality of the imported rosehips however fluctuates considerably due to the weather-dependent conditions.

Section *Caninae*

Most of the wild roses commonly found in Europe belong to the section *Caninae*, which is one of the ten sections in the genus *Rosa*. These so-called dogroses are important providers of rootstocks for ornamental roses and their rosehips bear a characteristic flavour desirable for traditional products. In addition, they show traits like a short, concentrated fruit ripening period and fruit that are suitable for desiccation. These traits make them appropriate to field production of rosehips (Uggla & Nybom, 1998). Another area where dogroses can be useful is resistance breeding. In times when increasingly few pesticides are permitted, and there is a decreasing acceptance of chemically treated food and growing resentments against regular spraying in home gardens, new ways to produce and grow healthy plants are essential.

A very important field of research in dogrose genetics is their unique form of meiosis, referred to as the *Caninae*-meiosis. In contrast to all the other sections of the genus *Rosa*, the meiosis here is heterogamous and leads to restricted genetic recombination. The basic haploid chromosome number of roses is 7, species in the *Caninae* section are polyploid with 2n = 28, 35 or 42. Through a special way of dividing the chromosomes unequally with only seven bivalents and the rest occuring as univalents, pollen grains with 7 chromosomes and egg-cells with 21, 28 or 35 chromosomes, depending of the species, are obtained (Täckholm, 1920). This means that inheritance is clearly matroclinal with only small contribution of the pollen parent.

In 1986, a project with dogroses started at the Department of Crop Science, Balsgård (Swedish University of Agricultural Sciences) in southern Sweden. Evaluation of F1-generations showed that these strongly resemble the seed parent in most characteristics (Werlemark & Nybom, 2001; Werlemark et al., 1999). Matroclinal inheritance was reflected also in the distribution of molecular markers in an RAPD-assay by Werlemark & Nybom (2001). In spite of this, some morphological traits like ovary length, orifice diameter, number of glandular hairs and characteristics of the sepals were found to be either intermediately or even patroclinally expressed (Werlemark & Nybom, 2001; Ritz & Wissemann, 2003). Mechanisms of inheritance should therefore be carefully investigated also for the even more desirable traits like disease resistance.

Important foliar diseases

Despite of being so popular, roses also have the reputation of being very disease-prone, and there are indeed many serious pathogens. This thesis is concerned with five different foliar fungi; blackspot, powdery mildew and rust being a common problem and two different leafspots that seem to be either only regionally spread or often overlooked.

Blackspot

Blackspot is often called the most serious disease in roses world-wide and it has attracted a lot of research. The causal organism, *Diplocarpon rosae* Wolf in its perfect stage and *Marssonina rosae* (Lib.) Lind in the imperfect, is a host specific pathogen that is mainly found growing on the upper leaf surfaces, but it can also attack the canes.

Typical for this disease are circular or irregularly coalescent spots, 2-12 mm in diameter with feathery margins (Horst, 1983). Due to ethylene production, the area around the affected tissue turns yellow, chlorosis spreads all over the leaflet and early abscission occurs. In addition to the easily recogniseable spots, more untypical symptoms without feathery margins can be found (Horst, 1983; Carlson-Nilsson, 2002). Blechert & Debener (2005) found eight different interaction types between host and pathogen by screening different rose species for their reaction to a single-spore isolate. Of those eight types, the first five make up the compatible reactions from fully to little susceptible. Only type 1 results in the commonly known symptoms, the other four compatible reaction types lead to spots with even borders. The remaining three are incompatible reactions where resistance is achieved by apoptose in types 6 and 7, which means that there is still visible evidence of the attack by the pathogen. Type 8 is resistant in a way that does not allow the pathogen to enter the tissue at all, and therefore, there is no macroscopic evidence of the fungal attack. The same race of *Marssonina rosae* can interact differently with different rose species or cultivars, and the same rose plant can interact differently with different *M. rosae* races. The interaction type is therefore a measurement of how easily a certain genotype of *M. rosae* can overcome the defence mechanisms of a certain rose genotype.

The fungus grows subcuticularly on the surface. Dark hyphae are visible together with black acervuli that release slimy masses of two-celled, hyaline conidia (15-25 µm x 5-7 µm). Blechert & Debener (2005) found acervuli scattered in high density when the interaction type was 1, whereas the other susceptible types were correlated with decreasing amounts of fruiting bodies. Apothecia of the perfect stage with two-celled ascospores are very rare. Conidia spread with water and need to be immersed in water for at least seven hours to infect. This makes control through climatic conditions possible in the greenhouse, but especially in rainy years the problem is very serious for outdoor roses.

Resistance is rare but has been found in different wild species (Svedja & Bolton, 1980; Wenefrida & Spencer, 1993; Byrne et al., 1996; Debener et al., 1998; De Vries & Dubois, 2001) and in some cultivars of the Old Garden Roses (Carlson-Nilsson, 2002). Both resistance through a dominantly inherited single gene (von Malek & Debener, 1998) and through a partially polygenic mechanism (Xue & Davidson, 1998) was reported, and since Blechert & Debener also found three incompatible interaction types (6-8), they propose to combine different kinds of resistance in breeding. This might provide a better protection against the pathogen which appears to contain several physiological races (Debener et al., 1998).

Powdery mildew

Sphaerotheca pannosa (Wallr. Ex Fr.) Lév., the pathogen causing powdery mildew of roses, is found wherever roses are grown. This fungus grows on the surface of all green tissues, mainly on leaves but also on young stems, flower buds and rosehips. *Sphaerotheca pannosa* is one of the most severe diseases in greenhouse production (Linde & Debener, 2003). First symtoms consist of reddish areas on young leaves. Those become curly with further growth, later the surfaces are covered with white mycelium and conidiophores of the fungus. Conidia (22.9-28.6 µm x 13.6-15 µm) are formed directly on the leaf surface in chains, leading to the characteristic powdery appearance, and are spread by wind (Horst, 1983). For conidia formation, high humidity is necessary. Liquid water, however, hinders germination and therefore epidemics occur when rainfall is low, the days are warm and dry and the nights cool and damp (Horst, 1983; Anonymous, 1988). Cleistothecia with ascospores are not important for spreading but for overwintering (Horst, 1983).

Schlösser (1990) reports about horizontal resistance, whereas Linde et al. (2004) identified a single gene, Rpp1, that carries resistance against at least one race of *S. pannosa*, and developed molecular markers for it. Several races could be identified in samples from three sites (Bender & Coyier, 1984; Linde & Debener, 2003), implying that the pathogen has high racial diversity and might easily overcome resistances.

Rust

Nine different species of *Phragmidium* have been reported to cause rust on roses (Horst, 1983) and four of them were reported for dogroses in Europe so far (Gäumann, 1959; Ritz et al., 2005). The most common species is apparently *Phragmidium mucronatum* (Pers.) Schlecht. and *Phragmidium tuberculatum* Mull., whereas *Phragmidium rosae-pimpinellifoliae* (Rabh.) Diet. is less common and *Phragmidium fusiforme* Schrot is mainly alpine (Gäumann, 1959; Ritz et al., 2005). Rust is widespread especially in temperate regions since it needs cool temperatures and moist conditions to develop. In susceptible plants, rust can lead to wilting and defoliation.

The disease occurs on all green parts of the plant, but is mainly found on the lower surface of the leaves. First symptoms are orange pustules of urediospores. In mild climates or in the greenhouse, this stage continues and thereby spreads the fungus with the wind and through insects. In colder areas, black teliospores are produced to overwinter. Depending on the species or cultivar, orange or brown discolourations of the tissue may appear on the upper leaf surface (Horst, 1983). Rust infects the tissue through stomatal openings (Horst, 1983), implying that the density of stomata on the leaves might have an influence on the severity of the infection.

There are no reports about plants that are completely resistant against all nine *Phragmidium* species nor of any identified resistance gene or resistance mechanism. There are lists of ornamental rose cultivars exhibiting at least a high tolerance against rust, but regional recommendations are important here since different species of the fungus might be most common in different areas (Pscheidt, 2005). Ritz et al. (2005) found *R. rubiginosa* to be the least susceptible species in the wild among three evaluated dogrose species.

Leafspot

There are several fungi that cause similar-looking leafspots on roses. Two of these fungi were investigated in this thesis, one will be referred to as *Sphaceloma*-leafspot, the other as *Septoria*-leafspot. Since it is not possible to distinguish between the two with the naked eye, "leafspots" is used for symptoms with unknown cause in the evaluations. Little information is available for these two diseases, either because they are not very common or because they are often overlooked and taken for blackspot.

Sphaceloma-leafspot

The best description available of the leafspot caused by *Sphaceloma rosarum* (Pass.) Jenkins (sexual stage: *Elsinoë rosarum*) was made by Jenkins in 1932. The disease is often called anthracnose and has spread all over the world. The disease can also affect canes and rosehips, but it is only noticed on the foliage in most reports. The fungus causes circular spots up to 0.5 cm in diameter on the leaves. In the early stage, only purple to dark brown spots are visible that can easily be taken for blackspot. When the spots enlarge, the center turns light whereas the margin stays dark. Depending on rose species and cultivar, the colour of the center varies between light brown, grey and white. The light shade is a result of a lifted cuticle or of an etiolation of the whole tissue. This destruction can cause the tissue under the cuticle to fall out, or the center of the lesion may become perforated, or the whole lesion can fall out, resulting in a shot-hole effect. Spots can even be found on veins and rachis.

Leaves affected by *S. rosarum* produce ethylen (McClellan, 1953), but different sources give different information about leaf yellowing. McClellan marks the absence of yellowing as an important distinction to blackspot, whereas Jenkins (1932) states that the common discoloration appears as a mixture of red and yellow. This corresponds to the drawing of the disease made by Margaret Senior in 1964 (front page). Most descriptions currently available for growers and home gardeners on the internet mention leaf yellowing and resulting defoliation, one article even reports that leaves may turn yellow, red yellow or reddish brown (Anonymous, http://www.caes.state.ct.us/PlantPestHandbookFiles/pphR/pphrose.htm, accessed 13-Feb-2006).

Symptoms on the canes are described as the occurrence of small raised lesions that are either circular or elongated parallel to the stem axis. The colour is brown, but again the centers turn white or ashen. Jenkins (1932) states that the lesions are generally not more than 2 mm in diameter, but they can coalesce. Lesions on rose hips resemble those on the canes.

The fungus produces one-celled hyaline conidia (5.9-7.4 µm x 2.8-5.5 µm) in light yellowish-brown acervuli that are hard to discover. The perfect stage, *Elsinoë rosarum*, produces hyaline ascospores (10-14 µm x 5-7 µm) with one to three septae in ascomata. The sexual form is scarce and was described on canes for the first time in 1957 by Jenkins & Bitancourt.

I have not found anything in the scientific literature about preferred climatic conditions and how the fungus spreads and overwinters in literature, but according to different internet pages, the pathogen is common after wet conditions, especially in springtime, spreads with splashing water and overwinters in old lesions on canes and fallen leaves (Hill, http://www.extension.iastate.edu/pages/hancock/hort/educ/roseanthracnose.html; Behrendt & Floyd, http://www.extension.umn.edu/projects/yardandgarden/diagnostics/roseanthrac.html; Rane, http://www.ppdl.purdue.edu/ppdl/weeklypics/6-14-04.html; Beckermann, http://www.extension.umn.edu/yardandgarden/YGLNews/YGLN-Feb0104.html#roses; Anonymous, http://www.colonialdistrictroses.org/sitebuildercontent/sitebuilderfiles/cwvoctober05.pdf; Chute & Chute, http://www.arsyankee.org/rosediseases.htm; Anonymous, http://www.extension.umn.edu/distribution/horticulture/components/6594-06.html; Anonymous, http://www.lfl.bayern.de/ips/gartenbau/09827/#top; Anonymous, http://www.fh-weihenstephan.de/fgw/infodienst/10-2004/ps.html, all accessed 13-Feb-2006). Interestingly, the disease seems to prefer dry springs in Colorado (Pottorff & Brown, http://www.ext.colostate.edu/pubs/garden/02946.html, accessed 13-Feb-2006).

There are no reports about resistance so far, but Jenkins (1932) mentions that she found no symptoms on ramblers in a big English garden which she visited in 1930, whereas all the other roses in that garden were infected.

Septoria-leafspot

The availability of information about the leafspot disease caused by *Septoria rosae* Desm. (teliomorph: *Sphaerulina rehmiana* Jaap.) is even more scarce than that about *Sphaceloma rosarum*. The name is only mentioned without a description in the Compendium of Rose Diseases (Horst, 1983) and I found it in none of the many internet pages for rose growers or home gardeners, except one from the Netherlands (Anonymous, http://home.wanadoo.nl/rmorssink/pag.gesl/h3rosa.html, accessed 26-Nov-2005) and Turkey (Cakir, http://www.bitkisagligi.net/Gul_Septoria_rosae.htm, accessed 28-Feb-2006). In Sweden, this disease was reported by Gram & Weber (1946) as a leafspot disease, while Nilsson & Åhman (1987) describe the leafspots and mention also attacks of the shoots. They state that the disease occurs mainly on certain types of *Rosa canina* but provide no further information in regard to this. The ecological flora of the British Isles at the University of York (Anonymous, http://www.york.ac.uk/res/ecoflora/cfm/ecofl/Results-path.cfm?mnuPathogen=Septoria+rosae&Submit=Search, accessed 28-Feb-2006) also reports about the disease in form of leafspots as a very common disease on *R. canina*.

