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CHARACTERIZATION OF *PUCCINIA RECONDITA*, THE CAUSAL AGENT OF BROWN RUST: A REVIEW

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Abstract
Brown rust caused by *Puccinia recondita* is a significant disease in cereal growing areas worldwide. On average, brown rust can cause yield losses from 10% to 40% resulting in economic losses. The disease damages the leaves, stems and glumes of cereals. Classification of the pathogen causing brown rust has undergone several revisions. There are two different opinions about the causal agent causing brown rust on rye and wheat. Some scientists consider that the causal agent of brown rust in wheat (*Triticum aestivum* L.) and rye (*Secale cereale*) is included in the broad species of *P. recondita* defined by Cummins, but other scientists consider that there are two species causing brown rust – *P. recondita* in rye and *P. triticina* in wheat. There are many studies about the races of *P. recondita* in wheat: in North America, 70 races are collected every year; in Canada, 35 races have been found; in Europe, 105 races have been found. Unfortunately, there are no studies about the races of the pathogen of rye. *P. recondita* is a heteroecious fungus with a complicated life cycle. For successful development, the fungus requires cereals as primary hosts and different alternative hosts, depending on the specialization of the pathogen. Specific studies about the biology, distribution and harmfulness of *Puccinia recondita* in Latvia are necessary. Monographic method was used for this study. The aim of this article is to summarize the information from the literature about *Puccinia recondita,* the causal agent of brown rust, with emphasis on the occurrence, harmfulness, taxonomy, and life cycle of *P. recondita* f. sp. *secalis*.
Key words: taxonomy, cereal, fungal diseases, rye, *Uredinales*.

Introduction

Brown rust (also called brown leaf rust) caused by *Puccinia recondita* (syn. *Puccinia triticina*) can infect wheat (*Triticum aestivum* L.), rye (*Secale cereale*), triticale (×*Triticosecale*), and barley (*Hordeum vulgare*). Brown rust is widespread in major wheat production regions such as America, Africa and Europe (Ordonez, German, & Kolmer, 2010; Huerta-Espino *et al*., 2011). Brown rust is the most widespread and prevalent disease of wheat in South America (German *et al*., 2007). In the USA, epidemics of brown rust on winter wheat have occurred in the southern part of the country more frequently than in the areas in north of the country. Brown rust is the most important wheat disease in Mexico (Roelfs, 1989). Level of yield losses caused by leaf rust are different, depending on various weather conditions, availability of inoculum and cultivar susceptibility (Teferi, 2015). The disease can cause yield losses in wheat from 5% to 10% in Canada, from 10% to 22% in the USA, and up to 40% in Mexico (Moschini & Perez, 1999).

Brown rust caused by *Puccinia recondita* f. sp. *secalis* occurs regularly in all areas where rye is growing. This disease is one of the most significant diseases of rye in Europe (Miedaner *et al*., 2012), and it is common also in Latvia (Bankina *et al.*, 2013). Early infection of brown rust in continental climates can cause yield losses of up to 40%, and if the epidemic is early and strong – even up to 60 – 80% in rye (Kobylanski & Solodukhina, 1996).

Puccinia recondita is a heteroecious fungus, macrocyclic, and has five distinct stages of development: teliospores, basidiospores, and urediniospores on cereal hosts, and pycniospores and aeciospores on the alternative hosts.

Genetic resistance is most commonly used to prevent yield losses caused by brown rust. The identification of pathogens' races is very important for the breeding of resistant varieties (Bolton, Kolmer, & Garvin, 2008).

There are many studies about the races of brown rust in wheat, but no research has been carried out on the races of *P. recondita* in rye.

The aim of this article is to summarize the information from the literature about *Puccinia recondita,* the causal agent of brown rust, with emphasis on the occurrence, harmfulness, taxonomy, and life cycle of *P. recondita* f. sp. *secalis*.

Materials and Methods

Monographic method was used for this study. Scientific literature from different countries related to *Puccinia recondita* (the causal agent of cereal brown rust), its biology, evolution and distribution was summarized.

Results and Discussion

Distribution and harmfulness of brown rust

Brown rust occurs on wheat (*Triticum aestivum* L.), rye (*Secale cereale*), triticale (×*Triticosecale*), and barley (*Hordeum vulgare*). The occurrence of brown rust is high in all regions where rye, wheat and triticale are produced. Under Latvia's climatic conditions, brown rust in rye sowings appears every year, but wheat and triticale sowings are seldom infected (Treikale, 2010, 2016).