Boerema (1963) uses the names leaf scorch or surface canker and confirms also that the symptoms occur mainly on wild species, but not on modern garden roses. He describes the symptoms on the foliage as angular, light green or yellow spots that are restricted by the veinlets and 0.5-1 mm in width. Later those spots turn to purple or dark brown in the center. Another variant consists of lighter brown spots that are surrounded by a purple border, thus making the spots appear more circular. Those spots reach up to 3 mm in diameter and are also often accompanied by yellowing. Both kinds of symptoms lead to a premature leaf drop in the case of a severe infection. Under wet conditions, small dots of creamy-white conidia tendrils are visible to the naked eye. On the canes, the symptom begins with purple spots that become longer parallel to the shoots. They can grow to a size of several cm and the older ones turn light brown in the center and often crack. They can girdle the shoots, thus leading to their dieback.

The fungus spreads via long, hyaline conidia (1.7-5.4 µm x 35-80 µm) with up to six septae that are formed in dark pycnidia. The spores emerge from the pycnidia as the already mentioned creamy-white tendrils. Small round fruiting bodies can be formed next to old pycnidia, those produce small, rod-shaped microconidia (2.5-3 µm x 0.5 µm). This spermagonial stage is characterised as an *Astromella* species. The sexual stage seems to have no importance. Since the conidia are very variable, the fungus has been described under many different names and therefore has many synonyms (Boerema, 1963): *Ascochyta rosarum* Lib., *Septoria rosae* Desm. var. *sempervirentis* Dur. & Mont., *Septoria rosae* Desm. var. *minor* Westend. & Wall., *Septoria rosarum* Westend., *Septoria rosae-arvensis* Sacc., *Septoria rosana* Thüm., *Phloeospora rosae* (Desm.) v. Höhn., *Cylindrosporium ramicola* Laub. and *Phloeospora rosae da Camara*.

Boerema (1963) provides one list of *Rosa* species that were mentioned as susceptible in more recent literature or found to be infected in the Netherlands and another list with species that did not show any signs of infection in spite of abundant inoculum sources. As already mentioned, he reports this leafspot only for wild species. Among the susceptible dogrose species are *R. canina*, *R. tomentosa*, *R. villosa* and *R. rubiginosa*. A selection, 'v.d.L.', of *R. rubiginosa* is, however, mentioned among those that lack symptoms. Thus, some kind of resistance seems to exist, and clearly there are differences among different species and perhaps even within species.

Aims

The aim of this work was to evaluate different species of dogroses, as well as some intra- and interspecific crosses for the occurrence of blackspot, powdery mildew, rust and leafspot in order to find more information about their reactions towards those diseases and about the way this is inherited especially in interspecific crosses. The work also included closer investigation of the symptoms with a microscope, especially of the two leafspot diseases, since there is only little information available so far.

Material and Methods

Plant material

The following species and subspecies belonging to section *Caninae* were used for the investigations: *R. canina* L., *R. dumalis* ssp. *corifoliia* (Fr.) A. Ped (syn. *R. caesia* SM.) and *R. dumalis* Bechst. ssp. *dumalis* of subsection *Caninae*; *R. rubiginosa* L. of subsection *Rubigineae*; *R. sherardii* Davies and *R. villosa* L. ssp. *mollis* (Sm.) Crep. of subsection *Vestitae*.

Plants in Field I originate from seeds collected in 1988 from wild rose populations in Scandinavia (Nybom et al., 1996) and are planted in a random order (Table 2). In addition to the dogrose species, there are also some plants of *R. spinosissima* L. (syn. *R. pimpinellifolia* L.) in this field. Those were evaluated but not used for the statistical analyses since they were too few. Field I was evaluated during the first half of September 2005.

Field II contained randomized seedlings originating from intra- and interspecific crosses conducted with wild-collected plants, namely *R. dumalis* ssp. *coriifolia* X *R. sherardii*, *R. dumalis* ssp. *dumalis* X *R. dumalis* ssp. *dumalis*, *R. dumalis* ssp. *dumalis* X *R. dumalis* ssp. *coriifolia*, *R. dumalis* ssp. *dumalis* X *R. villosa* ssp. *mollis*, *R. rubiginosa* X *R. rubiginosa*, *R. rubiginosa* X *R. dumalis* ssp. *dumalis*, *R. rubiginosa* X *R. sherardii*, *R. sherardii* X *R. sherardii*, *R. sherardii* X *R. villosa* ssp. *mollis*, *R. villosa* ssp. *mollis* X *R. villosa* ssp. *mollis* and *R. villosa* ssp. *mollis* X *R. sherardii* (Table 1). Crosses with less than seven plants were evaluated but excluded from the statistical analyses. Field II was evaluated during the second half of September 2005.

Field investigations

Evaluation of all diseases was conducted with a method previously used by Carlson-Nilsson & Davidson (2002). The plants were divided into a lower and an upper level and both were rated as follows: A = free of disease, B = low occurrence (up to 20% infected foliage), C = moderate occurrence (21-50%), D = severe occurrence (more than 51%). The two resulting scores were transferred into a figure between 0 and 9 according to the key (Table 3). This method not only produces an estimate of the occurrence and severity of the disease in different species and crosses, but also describes the infection pattern of each fungus. In order to obtain a less complicated overview, the values (1-9) produced by the key were also classed as follows: 0 = free, 1-3 = low, 4-6 = moderate and 7-9 = severe. Before the actual work started, I twice evaluated one test row in a field with wildroses of another section, in order to ensure repeatability of the evaluation data.

Due to anticipated problems with normality of data, only non-parametric statistical analyses were conducted. The computer programme SYSTAT 5.2 was used for these analyses; Kruskal-Wallis one-way analysis of variance and Spearman rank correlation coefficients.

In addition, I also took notes when plants showed distinctive features, like a considerable portion of dead canes without leaves or an accumulated incidence of spots on rosehips. Plants with very few leaves were omitted, while plants with only few leaves on one level were still evaluated considering those left. This can be a source of error, but since the cause of the leaf drop is unknown, it appeared to be the best alternative.

Microscope investigations

All closer investigations of the diseases were conducted with a Leitz Wetzlar 1.6 X stereomicroscope and a Olympus CH binocular microscope. Photos were taken with a Conica Minolta Dimage X 31 camera and Adobe Photoshop 7.0 was used for cropping and adjusting contrast and brightness.

Results

Survey of the diseases in the field

Powdery mildew was only found on very few plants, and then only on single fruits or leaves that were obviously mechanically damaged. Therefore, no statistical evaluations were performed for this disease. When all plants are considered together, blackspot was the least serious of the remaining diseases in both fields with 74% symptom-free plants in Field I and 53% in Field II (Figure 1). By contrast, very high numbers of moderately and severely affected plants were found for rust as well as for the leafspots, especially in Field II (Figures 2 and 3). For rust, a frequency distribution of evaluation values showed a prevalence of higher values in Field II (Figure 2), with only 1% free and 42% severly infected plants, compared to 14% free plants and 17 % severely infected plants in Field I (Figure 2). For leafspots, the differences between the fields were less pronounced. Thus, only 1% of the plants in Field I were free of symptoms, and none at all in Field II. However, the percentage of individuals with low occurrence of leafspots dropped from 34% in Field I to 20% in Field II, whereas "moderate" rose from 49% to 56% and "severe" from 16% to 24% (Figure 3).

There was at least one gap in the calculated disease values for all three diseases. For blackspot, considerably fewer plants were rated as 2 (B/B), than as for 1 or 3 (Figure 1), showing that *Marssonina rosae* is mainly found in the lower levels of the plant. For both rust and leafspots, comparatively few plants were evaluated as 3 (C/A), 6 (D/A) or 7 (D/B) (Figures 2 and 3), implying that these diseases are very evenly spread out in the plant. With leafspots the situation is, however, further complicated by the fact that two different fungi were involved.

Using the simplified scale with only four categories, the diseases show a more clear and characteristic pattern where a regression line can be inserted (Figures 4-6). The regression lines visualize the intensity of the increase of symptoms for each disease. A polynomic regression line fitted best for blackspot and leafspots, in both fields. For rust, a polynomic regression line was adequate only for Field I, whereas the data for Field II required a logarithmic regression line. All regression formulae reach fairly high coefficients of determination, only the formula for leafspots in Field II has a low value of 0.7938 (Figure 5). Therefore, the distribution of plants over the scale can be computed with high reliability by similar formulae in both fields for blackspot. For leafspots, similar formulae describe the distribution, but the formula for Field II is not very reliable. For rust, on the other hand, reliable formulae could be found for both fields, but they are not similar.

Differences among species in Field I

Variation between species in amount of disease symptoms was analysed by Kruskal-Wallis one-way analysis of variance. Highly significant results were obtained for all three diseases (blackspot, leafspots and rust), with $p = 0.000$

(Table 4). When similar analyses were performed with subsections as group variable, the result was quite different. For all three diseases, the three subsections seem to be rather similar, with $p = 0.343$ for blackspot, $p = 0.346$ for leafspots, and $p = 0.227$ for rust (Table 4). When the analyses were performed for the three taxa belonging to subsect. *Caninae*, *R. canina*, *R. dumalis* ssp. *coriifolia* and *R. dumalis* ssp. *dumalis*, their reaction to leafspots seemed to be very uniform with $p = 0.905$ (Table 4). For blackspot, there was also no significant difference, $p = 0.159$. Only with rust a significant difference could be found ($p = 0.025$). The two species belonging to subsect. *Vestitae*, *R. sherardii* and *R. villosa* ssp. *mollis*, did not differ for any of the three diseases; $p = 0.946$ for blackspot, $p = 0.476$ for leafspots, and $p = 0.630$ for rust. Since *R. rubiginosa* was the only species analysed in subsect. *Rubigineae*, interspecific comparisons could not be made.

Rosa spinosissima does not belong to the section *Caninae* and there were not enough plants for statistical data analysis. The leaves of this species however turned out to be very severely infected by *Sphaceloma rosarum* but by almost no other diseases. The symptoms of *Sphaceloma*-leafspot are very clear and easy to recognize, so this species might be ideal to gather spores from the field and as a standard in infection trials.

Differences among progeny groups in Field II

Pooling of progeny groups resulting from different crosses

Progeny groups resulting from intraspecific crosses with *R. dumalis* ssp. *dumalis* were compared by Kruskal-Wallis one-way analyses of variance (Table 5). Progeny groups 9001, 9002 and 9004 did not differ significantly; $p = 0.142$ for blackspot, $p = 0.465$ for leafspot and $p = 0.565$ for rust, and were therefore pooled into one group in the subsequent analyses. In contrast, the inclusion of progeny group 9007 resulted in much lower p-values both for blackspot ($p = 0.002$) and leafspot ($p = 0.000$). Interestingly, the deviant progeny group 9007 was the only group obtained by using a seed parent from population no. 1, whereas all the other groups had seed parents from population no. 4 (Table 1). Differences among the progeny groups were also illustrated in a histogram (Figure 7).

Comparison of all progeny groups derived from intraspecific crosses with *R. rubiginosa* indicated a significant deviation for leafspots ($p = 0.016$) but not for blackspot ($p = 0.746$) nor for rust ($p = 0.386$), illustrated also in the histogram (Figure 8). Exclusion of progeny group 9025, however resulted in $p > 0.5$ for all three diseases (Table 5). Therefore, all progeny groups except 9025 were pooled in the subsequent analyses.

The two progeny groups obtained from crosses between *R. rubiginosa* and *R. sherardii* did not differ sigificantly for any of the three diseases, and were therefore pooled in subsequent analyses (Table 5).

Comparison of the progeny groups

All the progeny groups (with some groups pooled as explained above) in Field II were compared by Kruskal-Wallis one-way analysis of variance, and proved to differ significantly for all three diseases (Table 4). Instead using subsections as a group variable also produced significant variation.

Subsection *Caninae*

Kruskal-Wallis one-way analysis of variance of all the progeny groups within subsection *Caninae* resulted in a significant difference only for the leafspots (Table 4). In this analysis, also progeny groups derived from interspecific crosses with one of the *R. dumalis* subspecies as seed parent (*R. dumalis* ssp. *dumalis* X *R. villosa* ssp. *mollis*, *R. dumalis* ssp. *coriifolia* X *R. sherardii*) were included because of the strong similarity with *R. dumalis* due to matroclinal inheritance.

Subsection *Rubigineae*

Kruskal-Wallis one-way analysis of variance of all progeny groups with *R. rubiginosa* as seed parent (*R. rubiginosa* X *R. rubiginosa*, *R. rubiginosa* X *R. sherardii*, *R. rubiginosa* X *R. dumalis* ssp. *dumalis*) resulted in significant difference for blackspot and rust, but not for leafspots.

Subsection *Vestitae*

Progeny groups belonging to subsection *Vestitae* were significantly different for blackspot and rust, but not for leafspots when investigated by Kruskal-Wallis one-way analysis of variance. Besides an interspecific cross of *R. sherardii,* a pooled group of two *R. sherardii* X *R. villosa* ssp. *mollis* crosses (9032 and 9034) belong to this subsection. Of two other progeny groups, *R. villosa* ssp. *mollis* X *R. villosa* ssp. *mollis* and *R. villosa* ssp. *mollis* X *R. sherardii*, only three single plants were available for evaluation, but since there are no other crosses with *R. villosa* ssp. *mollis* as seed parent it is useful to still include them.

Microscope investigations

Blackspot

In the beginning it was not easy to recognise *Marssonina rosae*, since the symptoms on dogroses look very different from the well-known symptoms on ornamentals. Smaller dark spots with an even and sometimes darker margin were most common (Figure 13). More 'classical' symptoms with large areas covered by blotches with slightly feathery margins were found only on a few of the *R. dumalis* ssp. *dumalis* individuals and on some plants in progeny groups with *R. dumalis* ssp. *dumalis* as seed parent (Figure 18b). In the microscope, mycelial strands were visible on the surface as well as acervuli, but not as dense as on the ornamental roses used for comparison. Conidia could easily be transfered to glass slides and were therefore used to verify the diagnosis. Yellowing was less intense on leaves with atypical symptoms.

Rust

At the beginning of autumn, rust could be found on virtually every leaf gathered from either field. Most leaves were completely covered either with orange urediospores or black teliospores or both, only plants belonging to *R. rubiginosa* were slightly better (Figure 14). Even insects and mites were covered with urediospores. Teliospores had five to seven septae. Rust attacked mainly leaves, whereas shoots and fruits were affected only if already damaged by something else.

Typically, spores occurred mainly on the lower leaf surface. Spores also on the upper surface were typically found on plants belonging to *R. sherardii* and *R. villosa* ssp. *mollis* or to progeny groups with these species as seed parent. This group also had a tendency to show orange spots on the upper leaf surface, the same could sometimes be found on plants belonging to *R. rubiginosa* or its progeny groups, however, here the spots were darker. Plants belonging to subsection *Caninae* never showed symptoms on the upper leaf surface. Those differences are not very distinct and they do not correlate with the data about susceptibility of the different species, since the most susceptible plants can be found in subsection *Caninae* as well as *Vestitae*.

Leafspot

Until recently, only *Sphaceloma*-leafspot had been diagnosed in the dogrose fields at Balsgård. Especially on plants belonging to subsection *Vestitae*, leafspot symptoms however were somewhat atypical, with small spots covering the leaves very densely. Microscope studies showed the presence of a different fungus, determined as *Septoria rosae* by Professor Uwe Braun from Halle, Germany.

Sphaceloma rosarum

The leafspots caused by *Sphaceloma rosarum* differed considerably in appearance. Colour and size of the round lesions with darker margin were very variable and therefore the pathogen was hard to distinguish from other leafspot fungi. In contrast to *Septoria rosae*, no growth of the fungus was visible on the surface and the dead tissue in the center of the lesions often looked like it was peeling off. The lesions reached over the veins and were not restricted by them. Sometimes yellowing occurred, but a reddish discolouration of the leaves was more common. The foliage mostly stayed green on *R. rubiginosa* and its progeny.

On *R. spinosissima* the margins were purple and the centers almost white (Figure 15a), and shot-holes were common. Interestingly, the lesions were often located on the middle vein. On *R. canina*, *R. rubiginosa*, *R. dumalis* ssp. *dumalis* and plant belonging to progeny groups with these species as seed parents, the spots were also almost white in the center. Plants belonging to species with hairy leaves (*R. sherardii*, *R. villosa* ssp. *mollis*, *R. dumalis* ssp. *coriifolia*) or to progeny groups with such species as seed parents, commonly had light brown spot centers, and the margins were more dark brown than reddish. Ornamental cultivars, examined for comparison, similarly exhibited a range of different symptoms. In contrast to the wild species, where I could not find any asexual fruiting bodies, acervuli were often clearly visible as black dots (Figure 15d), but I could not find any conidia in them. Ascostromata containing four-celled slightly colored ascospores were present, albeit seldomly, on *R. spinosissima* leaves (Figure 15c), but never noticed on any other species. In general, sexual as well as asexual spores were very hard to find on the leaves.

Septoria rosae

The spots caused by *Septoria rosae* did not reach the size of those caused by *Sphaceloma rosarum*. On plants belonging to *R. canina*, *R. dumalis* ssp. *dumalis* and to progeny groups with *R. dumalis* ssp. *dumalis* as a seed parent, the purple margin of the lesions was sometimes very slim and they therefore looked angular (Figure 17c). On plants belonging to *R. dumalis* ssp. *coriifolia*, *R. villosa* ssp. *mollis*, *R. sherardii* and to progeny groups with one of these species as seed parent, broader margins leading to rounder spots were more common. The symptoms were clearly restricted by the veinlets and showed no peeling off in the centre, and the leaf surface stayed intact. The mycelium of this fungus is visible with a microscope (Figure 17e) and the worm-like creamy-white spore tendrils that emerge from the dark pycnidia are very typical (Figure 17d, g, j). Sometimes the centres of the spots appeared to be white, due to fluffy masses of conidia (Figure 17f), that can pile up around the pycnidia (Figure 17j). Heavily infected leaves had big dull brown blotches containing white spots caused by the mentioned spore tendrils and fungal growth. Both of those fungal structures could always be found after rain or high humidity and were triggered by storing leaves for a few days in a moist Petri dish. Sometimes micro conidia were formed in black stromata on those areas with far advanced infection.

Septoria rosae caused yellowing and leaf drop, especially on plants belonging to *R. sherardii*, *R. villosa* ssp. *mollis* and progeny groups with one of these species as seed parent, where it seemed to be at least as serious as *Sphaceloma rosarum*. *Septoria rosae* is sometimes found on plants belonging to the subsection *Caninae*, but apparently less common than *Sphaceloma*-leafspot. No *Septoria*-leafspot was found on plants belonging to *R. rubiginosa* or to progeny groups with this species as seed parent, and also not on *R. spinosissima*.

Combined infections

Pairwise co-occurrence of diseases on the same individual was analysed for the two fields separately with Spearman correlation coefficients (Table 6). In Field I, only a negative correlation between leafspots and blackspot was significant. The same was found in Field II, as well as a negative correlation between rust and blackspot. However, both had only a low significance, whereas rust and leafspots in this field showed a positive correlation with high significance.

Occasionally different fungi had infected the same leaf (Figure 18). Especially rust was omnipresent and there was no difference in the extent of rust infection between leaves that were free from other fungi and those that were affected by one or two of the fungus species. Blackspot and *Sphaceloma*-leafspot could also be found together on the same leaves, sometimes the lesions were even in direct contact (Figure 18c). On heavily affected leaflets, one of these two fungi was, however, always more prevalent (Figure 18a).

When both leafspot species were found on the same plant, attacks of *Sphaceloma*-leafspot were mostly confined to the upper parts. Symptoms of *Septoria*-leafspot were apparently often more severe in the lower parts of the plants.

Symptoms of unknown fungi

Dieback and spots on the fruits

Especially plants belonging to *R. dumalis* and to progeny groups with this species as seed parent, often suffered from severe defoliation, particularly in the lower parts of the plants. This lack of leaves could be found also on the other species, although to a minor extent on *R. rubiginosa* and its progeny. This rendered an evaluation of leaf symptoms for many plants impossible or at least difficult and ambiguous. One of the reasons for this leaf fall seems to be a fungal cane disease causing dark spots on shoots and fruits, that finally leads to dieback of the shoots. Since the symtoms could be found on all the other species as well, further investigation seemed to be warranted.

The first symptoms are small dark red to brown raised spots on the shoots (Figure 16). As they increase in size, the centres turn light and the epidermal tissues dry out and often crack. Spots can coalesce, forming light cankers with reddish margins that can girdle the shoot leading to defoliation and subsequent death. The dead shoots or shoot tips are dried out and crack easily. Black fruiting bodies can be seen on the light, almost white cankers. Investigation with a light microscope revealed two different types of black fruiting bodies. The smaller ones contained hyaline elliptic conidia and the bigger ones four-celled ascospores (Figure 19).

Fruits on affected shoots often showed similar spots, again most common on the *R. dumalis*-plants. Only plants belonging to subsection *Rubigineae* were almost free from this kind of spots. The spots apparently start out as small dark pits that develop light centres and eventually coalesce. Like on the shoots, the epidermal tissues dry out and often crack. In small spots, the whole dried out centre can fall out, leaving the spot without protecting epidermis (Figure 20). In extreme cases, the whole fruit dries out, the epidermis turns white and only the spots stay dark (Figure 20c). In parts of this dead epidermis, mycelium of the fungus growing through the cells was visible around the region of dark cells when examined in the microscope. Unfortunately, I did not find spores in the lesions.

White sprinkles on fruits of *R. rubiginosa* and its progeny

Plants belonging to *R. rubiginosa* or to progeny groups with this species as seed parent, very often showed several white flecks on the fruits, as if they had been sprinkled with dye. First I took them as the beginning of powdery mildew and expected to find the typical symptoms later in autumn together with a spreading to the leaves. But this never happened, the *R. rubiginosa* fruits instead looked healthier than fruits of other species until late in the season, completely lacking the dark spots caused by *Sphaceloma rosarum* or *Septoria rosae*. Unlike all the other species, they were seldomly affected by grey mould or the rosehip fly (*Rhagoletis basiola*). In the microscope, the white flecks seem to be caused by dead cells of the epidermis, similar to the spots caused by leafspot on the fruits, but in *R. rubiginosa* only the outmost layer of cells was affected (Figure 21).

Discussion

Field evaluation methods

The original nine-step evaluation scale involves separate assessments of the upper and lower parts of the plants. Gaps in the frequency diagrams of the evaluation scores tell us that those particular combinations of symptoms in upper versus lower parts of the plant are uncommon. Thus, we can see that blackspot is found mainly in the lower parts, whereas rust and leafspots are, in general, spread equally over the plant.

Using a simplified scale with only four steps saves time and effort, and produces a more easily interpretable histogram. For evaluation of blackspot, mainly the lower level of the plant needs to be examined. For rust and the leafspots, the whole plant should be embraced. Although the simplified scale could be sufficiently informative in many situations, the system with two levels makes it necessary to examine each plant more closely, thus raising the probability of finding distinctive features. For proper assessment of each of the two leafspot diseases, a completely new evaluation method would, however, be required.

Powdery mildew

The general absence of powdery mildew in both fields is remarkable since this cannot be due to unfavourable weather conditions or lack of inoculum. In a field with wild roses of a different section, close to Field II, powdery mildew was definitely a problem; with plants ranging from free of symptoms to severely affected. Obviously the fungus had adequate conditions for developing and inoculum was present in sufficient amounts.

Interestingly, powdery mildew had caused problems on the dogrose plants in previous years. Olsson et al. (2000) report about *R. villosa* ssp. *mollis* plants from one collection site that were too heavily affected by *Sphaerotheca pannosa* to be used for analyses of leaflet shape and RAPD variation, Werlemark et al. (1999) had the same problem with *R. rubiginosa* X *R. dumalis* ssp. *dumalis* and *R. dumalis* ssp. *dumalis* X *R. rubiginosa* crosses. Werlemark & Nybom (2001) mention one *R. villosa* ssp. *mollis* X *R. sherardii* cross that had leaves that were so malformed that they could not be analysed. Carlson-Nilsson & Uggla (2005), who evaluated crosses of the same species, found little powdery mildew, but state that *R. rubiginosa* as seed parent seems to have a positive influence on resistance.

Apparently a protecting mechanism is somehow acquired, possibly when a certain age is reached or when infection with other fungi is very severe. Morphological barriers seem not to be important for resistance (Mence & Hildebrandt, 1966; Conti et al., 1985), but instead Conti et al. (1986) suggest the accumulation of phenolic compounds at the infection site as a possible mechanism. Hajlaoui et al. (1991) found that the formation of papillae can restrict the growth of the infection peg of the pathogen, and that cellulose-rich collars were formed around the haustorial neck in less susceptible plants. Ferrero et al. (2001) report of a lower cuticle transpiration rate in one resistant genotype compared to susceptible genotypes. Possibly, the plant metabolism changes with age, but changes of the transpiration rate should only occur through the life cycle of the single leaf, not for all leaves trough the life cycle of the plant.