Wheat brown rust can cause a reduced number of kernels per head and kernel weight (Kolmer, 2013). Grain losses can reach up to 30 – 70% even in susceptible varieties in South America (Ordonez, German, & Kolmer, 2010). Different results have been obtained in Europe, where yield losses in susceptible cultivars reached 14 – 29%, mainly due to reductions in kernel weight (Huerta-Espino *et al*., 2011). Findings of American researchers confirm that yield losses caused by rust can make 5 – 15% in Canada, 10 – 22% in the USA, 9 – 51% in Argentina, and even up to 40% in Mexico (Moschini & Pérez, 1999).

Brown rust in rye can cause significant yield losses, especially when infection is early. In continental climates, yield losses can reach up to 40%, and if the epidemic is early and strong – even up to 60 – 80% (Kobylanski & Soludhkina*,* 1996). Disease severity in Latvia in some years increased up to 15% (Treikale, 2010, 2016).

Brown rust is a significant disease for winter triticale in Poland, and the infections caused by *P. recondita* can result in substantial yield losses (Wooe, Maekowiak, & Cichy, 1994).

Harmfulness of brown rust depends on the time of infection – earlier appearance of disease leads to more substantial yield losses.

There are findings which confirm that brown rust infection depends on the cultivar. In Finland, rye cultivars differed in brown rust infection level; however, the effect of cultivar was also directly related to the time and location of sowing (Serenius *et al*., 2005). In Latvia, observations showed that disease severity differed depending on the cultivar, but clear regularities were not found (Bankina *et al*., 2013).

Characterisation of the pathogen

Causal agents of brown rust belong to the genus *Puccinia*, family *Pucciniaceae*, order *Pucciniales*, phylum *Basidiomycota* in the kingdom *Fungi*.

The classification of these pathogens has undergone several revisions. The fungi develop on two different hosts: uredospores, teliospores and basidiospores develop on the principal host, and pycniospores and aeciaspores develop on the alternative host. At the beginning, the causal agent of brown rust was designated as *Uredo rubigo-vera* in 1815 by Augustin de Candolle. Winter in 1884 placed the causal agent of this disease in the species complex of *P. rubigo-vera*. Eriksson in 1899 was the first one to report *Puccinia triticina* as a single species. At the beginning of the 20th century, it was adopted by many scientists in North America and Europe that some species infect rye, wheat, barley, and few grasses; at that time, the species' name was *P. rubigo-vera*. The alternative hosts of *P. rubigo-vera* were supposed to be the plants from the family *Boraginaceae.* When Plowright described the new species as *Puccinia perplexans* in 1885, it was considered that more than one species can cause brown rust on various plants. Later, many species were described and named according to host specialization. The classification of causal agents of brown rust proceeded to be modified from time to time (Liu *et al*., 2013).

In 1894 and 1899, Eriksson and Henning described many species (*P. agropyrina*, *P. bromina*, *P. dispersa*, *P. glumarum*, *P. holcina*, *H. mollis*, *P. simplex*, *P. triseti*, *P. triticina*), which before were grouped as one species – *Puccnia rubigo-vera*. Arthur and Fromme, in contrast, united all forms of *P. rubigo-vera* with alternative host plants from *Ranunculaceae* family into one species with one name – *Dicaeoma clematidis.* Mains in 1933 suggested to place all featured species causing brown rust back into one species under name *Puccinia rubigo-vera.* In 1934, Arthur accepted the causal agents of brown rust as one species *P. rubigo-vera*. Cummins and Caldwell in 1956 suggested *Puccinia recondita* as the valid binomial for the causal agents of brown rust of grasses and cereals. This broad species concept was widespread in North America (Huerta-Espino *et al*., 2011).

P. recondita has alternative hosts in four families of plants (*Balsaminaceae*, *Boraginaceae*, *Hydrophyllaceae*, and *Ranunculaceae*). Cummins in 1956 and Caldwell in 1971 placed all causal agents of brown rust into one species, because of spore morphology and host range was similar. Other scientists arranged these pathogens into more than one species, because of small but permanent differences in the morphology of teliospores, aeciospores and uredospores (Savile, 1984). There are two diverse opinions about the *P. recondita* complex: some of researchers hold the opinion that the causal agent of brown rust in wheat and rye is included in the broad species of *P. recondita*, but some consider that there are two species that cause brown rust – *P. recondita* in rye and *P. triticina* in wheat.

The causal agents of cereal brown rust have been divided into various species including *Puccinia aegilopis* (Maire, 1914), *Puccinia dispersa* (Gaumann, 1959), *Puccinia persistens* (Urban, 1992), *P. rubigo-vera* (Arthur, 1934), *Puccinia tritici-duri* (Viennot-Bourgin, 1941), and *Puccina triticina* (Savile, 1984), and *P. recondita* as well (Cummins, 1971). The causal agent of brown rust in wheat and rye is included in the broad species of *P. recondita*; however, some scientists separated this pathogen into two species – *P. recondita* (rye group) and *P. triticina* (wheat group) (Savile, 1984; Swertz, 1994) or *P. persistens* spp. *triticina* (Urban & Markovi, 1992). Generally, the conception of the *P. recondita* complex as a single broad species is more accepted in the USA than in Europe where the conception of more narrowly described brown rust species dominates. The name *Puccinia recondita* f. sp.

secalis is the most accepted name for the causal agent of rye brown rust (Anikster *et al*., 1997).

P. recondita has different alternative hosts depending on their specialization: principal host – cultivated wheat; alternative hosts – meadow rue (*Thalictrum speciosissimum*), *Triticum turgidum* ssp. *durum* and blue bugloss (*Anchusa italic*), rye and bugloss (*Lycopsis arvernsis*) (Urban & Markovi, 1992). The alternative hosts of *P. recondita* from wild wheat species are poorly investigated; however, several species in the *Boraginaceae* family have been found.

Depending on genome size and host range, Anikster *et al*. (1997) separated *P. recondita* on rye, wheat and grasses (*Aegilops* spp.) into two groups. Group one infects wheat, and group two infects rye and grasses. Isolates of each group are interfertile, and selections of groups are not sexually consistent. In group one, there are isolates of *P. recondita* and *Thalictrum speciosissimum* is the alternative host. Group two comprises isolates that have few species from the *Boraginaceae* family as the alternative hosts (Anikster *et al*., 1997). The most accepted names of brown rust causal agents are: *P*. *recondita* f. sp. *tritici* and *P*. *recondita* f. sp. *secalis*.

In the taxonomic hierarchy, race is an informal rank, under the level of subspecies. Race nomenclature was uncomplicated as long as the early standard differentials were applied and a key was contended for the identification of races. The introduction of new hosts required additional names. This pursued in many systems of nomenclature; however, none of them was fully satisfactory. In North America in 1980, leaf rust researchers used a formula system similar to that made by Green for wheat stem rust (Green, 1981).

Mains and Jackson in 1921 and 1926 were the first to research the physiologic specialization of *Puccinia recondita* f. sp. *tritici*. They found twelve races by infection types on 11 plants. The researchers developed their own systems of race designation and analysis (Long & Kolmer, 1989).

Populations of brown rust causal agents are extremely different in the world. Each year in North America, more than 70 races are collected. The fungus has an inherent mutation mechanism to produce races that are still unknown, even without sexual stage of development (Huerta-Espino *et al*., 2011). From 1997 to 2007 in Canada, 35 races were found. In Europe, from 2608 isolates 105 races were identified (Mesterhazy *et al*., 2000). Goyeau *et al*. in 2006 France identified 104 races. The identification of rust races has changed recently because genetic markers were introduced (Ordonez, German, & Kolmer, 2010). Virulence studies of *P. recondita* f. sp. *tritici* have been conducted in the former Czechoslovakia, where 14 races of this pathogen were found (Hanzalova *et al*., 2008). In France, pathogens were reported to be diverse for virulence despite that there are only a few specific resistance genes (Goyeau *et al*., 2006). In Hungary, it was found that the main races in the population are the races 77 and 61 (Manninger, 2006). As uredospores of *P. recondita* are dispersed by wind, it can be assumed that the main virulence phenotypes might be discovered in many countries in Europe, which was the case from 1960 to 1980 for race 77 (Zadoks & Bouwmann, 1985). A large study of *P. recondita* virulence in the west of Europe was conducted in 1995 (Park & Felsenstein, 1998), which was significant in that a big number of collections were achieved from a few of different countries and were featured for virulence using the differential set and description nomenclature. A total 850 isolates were collected and 53 races were identified in France, Germany, Austria, Belgium, Italy, Switzerland, and the UK. Four races were found on 64% of isolates, and they were reported to be widespread all over Western Europe. Three of the four dominant races were also found in collections from Estonia, Finland Poland and Hungary. Unfortunately, there are no studies about the races of *Puccinia recondita* f. sp. *secalis*.