Blackspot

The microscopic symptoms of *Marssonina rosae* on dogroses are rather different from the symptoms on ornamental roses. The dogrose symptoms do, however, fit with the description of the different reaction types given by Blechert & Debener (2005); the bigger blotches with slightly fringed margin may represent reaction types 2 or 3, while the smaller spots on *R. rubiginosa* with even margins may represent type 4. It is important to realise that even the small spots with darker margins can also be caused by *Marssonina rosae*, instead of *Sphaceloma rosarum* or *Septoria rosae*. Although blackspot can be a problem on dogroses, it is probably not able to spread as intensely as it does on most ornamental roses, since interaction types of lower compability lead to a decreasing ability of the pathogen to produce inoculum (Blechert & Debener, 2005).

Blackspot is usually a serious problem in roses and it was the main disease recorded by Uggla & Carlson-Nilsson (2005) in progeny derived from crosses with *R. dumalis* ssp. *dumalis* and *R. rubiginosa* as seed parents. The low incidence of blackspot in my study is therefore very surprising but the evaluation needs to be repeated over several years before drawing any final conclusions about possible resistance. Later in the season, after the evaluations, blackspot became far more common on all investigated species. One possibility is that late infections are able to overcome the defence mechanisms of the plant because of decreasing vigour in autumn. Thus, Xue & Davidson (1998) report that *Marssonina rosae* progresses faster on old leaves. But Carlsson-Nilsson (2002), however, describes a year-to-year variation in disease development; the peak of the infection can be very late in one year due to less favourable conditions during the summer, but very early in another year, thus causing considerable damage.

Taxa in subsect. *Caninae* did not show much variation in blackspot scores, neither among the species in Field I nor among the progeny groups in Field II. There was, however, one progeny group among the intraspecific crosses of *R. dumalis* ssp. *dumalis* which differed from the group also for blackspot. Therefore, variance might be present but hidden due to the low occurrence of blackspot. Significant differences were found for subsect. *Rubigineae* and *Vestitae* in Field II, but this was not true among the pure species in Field I. Furthermore, there was no significant variance in blackspot susceptibility among the intraspecific crosses of *R. rubiginosa* in Field II. Therefore, differences in reaction to diseases among the crosses in Field II may be due to influences by the pollen parents of other subsections.

Rust

Rust showed similar symptoms to those on ornamental cultivars with only marginal differences between the species. This was the first time that rust was a major problem on roses at Balsgård. By contrast, Uggla & Carlson-Nilsson (2005) found almost no symptoms during their evaluations in 1997 and 1998.

The teliospores with five to seven septae suggest that the pathogen could be *Phragmidium mucronatum* if dogroses in Sweden are only attacked by one (or several) of the four species reported from central Europe (Gäumann, 1959). Still, more than one species of *Phragmidium* might be present, and more research is therefore needed for a proper determination of the species responsible for infecting dogroses in southern Sweden.

Rust was common in Field I, but much worse in Field II. Analyses of the evaluation results produced two different regression lines, one polynomic (Field I) and one logarithmic (Field II). This difference is probably not due to differences of the plant material nor to the location of the fields. Later in autumn, symptoms of rust were more severe in Field I than at the time of the evaluation, suggesting that the difference in disease development is mainly an effect of the time lapse between evaluating the two fields.

The hairy leaves of plants belonging to subsect. *Vestitae* and to *R. dumalis* ssp. *coriifolia* seemed to be covered by spores, but since the glabrous-leaved *R. canina* and *R. dumalis* ssp. *dumalis* had rust to a similar extent, the hairs can not be crucial for attaching the spores to the leaves. A lower incidence of rust was found only on *R. rubiginosa* which has glabrous but glandular leaves.

The significant differences found between the progeny groups of subsect. *Rubigineae* and also *Vestitae* indicate some influence of the pollen parent. Interestingly, a corresponding difference could not be found for subsect. *Caninae* in Field II. The progeny groups belonging to this subsection were all either obtained by intraspecific crosses or by combining a seed parent of subsect. *Caninae* with a pollen-parent of subsect. *Vestitae*. A closer look at the performance of these two subsections in Field II reveals the same extremely high susceptability, and therefore the identity of the pollen parent did, in all likelihood, not make a noticeable difference.

Leafspots

Sphaceloma rosarum

A considerable range of symptoms was caused by *Sphaceloma rosarum* and especially spots with centres that are not very light can easily be taken for blackspot. The fact that spores are hard to find on the lesions renders future research difficult. More knowledge is needed about the severity of this disease and whether it causes substantial economical loss in rose production. To identify resistant plants, a reliable method for infection tests must be developed. For this, information is needed about growth and development of the fungus, e. g. what are the best conditions for infection, how long does it take from the infection until the first spots are visible and what conditions favour the development of fruiting bodies and spores. Among others, histological methods might be useful for this purpose.

The few plants analysed of *R. spinosissima* showed abundant symptoms of *Sphaceloma rosarum*, but little evidence of having been infected by other foliar diseases. Therefore this species, or at least the genotype used at Balsgård, would be ideal for producing inoculum for infection tests with this pathogen.

Septoria rosae

Septoria rosae is easily confused with *Sphaceloma rosarum*. Reliable diagnosis can only be made with a microscope, preferably when plants have been exposed to moist conditions that trigger the release of characteristic spore tendrils. If no spore tendrils are present, the symptoms can resemble blackspot even under the microscope. Some fungal growth is visible and the dark pycnidia can be taken for the black acervuli of *Marssonina rosae*.

Conidia are often found in large amounts, indicating that it would be easier to develop an infection test for *Septoria rosae* than for *Sphaceloma rosarum*. It would, however, be prudent to first determine how serious this pathogen really is and which species it can infect.

Unfortunately, it was not possible to distinguish the two leafspot species in the field. *Sphaceloma*-leafspot was first found in 1996 in Balsgård (Carlson-Nilsson, 2000), but Uggla & Carlson-Nilsson (2005) state that it has become more serious in later years. *Septoria*-leafspot was never found before, and it is not clear how serious this disease is in general on dogroses.

Regression analyses of the field evaluation results for both diseases combined, produced two similar polynomic formulae. Possibly the symptoms were caused mainly by *Sphaceloma rosarum* at the time when Field I was investigated, and therefore the regression coefficient indicates a high reliability of the formula for this field. Two weeks later, however, when Field II was evaluated, the leafspot symptoms were produced by both diseases, resulting in a regression formula with low reliability. This theory fits with the temperature range, 16-18°C, reported on a Turkish web page about *Septoria rosae* (Cakir, http://www.bitkisagligi.net/

Gul_Septoria_rosae.htm, accessed 28-Feb-2006). Possibly this species can spread only during cooler conditions, whereas *Sphaceloma rosarum* is able to proliferate during the whole season.

Cane dieback was observed on many plants together with purple spots on the green branches. In general, cankers and dieback are caused mainly by three fungal diseases, namely *Coniothyrium wernsdorffiae*, *Coniothyrium fuckelii* (teleomorph: *Leptosphaeria coniothyrium*) and *Cryptosporella umbrina* (teleomorph: *Diaporthe umbrina*) (Pataky, 1990). These species as well as other fungi mentioned in this context in the literature (Horst, 1983) do match the observed symptoms, but not the two observed kinds of black fruiting bodies containing one-celled conidia or four-celled spores (Figures 19 d, g). Additionally, I found no evidence in the literature that those fungi also attack fruits. The fruiting bodies and spores discovered on the cankers instead match *Sphaceloma rosarum* / *Elsinoë rosarum*, which is said to be able to infect not only the leaves but also stems, rosehips and pedicels, where it produces spots with ashen centers (Horst, 1983). *Septoria rosae* also causes similar symptoms (Boerema, 1963) but since I never found any of the conidia typical for this species on the branches, it seems unlikely that it was responsible for the cane dieback. There were also other fungi on the damaged canes, including *Botrytis*-infections, suggesting that cane dieback may be a complex process involving several pathogens.

Similar looking spots, dark lesions with light centers, commonly affected the fruits of all plants except those belonging to subsect. *Rubigineae* and seemed to seriously damage the fruits.

Dead epidermis cells caused white sprinkles on fruits of *R. rubiginosa* and its progeny, similar to the symptoms caused by thrips, but no mites or insects were present. In all likelihood, these symptoms were caused by an incompatible reaction towards a fungus, possibly *Sphaceloma rosarum*. Infection would stop when the fungus starts to invade the fruit via the epidermis, causing the cells to die in apoptosis together with the pathogen.

The three subsections differed significantly in leafspot susceptibility. Comparisons within the subsections yielded significant variation only among the progeny groups belonging to subsect. *Caninae*. However, since the evaluation scores included two different fungi, no conclusions can be drawn about inheritance. Plants of subsect. *Rubigineae* were not found to be affected by *Septoria rosarum*, neither plants belonging to *R. rubiginosa* in Field I and its intraspecific crosses in Field II nor interspecific crosses with pollen parents belonging to other, apparently susceptible species. This suggests matroclinally inherited resistance. Overall occurrence of leafspots was lowest in subsect. *Rubigineae* and symptoms on canes and fruits were also fewer, suggesting that at least some tolerance to *Sphaceloma rosarum* was transmitted through the seed parent.

Combined infections

Infections with different fungi could be found on the same plants, the same leaves and even the same leaflets. Rust was present on all leaves to a similar extent, regardless of infections by other fungi, and therefore does not seem to interact with any of these other fungi. *Sphaceloma*-leafspot and blackspot seem to be able to co-exist in close proximity, but one of them was always prevalent on a leaflet. Probably the first arriving pathogen occupied most of the space without any further interactions. I could not find blackspot and *Septoria*-leafspot on the same plant but this might be different in a year with more blackspot. Since the positive correlation between rust and leafspots is significant only for Field II where both diseases were very severe and present on 99 respectively 100 % of the plants, their counter-influence is not proven. The negative correlation between blackspot and the other two diseases is interesting but the incidence of blackspot was too low to allow any definite conclusions.

Septoria rosae appears to cause more damage in the lower levels of the plant than in the upper levels. Plants heavily infected with this leafspot showed symptoms of *Sphaceloma rosarum* mainly in the upper levels, suggesting an adversary effect between the two fungi but this needs empirical verification.

Variability and disease inheritance

Significant variation in disease susceptibility was found among subsections, species and progeny groups, thus fulfilling a basic requirement for plant breeding: the existence of genetic variability. Three species of subsect. *Caninae* were investigated in Field I, and these varied significantly only for rust. When progeny groups having one of these species as seed parent were compared (Field II), significant variation was instead found only for leafspots. A deviant progeny group among the several groups derived from intraspecific crosses of *R. dumalis* ssp. *dumalis* originated from a seed parent which had been collected from a population in an area where none of the other parental plants grew. Possibly there would be even more variability in this taxon if material from a wider geographic range had been investigated. The material of subsect. Caninae used at Balsgård seems not promising for breeding because of the high average values for rust and leafspots (Figure 10).

Only one of the analysed species, *R. rubiginosa*, belongs to subsect. *Rubigineae*. The progeny groups with this species as seed parent had the lowest values for all three diseases, with all averages below 5 on the nine-step evaluation scale, and were apparently not infected by *Septoria*-leafspot (Figure 9). This could be due to the glabrous leaves with aetherical oils. Ritz et al. (2005) found the lowest incidence of rust on *Rosa rubiginosa* when compared to *R. canina* and *R. corymbifera*. They propose that this was due mainly to the fact that *R. rubiginosa* is less common in Germany than the other two species, and the pathogen might therefore be better adapted to those than to *R. rubiginosa*. Similarly, of the species used in my study, *R. rubiginosa* is the least common in Sweden.

Rosa rubiginosa was found to be very homogenous by Nybom et al. (1998). Nevertheless, one progeny group among the intraspecific crosses was found to differ significantly from the others for leafspots. This progeny group was obtained by selfing a plant that had already been noted as having a different leaflet shape compared to other plants of *R. rubiginosa* (Nybom et al., 1998). Three subspecies are often recognized in *R. rubiginosa*; ssp. *rubiginosa*, ssp. *umbellata* and ssp. *columnifera*, but these differ mainly in the sepal morphology (Henker, 2000). Most of the *R. rubiginosa* plants at Balsård are likely to belong mainly to ssp. *columnifera* (Gun Werlemark, pers. comm.) but maybe the seed parent of the deviating progeny group should be treated within one of the other subspecies. Anyway, the intraspecific variation in *R. rubiginosa* could be useful for breeding, especially since the deviating progeny group showed less susceptibility than the rest.

Investigation of the *R. rubiginosa* progeny groups also showed that the cross with *R. sherardii* as pollen parent had a much higher incidence of blackspot than the intraspecific crosses, and the hybrid with *R. dumalis* ssp. *dumalis* a much lower value (Figure 11). This is somewhat surprising since *R. sherardii* in Field I had a very much lower incidence of blackspot than *R. rubiginosa*.

No difference in disease scorings was found between the two species belonging to subsect. *Vestitae*: *R. sherardii* and *R. villosa* ssp. *mollis*. Nybom et al. (1998) found a close relationship between these taxa also for molecular markers. Since values were very high for both rust and leafspots this subsection does not appear to be very promising for plant breeding purposes (Figure 12).