Resistance

There is only fragmentary information about the rye varieties resistant to *P*. *recondita* f. sp. *secalis*. Kornicke and Werner (1885) were the first to report the discovery of resistant rye cultivars. Later, many scientists observed a higher degree of resistance in some of the cultivars (Novikov, 1907; Yachevsky, 1909; Mains & Leighty, 1923; Dmitriev, Talchuk, & Serova, 1982). Meantime, genotypes resistant to leaf rust have been detected in many populations of wild perennial rye and in cultivars bred in Russia, Ukraine, Belarus, Poland, Germany, Austria, Hungary, and Canada (Kobylyanskii, 1982; Kobylyanskii & Soludhkina, 1996).

There is information that 71 brown rust resistance genes have been found in wheat to chromosome position and specified gene names. The study of genetic analysis of the causal agent of rye brown rust helped to identify two dominant resistance genes Pr1 and Pr2. These two genes demonstrated to be against a local brown rust population and single-pustule isolates as well (Wehling *et al*., 2003). Earlier, resistance genes Pr1 and Pr2 had names Lr-a and Lr-b (Linz & Wehling, 1998). Studies in Germany showed that there were three dominant genes of resistance to brown rust (*Puccinia recondita* f. sp. *secalis*). Resistance genes Pr3, Pr4, and Pr5 were recognized using genetic analysis of resistance to brown rust in rye. These genes – Pr3, Pr4, Pr5 confer resistance to many isolates of single-pustules (Roux *et al*., 2004).

Many resistance genes are beneficial in seedlings; they stay effective till the adult stage of the plant. Genes like Lr1, Lr10, and Lr21 are excelent examples

of race-specific resistance genes that are beneficial in seedlings and adult plants (Dyck & Kerber, 1985). At first, leaf rust resistance genes – Lr1, Lr2a, Lr3, Lr10, Lr11 were characterized in wheat *T. aestivum*, and then, in species connected to wheat, such as *Aegilops elongatum*, *A. umbellulata*, *T. tauschii*, *Aegilops elongatum* and *S. cereale*. It has been proven that race-specific seedling resistance genes are very weak to selection and could increase virulent races in leaf rust populations. Primarily, multiple wheat cultivars were resistant when they were first created, but as new brown rust races appeared, the seedling resistance decreased and, as a result, the resistance of cultivars decreased. In regions where winter wheat and rye are grown, the selection of virulent races can happen comparatively fast. Race-specific resistance genes that are normally expressed in the adult stage of plant but weakly expressed in seedlings have been characterized as well. Such resistance genes as Lr12 and Lr13 were obtained from wheat, while other genes like as Lr22a and Lr37 were obtained from *A. ventricosa* and *T. auschii* (Kolmer *et al*., 2008). When plants have seedling resistance genes to disease, then, at the adult stage of the plant, resistance genes have eroded the effectiveness of resistance (Dyck & Johnson, 1983). A partial type of resistance is normally expressed in adult plants; however seedlings can also be sensitive. A clue to the characteristics of these genes is that they present resistance to many known races of *P. recondita* that do not express race specificity. These genes individually do not provide full resistance, but resistance of these genes appears by sensitive infection types that do not produce uredinia. The most familiar and mostly described of these genes is the gene Lr34 (Kolmer *et al*., 2008). Wheat cultivars with the gene Lr34 also have a diverse phenotype of leaf necrosis that appears separately from rust infection. Leaf rust resistance genes Lr46, Lr67, and Lr68 are also liable for adult-plant resistance (Herrera-Foessel *et al*., 2012).

Life cycle

Puccinia recondita is a heteroecious fungus, macrocyclic, and has five distinct stages of teliospores, basidiospores, and uredospores on cereal hosts, and pycniospores and aeciospores on the alternative hosts (Kolmer, 2013).

The uredospores of uredinia are typical symptoms of brown rust. The diameter of uredinia can reach even 1.5 mm, their colour is orange to brown, their shape is round to ovoid. Uredinia are scattered on both sides of leaf surfaces. Uredospores release from uredinia, their average size is 20 mm in diameter, and colour – orange-brown. Uredospores have up to eight germ pores scattered in dense walls (Bolton, Kolmer, & Garvin, 2008). There can be thousands of spores in each pustule. Under severe epidemics of leaf rust, pustules are able to develop on the beards and glumes of heads or sometimes on the stem underneath the head. Late in the growing season, leaf rust may get very severe, which can result in leaf death. This is characteristic of America. Telia with black teliospores were produced on the leaves later in the season. Telia develop beneath epidermis, primarily on leaf sheets and blades. Telia are not always formed, especially if brown rust infection occurs late in the growing season (Dyck & Kerber, 1985).

Symptoms depend on the level of cultivar resistance; there are cultivars that are completely susceptible and have big uredinia without causing necrosis or chlorosis in the plant tissues. Varieties that are resistant are described by different responses – from small spots to small- to medium-size uredinia that could be surrounded by necrotic and chlorotic areas (Kobylanski & Soludhkina, 1996).

P. recondita spores are spread by splashing water and wind. Optimal environmental conditions for disease development are temperatures ranging from 15 °C to 20 °C, but the fungus can develop at the temperature of 2 – 35 °C. The fungus needs aproximately six hours of moisture on leaves to start developing. With much moisture and suitable temperatures, lesions are formed within 7 – 10 days, and spore production reduplicates another uredospore generation (Kolmer, 2013).

Normally, *P. recondita* develops from autumn infections. Usually, the disease appears first on lower leaves and then moves forward up the plant to the upper leaves of the infected plant until summer. However, infections ordinarily occur first on the upper leaves of the plant, which happens because of the wind-blown spores that are laid out of the air in the course of spore showers (Roelfs, Singh, & Saari, 1992).

The teliospores of *P. recondita* are made under the epidermis of blades under senescence or unfavourable conditions and remain with the leaves. Leaves can be moved or dispersed by wind, animals or humans at remarkable distances. Basidiospores need humid conditions to form and release, and moisture limits their spread. Basidiospores are also translucent and sensitive to light, that limits traveling further to perhaps tens of metres. The pycniospores are usually carried by insects to other sites of infection where the fusion of two genetically divergent cells happens, which reestablishes the dikaryotic nuclear condition (Cummins & Caldwell, 1956). The dikaryotic aecium grows on the underneath of the leaf surface, and within these, chains of aeciospores are produced. When the aecium has developed, the aeciospores are released and dispersed by wind to infect their cereal host. Several generations of uredo spores develop on the cereal host as long as favourable conditions are available. Teliospores develop in the late of the season or under unfavourable conditions. The

sexual cycle of brown rust is related to the presence of an appropriate alternative host. Meadow rue, the alternative host for *P. recondita* in wheat, *Thalictrum speciosissimum* L., is characteristic to southwest Asia and southern Europe and does not occur naturally in North America (Samborski, 1985). There are no studies of aeciospores or pycnia produced on either or *T. glaucum* or *T. speciosissimum* in North America. Species of *Thalictrum* are resistant to basidiospore infection caused by *Puccinia triticina* (Saari, Young, & Kernkamp, 1968). As a result, *P. recondita* is found only as uredinial infection on wheat in the majority of rye and wheat growing areas all over the world. Aeciospores produced on *Thalictrum* spp. follow from basidiospore infection from different *Puccinia* spp., often have ITS DNA sequences and do not infect wheat, which are very much related to uredinial collections from *Elymus glaucus*.

The urediniospores are scattered by winds and they infect cereal crops developing furthermore (Roelfs, 1989). Ultimately, brown rust uredinial infections could be found by mid-June on spring wheat. Many winter cereal cultivars are sensitive to brown rust, which lets a huge population of *P. recondita* to overwinter across a big geographic region on an annual basis (Saari, Young, & Kernkamp, 1968).

Conclusions

Brown rust is a significant disease wherever rye and wheat are grown, and it can cause substantial yield losses. After many revisions in taxonomy of the causal agent of brown rust in rye and wheat, there are still different opinions, but the most accepted point of view is that there is one species causing brown rust – *P. recondita* with different specialized forms (f. sp.).

The life cycle of brown rust is complicated, and it depends both on the primary and alternative hosts and on environmental conditions.

Further research about the biology, distribution and harmfulness of *Puccinia recondita* in Latvia is needed.

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