Conclusions

Dogroses unfortunately do not appear to be resistant to foliar fungi, and there was no evidence of dominantly inherited resistance genes in the investigated material, which could have been introduced easily into new rose cultivars.

In 2005, *Marssonina rosae* was apparently not the major problem, but instead leafspots and rust. The extreme incidence of *Phragmidium* may be due to exceptional weather conditions since such high levels of rust infection had never been reported before. The leafspot fungus *Sphaceloma rosarum*, however, definitely seems to cause increasing problems. Another leafspot fungus that had never been noted before at Balsgård was identified as *Septoria rosae*. It is not yet clear how serious its impact is on dogroses, but it should be included in future observations. In many plants, canes and fruits had been seriously damaged. The fungus responsible for this was probably *Sphaceloma rosarum* but *Septoria rosae* can also cause cane damage, and more research is needed to determine what fungus is involved.

Evaluation of several different species from the subsections *Caninae*, *Rubigineae* and *Vestitae* indicates that *R. rubiginosa* is the healthiest of the studied species. The other species of subsect. *Rubigineae* should, however, be investigated since some of them might be even more advantageous for use as donors of disease resistance. Since there is evidently some intraspecific variation, it might be necessary to screen plants collected from many different populations in order to find the best genotypes.

Possibly the *R. rubiginosa* plants used at Balsgård are resistant against *Septoria rosae*, but all of the other four evaluated fungi were found. The better overall disease tolerance (horizontal resistance) of this species may be connected to morphological factors like the number of stomata or the production of essential oils in the leaf glands. It is also possible is that the pathogens are less adapted to *R. rubiginosa* because it is the least common of the evaluated *Rosa* species.

In general, disease susceptibility in experimentally derived progeny groups was strongly influenced by the seed parent, but a paternal contribution was also evident in several progenies.

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Finally my thesis is finished and I learned a lot about roses and their diseases, about the writing of scientific texts and the research of literature. It is as important for me that I also got to know another country and some of the people living there. This would not have been possible without help,

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It was not easy to find out which second fungus caused leafspots on the roses, so I am very grateful that Prof. Uwe Braun from Halle, Germany, determined it as *Septoria rosae*.

The copyright for the painting by Margaret Senior is held by NSW Agriculture, Australia, and I am very happy to be able to use it.

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Tables

Table 1. Progeny groups used for the disease evaluations in Field II. The two last digits in the numbers of the parents identify the individual plant used in the crossings whereas the first 1 or 2 digits refer to the population from where the parent plants were originally collected.

cross	cross number	parents	number of individuals
R. dumalis ssp. *coriifolia* X *R. sherardii*	9011	-	8
R. dumalis X *R. dumalis* ssp. *coriifolia*	9006	-	4
R. dumalis ssp. *dumalis* X *R. dumalis* ssp. *dumalis*	9007	112 X 409	25
R. dumalis ssp. *dumalis* X *R. dumalis* ssp. *dumalis*	9004	407 X 409	22
R. dumalis ssp. *dumalis* X *R. dumalis* ssp. *dumalis*	9005	407 X 504	6
R. dumalis ssp. *dumalis* X *R. dumalis* ssp. *dumalis*	9002	409 X 407	12
R. dumalis ssp. *dumalis* X *R. dumalis* ssp. *dumalis*	9001	409 X 409	15
R. dumalis ssp. *dumalis* X *R. sherardii*	9013	-	2
R. dumalis ssp. *dumalis* X *R. villosa* ssp. *mollis*	9009	504 X 105	21
R. rubiginosa X *R. dumalis* ssp. *dumalis*	9030	1302 X 504	17
R. rubiginosa X *R. rubiginosa*	9027	1102 X 1109	15
R. rubiginosa X *R. rubiginosa*	9028	1102 X 1305	22
R. rubiginosa X *R. rubiginosa*	9025	1109 X 1109	7
R. rubiginosa X *R. rubiginosa*	9029	1302 X 1102	25
R. rubiginosa X *R. rubiginosa*	9031	1401 X 1401	10
R. rubiginosa X *R. rubiginosa*	9033	1408 X 1408	11
R. rubiginosa X *R. sherardii*	9032	1401 X 1402	17
R. rubiginosa X *R. sherardii*	9034	1408 X 1402	15
R. sherardii X *R. sherardii*	9018	315 X 314	21
R. sherardii X *R. villosa* ssp. *mollis*	9020	315 X 105	58
R. villosa ssp. *mollis* X *R. sherardii*	9017, 9021, 9023	-	3
R. villosa ssp. *mollis* X *R. villosa* ssp. *mollis*	9014	105 X 105	5

Table 2. Species used for the disease evaluations in Field I

species	number of individuals
R. canina	42
R. dumalis ssp. *coriifolia*	22
R. dumalis ssp. *dumalis*	98
R. spinosissima	4
R. rubiginosa	122
R. sherardii	44
R. villosa ssp. *mollis*	14

Table 3. Evaluation key and resulting rating for blackspot, leafspots and rust; and the four major disease incidence categories used for obtaining an overview. A = free of disease, B = low occurrence (up to 20% infected foliage), C = moderate occurrence (21-50%), D = severe occurrence (more than 51%).

<table>
<tr><th>level I</th><th>level II</th><th>final rating</th><th>disease categories</th></tr>
<tr><td>A</td><td>A</td><td>0</td><td>Free</td></tr>
<tr><td>A</td><td>B</td><td>1</td><td rowspan="3">Low</td></tr>
<tr><td>B</td><td>B</td><td>2</td></tr>
<tr><td>C</td><td>A</td><td>3</td></tr>
<tr><td>C</td><td>B</td><td>4</td><td rowspan="3">Moderate</td></tr>
<tr><td>C</td><td>C</td><td>5</td></tr>
<tr><td>D</td><td>A</td><td>6</td></tr>
<tr><td>D</td><td>B</td><td>7</td><td rowspan="3">Severe</td></tr>
<tr><td>D</td><td>C</td><td>8</td></tr>
<tr><td>D</td><td>D</td><td>9</td></tr>
</table>

Table 4.. Variation in disease incidence estimated for each of three diseases (blackspot, leafspots and rust) separately by Kruskal-Wallis one-way analysis of variance using subsections, species and progeny groups as grouping variables. Progeny groups obtained from crosses involving the same species were pooled when not significantly different (Table 5). The p-values refer to the probability that the compared groups are similar.

			p-value		
	Investigated groups	Variable	blackspot	leafspots	rust
Field I (pure species)	Subsection *Caninae*[1)] Subsection *Rubigineae*[2)] Subsection *Vestitae*[3)]	Species	0.000	0.000	0.000
	Subsection *Caninae*[1)]	Species	0.159	0.905	0.025
	Subsection *Vestitae*[3)]	Species	0.946	0.476	0.630
	Subsection *Caninae*[1)] Subsection *Rubigineae*[2)] Subsection *Vestitae*[3)]	Subsecti on	0.343	0.346	0.227
Field II (crosses)	Subsection *Caninae*[4)] Subsection *Rubigineae*[5)] Subsection *Vestitae*[6)]	Progeny group	0.000	0.000	0.000
	Subsection *Caninae*[4)]	Progeny group	0.936	0.000	0.460
	Subsection *Rubigineae*[5)]	Progeny group	0.000	0.222	0.003
	Subsection *Vestitae*[6)]	Progeny group	0.027	0.502	0.009
	Subsection *Caninae*[4)] Subsection *Rubigineae*[5)] Subsection *Vestitae*[6)]	Subsecti on	0.000	0.000	0.000

[1)] *R. canina*, *R. dumalis* ssp. *dumalis*, *R. dumalis* ssp. *coriifolia*
[2)] *R. rubiginosa*
[3)] *R. sherardii*, *R. villosa* ssp. *mollis*
[4)] *R. dumalis* ssp. *coriifolia* X *R. sherardii*, *R. dumalis* ssp. *dumalis* X *R. dumalis* ssp. *dumalis*, *R. dumalis* ssp. *dumalis* X *R. sherardii*, *R. dumalis* ssp. *dumalis* X *R. villosa* ssp. *mollis*
[5)] *R. rubiginosa* X *R. dumalis* ssp. *dumalis*, *R. rubiginosa* X *R. rubiginosa*, *R. rubiginosa* X *R. sherardii*
[6)] *R. sherardii* X *R. sherardii*, *R. sherardii* X *R. villosa* ssp. *mollis*, *R. villosa* ssp. *mollis* X *R. villosa* ssp. *mollis*, *R. villosa* ssp. *mollis* X *R. sherardii*

Table 5. Variation in disease incidence estimated for each of three diseases (blackspot, leafspots and rust) separately by Kruskal-Wallis one-way analysis of variance using progeny groups as grouping variables. The p-values refer to the probability that the compared groups are similar.

		p-value		
Investigated crosses	Variable	blackspot	leafspots	rust
R. dumalis ssp. *dumalis* X *R. dumalis* ssp. *dumalis* crosses no. 9001, 9002, 9004, 9007	progeny group	0.002	0.000	0.103
R. dumalis ssp. *dumalis* X *R. dumalis* ssp. *dumalis* crosses no. 9001, 9002, 9004	progeny group	0.142	0.465	0.565
R. rubiginosa X *R. rubiginosa* crosses no. 9025, 9027, 9028, 9031, 9033	progeny group	0.746	0.016	0.386
R. rubiginosa X *R. rubiginosa* crosses no. 9027, 9028, 9031, 9033	progeny group	0.527	0.649	0.643
R. rubiginosa X *R. sherardii* crosses no. 9032, 9034	progeny group	0.833	0.080	0.726

Table 6. Analyses of co-occurrence of the different diseases (blackspot, leafspots and rust) in the two fields, reported as a matrix of Spearman rank correlation coefficients. Since total number of observations is 346 in Field I and 348 in Field II, the coefficent must reach at least ±0.195 for $p < 0.05$, ±0.254 for $0.05<p<0.01$, and ±0.321 for $p<0.001$.

	blackspot		leafspots	
	Field I	Field II	Field I	Field II
leafspots	**-0.309**	**-0.217**		
rust	-0.019	**-0.196**	-0.062	**0.476**

Figures

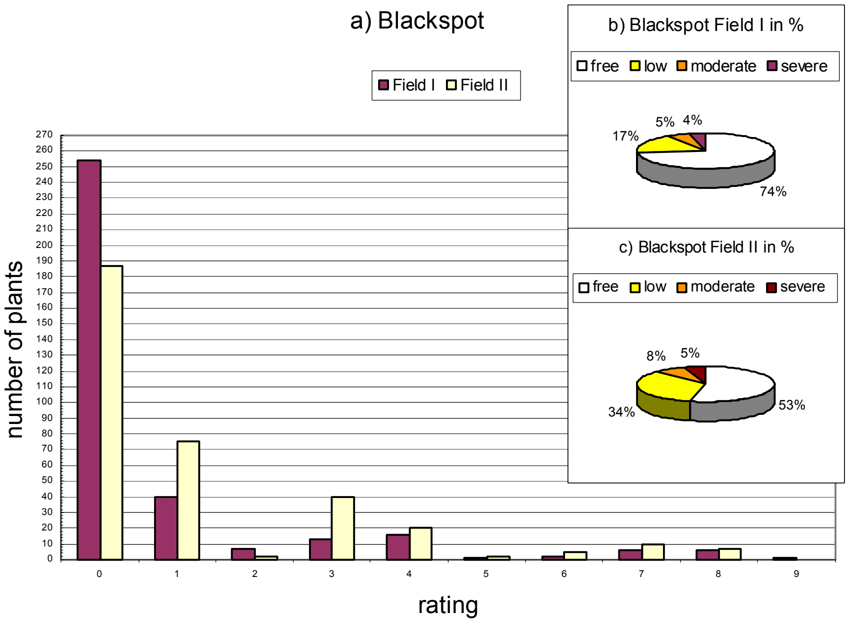

Figure 1. Blackspot on all plants in Field I and Field II, in absolute numbers and as percentages. a) The absolute numbers of plants with the different evaluation key values (1-9) are compared for both fields, b) Percentage of plants in Field I that belong to the four major disease incidence categories, c) Percentage of plants in Field II that belong to the four major disease incidence categories.

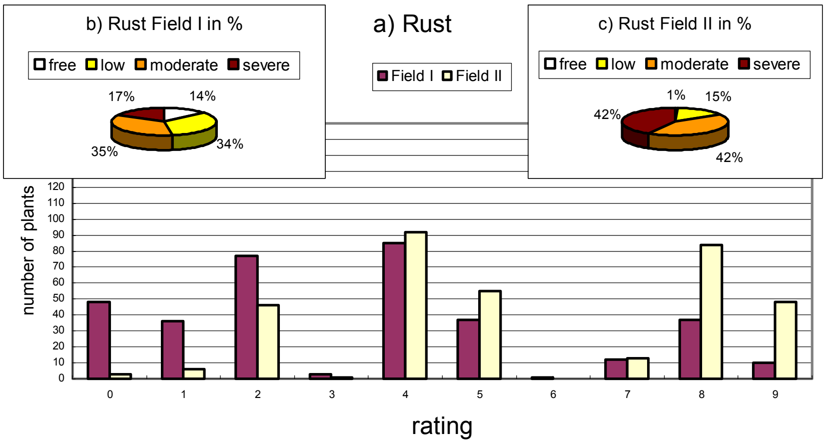

Figure 2. Rust in Field I and Field II, in absolute numbers and as percentages. a) The absolute numbers of plants with the different evaluation key values (1-9) are compared for both fields, b) Percentage of plants in Field I that belong to the four major disease incidence categories, c) Percentage of plants in Field II that belong to the four major disease incidence categories.

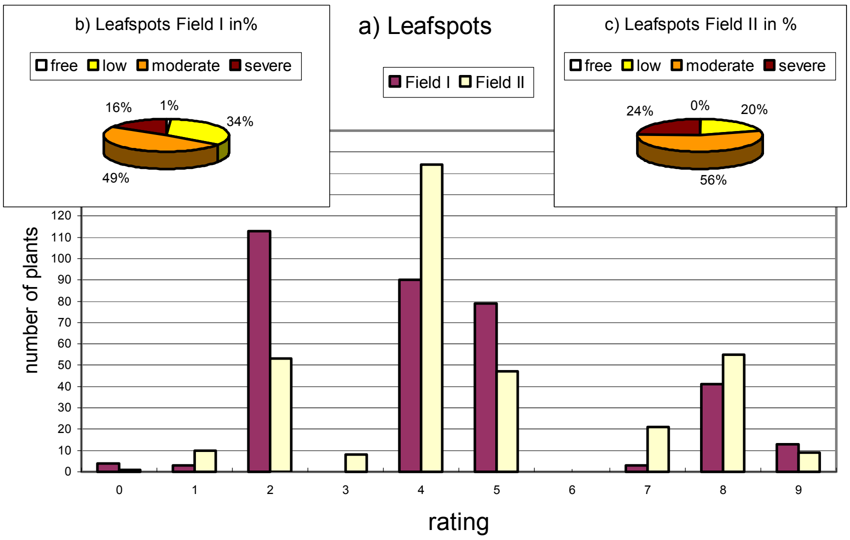

Figure 3. Leafspots in Field I and Field II, in absolute numbers and as percentages. a) The absolute numbers of plants with the different evaluation key values (1-9) are compared for both fields, b) Percentage of plants in Field I that belong to the four major disease incidence categories, c) Percentage of plants in Field II that belong to the four major disease incidence categories.

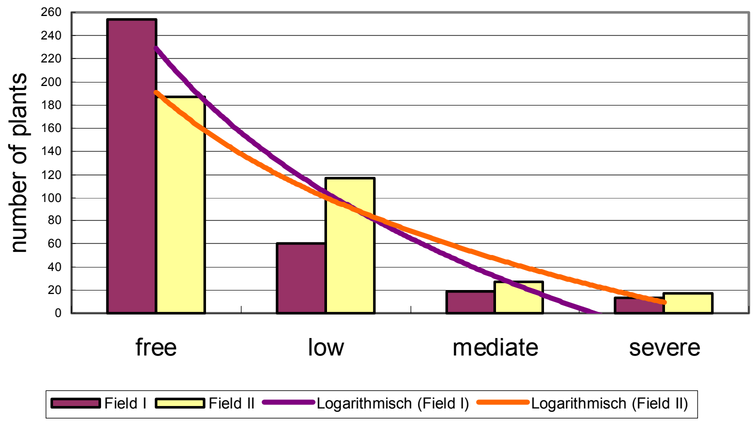

Figure 4. Number of plants in the four majour disease incidence categories when scored for blackspot in Fields I and II, with fitted regression lines (both logarithmic). Field I: y = -179.32Ln(x) + 228.97; R^2 = 0.9004; Field II: y = -131.12Ln(x) + 191.18; R^2 = 0.9609

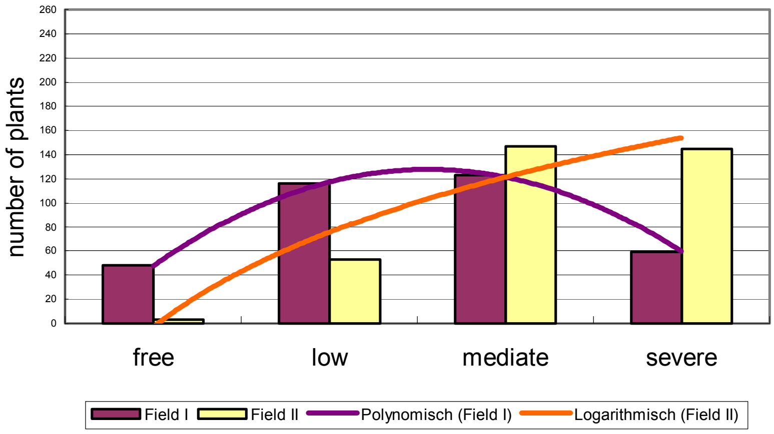

Figure 5. Number of plants in the four majour disease incidence categories when scored for rust in Fields I and II, with fitted regression lines. (polynomic for Field I; logarithmic for Field II). Field I: $y = -56x^2 + 301.2x – 246.5$; R^2 = 0.9634; Field II: $y = -44x^2 + 257.2x – 226$; R^2 = 0.7938

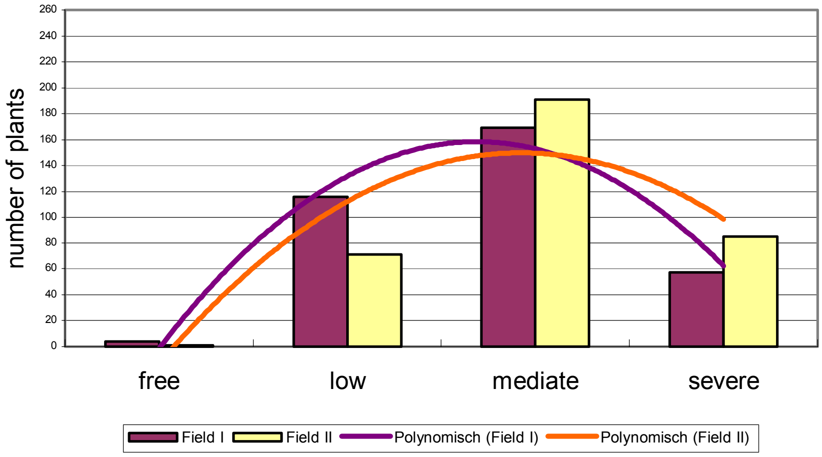

Figure 6. Number of plants in the four majour disease incidence categories when scored for leafspots in Fields I and II, with fitted regression lines (both polynomic). Field I: $y = -33x^2 + 169x - 88.5$; $R^2 = 0.9989$; Field II: $y = -44x^2 + 257.2x - 226$; $R^2 = 0.7938$

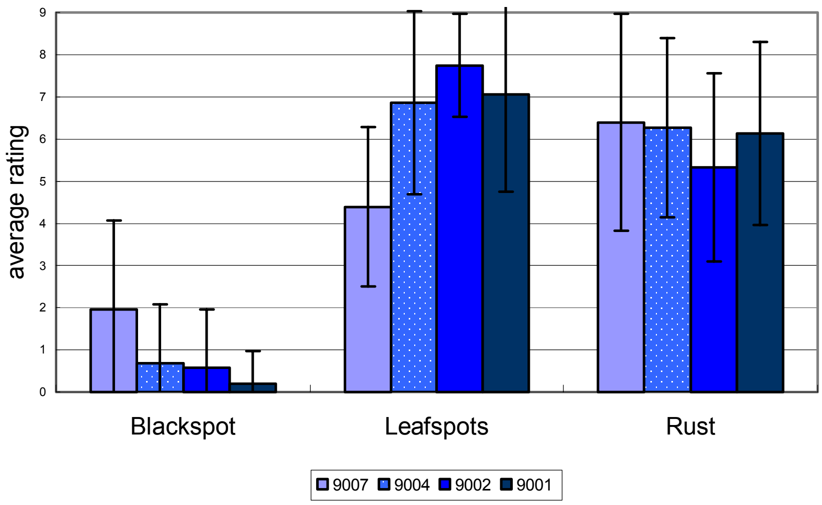

Figure 7. Average disease incidence in four different *R. dumalis* X *dumalis* progeny groups.

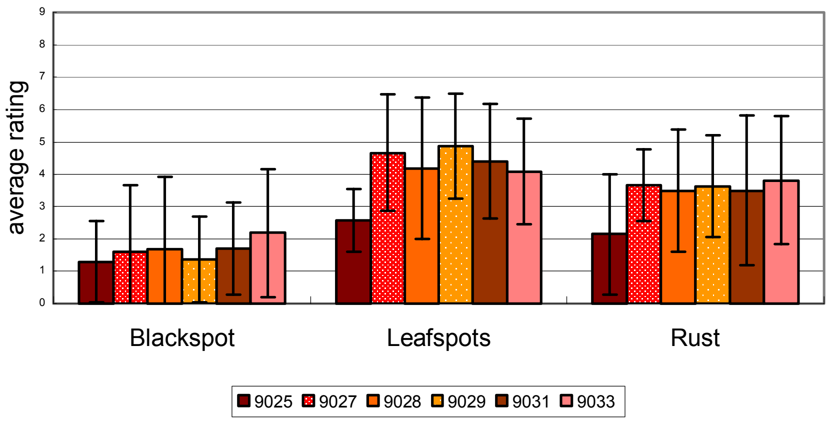

Figure 8. Average disease incidence in six different *R. rubiginosa* X *rubiginosa* progeny groups.

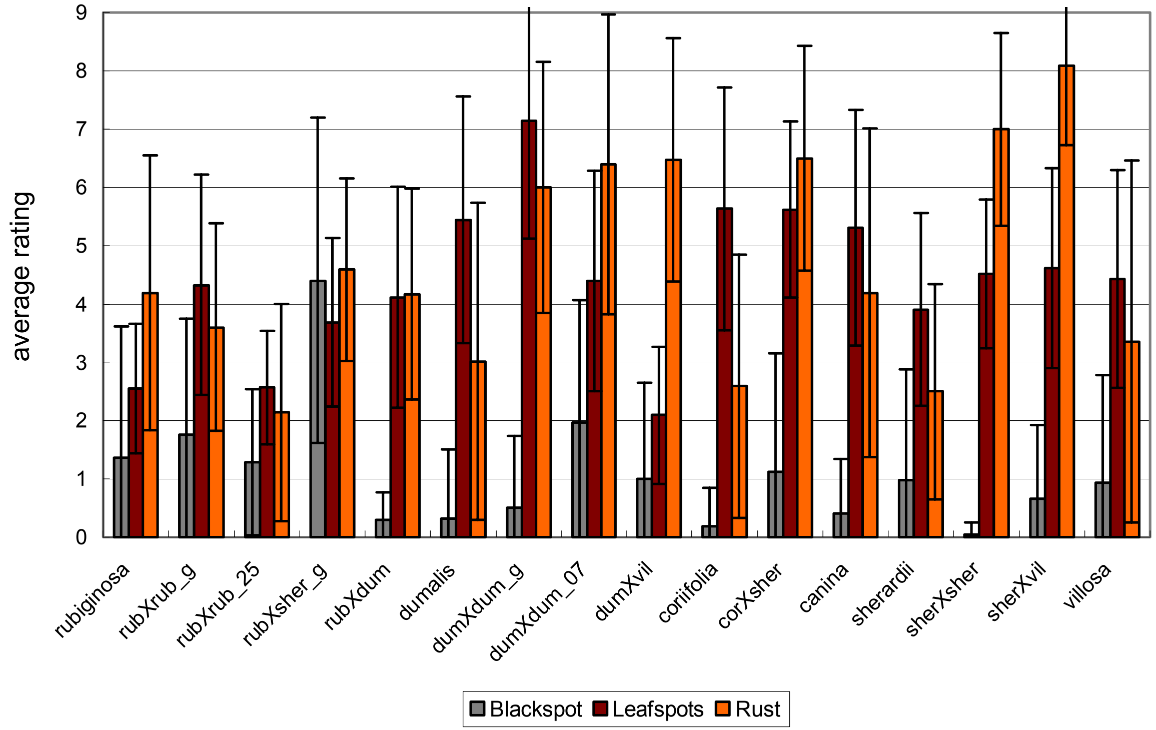

Figure 9. Overview of the average disease rating for plants obtained both from seed collections in wild populations (Field I) and from directed crosses (Field II). Progeny groups in Field II were pooled when not significantly different. More information about the origination of the progeny groups is given in the Figure legends for Figures 10-12.

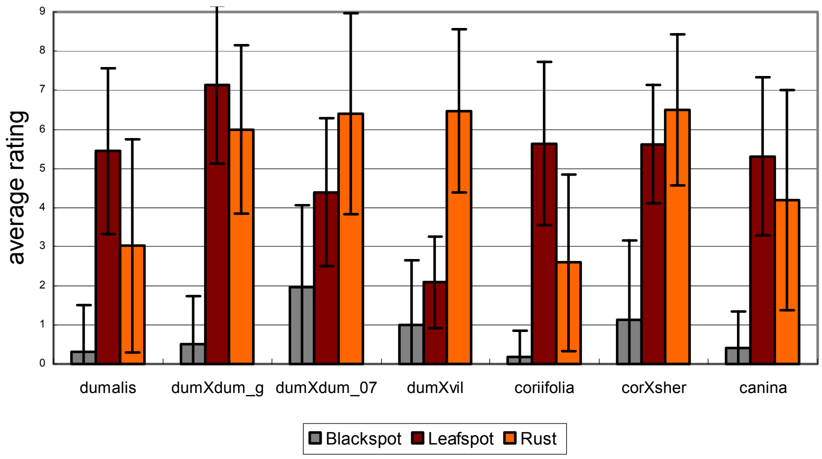

Figure 10. Average disease rating in subsect. *Canina*e for plants obtained both from seed collections in wild populations and from directed crosses. Progeny groups in Field II were pooled when not significantly different.
dumalis = *R. dumalis* ssp. *dumalis* (Field I), dumXdum_g = *R. dumalis* ssp. *dumalis* X R. *dumalis* ssp. *dumalis* crosses 9004, 9002, 9001 (Field II), dumXdum_07 = *R. dumalis* ssp. *dumalis* X R. *dumalis* ssp. *dumalis* cross 9007, dumXvil = *R. dumalis* ssp. *dumalis* X R. *villosa* ssp. *mollis* cross (Field II), coriifolia = *R. dumalis* ssp. *coriifolia* (Field I), corXsher = *R. dumalis* ssp. *coriifolia* X R. *sherardii* cross (Field II), canina = *R. canina* (Field I)

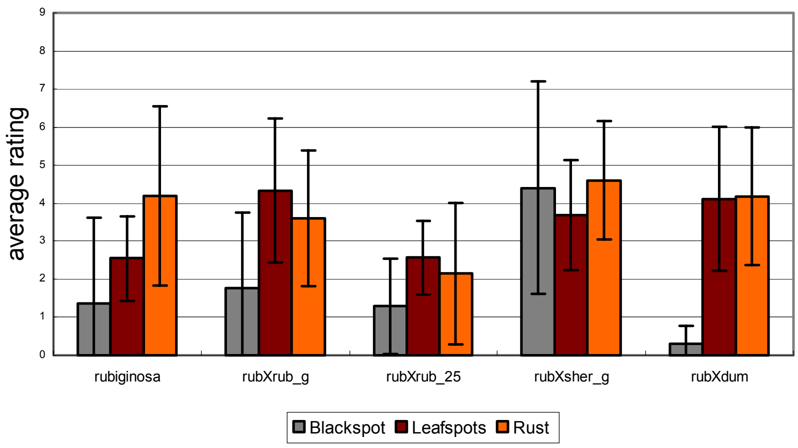

Figure 11. Average disease rating in subsect. *Rubigineae* for plants obtained both from seed collections in wild populations and from directed crosses. Progeny groups in Field II were pooled when not significantly different.
rubiginosa = *R. rubiginosa* (Field I), rubXrub_g = *R. rubiginosa* X *R. rubiginosa* crosses 9027, 9028, 9029, 9031, 9033 (Field II), rubXrub_25 = *R. rubiginosa* X *R. rubiginosa* cross 9025 (Field II), rubXsher_g = *R. rubiginosa* X *R. sherardii* crosses 9032, 9034 (Field II), rubXdum = *R. rubiginosa* X *R. dumalis* ssp. *dumalis* cross (Field II).

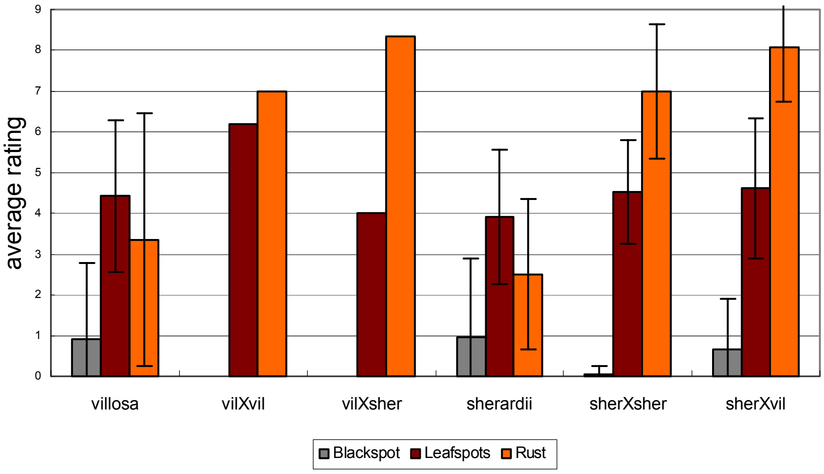

Figure 12. Average disease rating in subsect. *Vestitae* for plants obtained both from seed collections in wild populations and from directed crosses. Progeny groups in Field II were pooled when not significantly different.

villosa = *R. villosa* ssp. *mollis* (Field I), vilXvil = *R. villosa* ssp. *mollis* X R. *villosa* ssp. *mollis* cross (Field II), vilXsher = *R. villosa* ssp. *mollis* X R. *sherardii* cross (Field II), sherardii = *R. sherardii* (Field I), sherXsher = *R. sherardii* X *R. sherardii* cross (Field II), sherXvil = *R. sherardii* X *R. villosa* ssp. *mollis* cross (Field II).

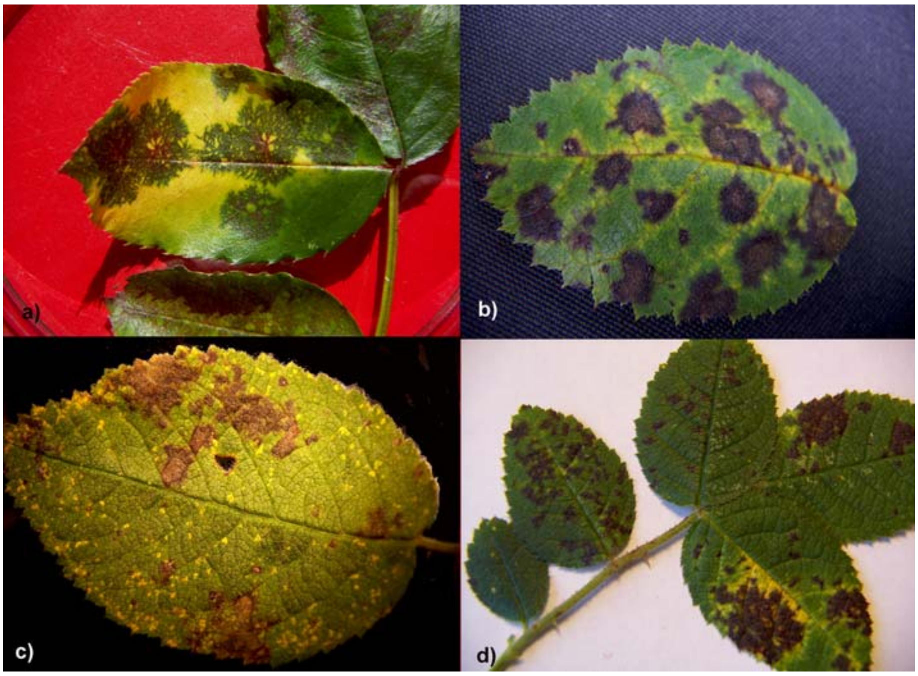

Figure 13. Symptoms of *Marssonina rosae* on ornamental and wild roses

a) typical symptoms on an ornamental rose: lesions with feathery margins resulting in a star-like shape

b) brown blotches on *R. rubiginosa* with dark border producing symptoms that resemble leopard flecks

c) light brown symptoms on *R. sherardii* (the yellow spots are due to rust)

d) very small black spots on *R. rubiginosa*

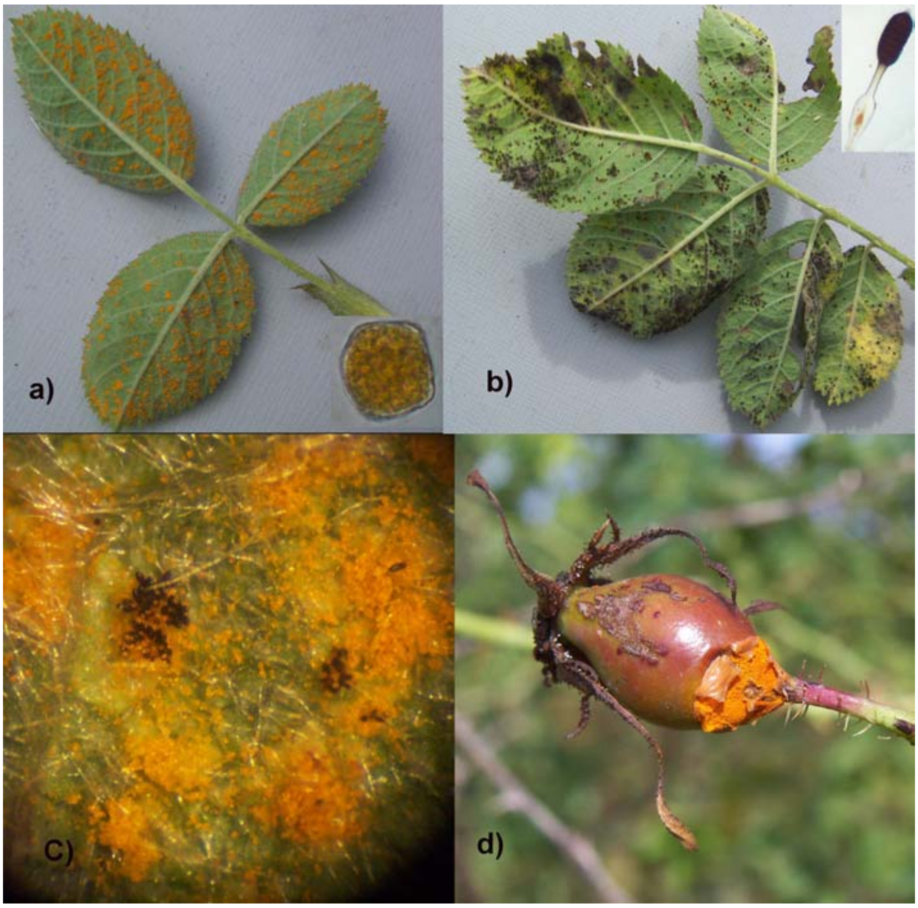

Figure 14. *Phragmidium* spec.

a) orange urediospores covering the lower leaf surface of a *R. sherardii* X *R. villosa* offspring (small picture: microscopic view (X 400) on a spore)

b) black teliospores on a leaf of the same plant (small picture: microscopic view (X 100) on a teliospore)

c) microscopic view (X 1.6): orange urediospores and black teliospores in clusters on the hairy epidermis typical for plants of subsect. *Vestitae*

d) unusual case: rosehip with rust on an injury

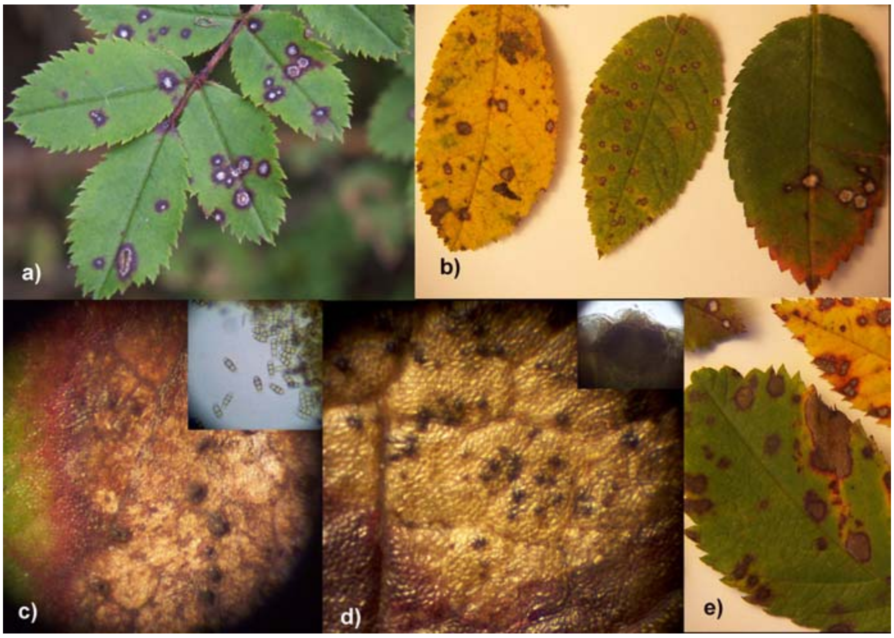

Figure 15. Leafspots caused by *Sphaceloma rosarum*

a) typical, easily recocnizable symptoms on *R. spinosissima*: circular spots with white centre and dark purple margin

b) various symptoms caused by *Sphaceloma rosarum* on roses of subsect. *Vestitae* and an ornamental cultivar: with strong yellowing, small colour change, turning reddish

c) microscopic view (X 1.6): symptoms on *R. spinosissima*; the black fruiting bodies produce ascospores (small picture, X 400)

d) microscopic view (X 1.6): leafspot on an ornamental rose, small picture: cut through one of the tiny black acervuli (without spores, X 100)

e) coalescing spots, forming big blotches

Figure 16. Severe case of *Sphaceloma rosarum*

heavy infection of a plant belonging to *R. rubiginosa*; spots on leaves, fruits and bark; dead tip (topmost arrow)

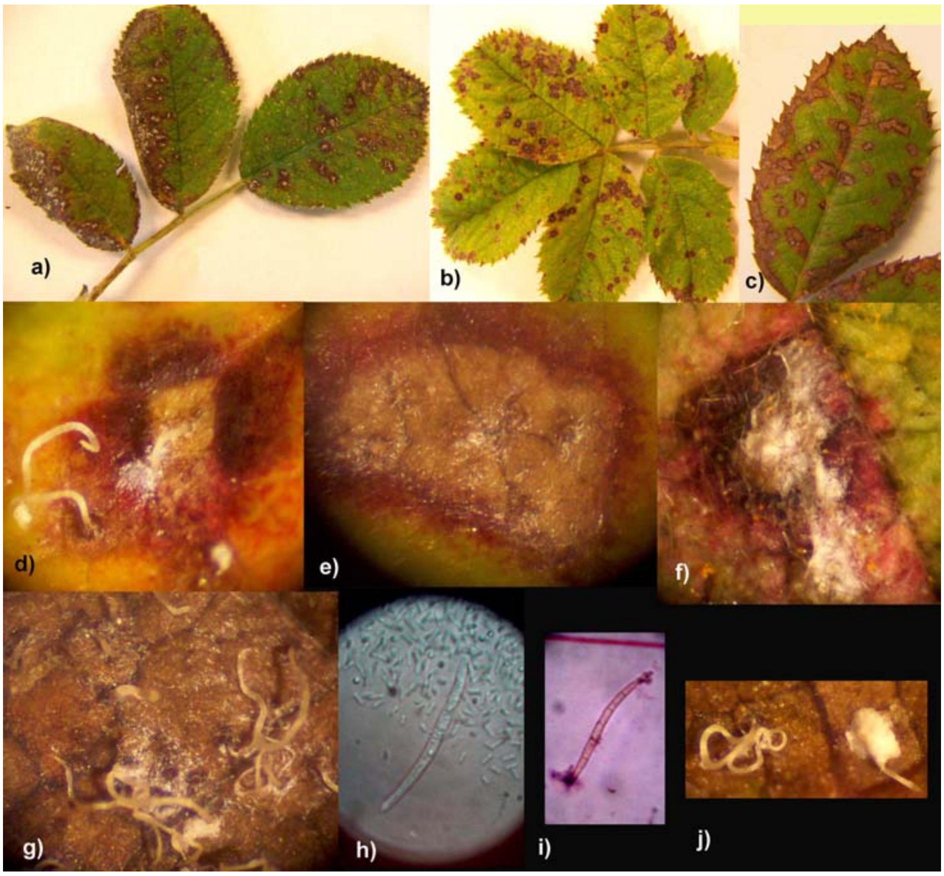

Figure 17. Leafspots caused by *Septoria rosae*

a) *Septoria rosae* on *R. sherardii* X *R. sherardii*: spots coalescing, forming grey areas with white structures
b) similar symptom on *R. villosa* ssp. *mollis*
c) angular spots on *R. dumalis*: lesions are restricted by the veinlets
d) microscopic view (X 1.6): spot with broad purple margin in chlorotic tissue, white tendrils of conidia emerging from dark pycnidia
e) microscopic view (X 1.6): spot with mycelium slightly visible on the surface
f) microscopic view (X 1.6): leafspot covered with white mass of conidia
g) microscopic view (X 1.6): heavily infected part of a big part of the leaf
h) microscopic view (X 400): long conidia with a mass of smaller, rod-shaped microconidia
i) microscopic view (X 400): stained conidia with visible septae
j) microscopic view (X 400): creamy-white tendrils of conidia and typical white heaps of conidia

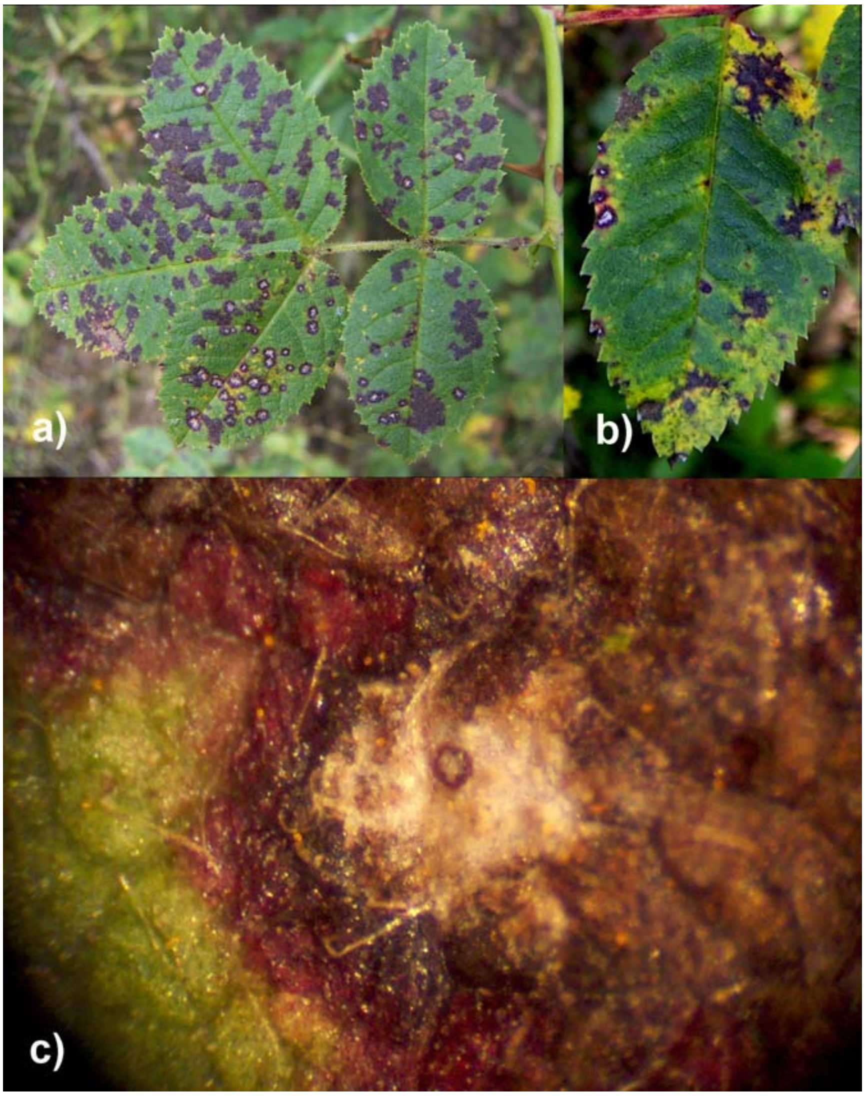

Figure 18. Different fungi infecting the same leaves

a) Rust, blackspot and *Sphaceloma*-leafspot on *R. rubiginosa* X *R. rubiginosa*

b) Blackspot and *Sphaceloma*-leafspot on plant of *R. dumalis* X *R. dumalis*

c) microscopic view (X 1.6): spot caused by *Sphaceloma rosarum* adjacent to symptoms of blackspot, *Marssonina rosae*

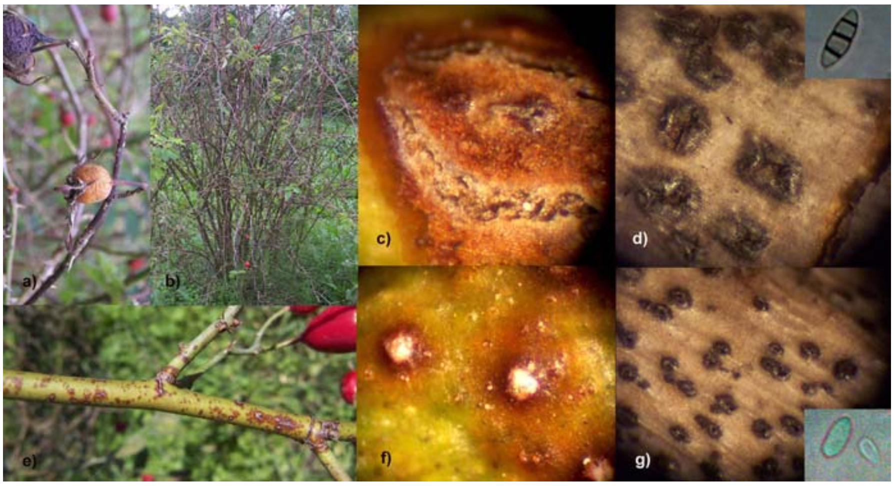

Figure 19. Cane disease probably caused by *Sphaceloma rosarum*

a) dead shoot with desiccated rosehips

b) plant almost without leaves in september and with mostly dead shoots, frequently found especially in *R. dumalis*

c) microscopic view (X 1.6): older lesion; the dry brownish tissue is bursting

d) microscopic view (X 1.6): white area on dead shoot tip; fruiting bodies of the sexual stage (small picture: ascospore, X 600)

e) infected shoot: small purple spots as well as bigger lesions visible

f) microscopic view (X 1.6): emerging symptoms; minute, elevated spots with a light centre and a purple margin

g) microscopic view (X 1.6): white area on dead shoot tip; fruiting bodies of the asexual stage (small picture: conidia, X 600)

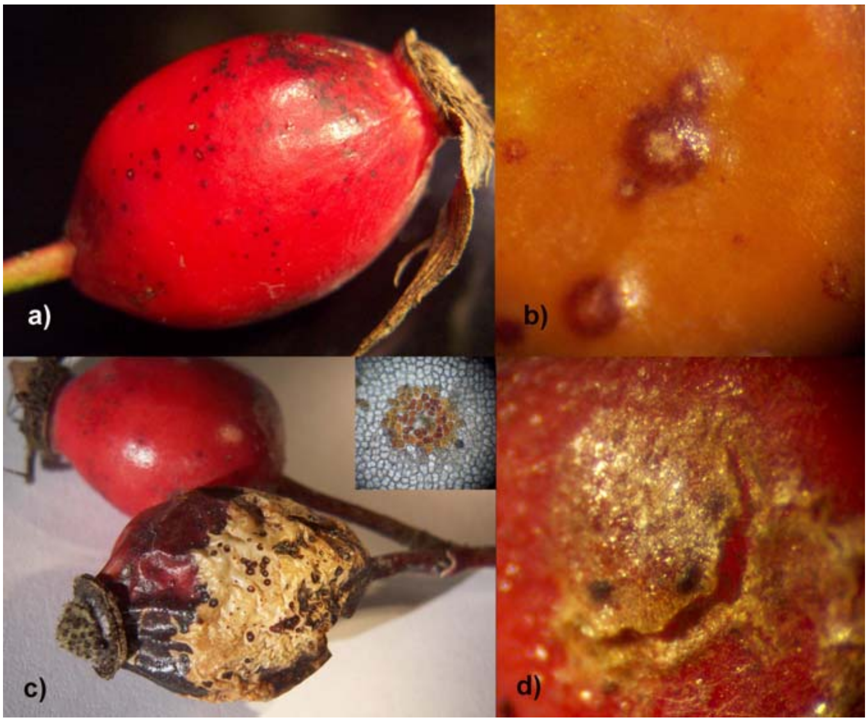

Figure 20. Symptoms on the fruits probably caused by *Sphaceloma rosarum*

a) common symtoms on the fruits: dark sprinkles that can coalesce, older lesions develop light centres

b) microscopic view (X 1.6): emerging symptoms; dark, elevated spots with light centre

c) extreme case: a big part of the epidermis is desiccated and white; small picture: piece of dead epidermis with coloured spot, the transparent cells around the coloured ones are invaded by mycelium (microscopic view, X 100)

d) microscopic view (X 1.6): older lesion; the epidermal tissue is dead and cracks

Figure 21. Special symptoms found only on rosehips of *R. rubiginosa*

a) white sprinkles common on rosehips of *R. rubiginosa*

b) microscopic view (X 1.6): a thin layer of dead cells results in a light discolouration