Role of Alternate Hosts in Epidemiology and Pathogen Variation of Cereal Rusts

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Keywords

Abstract

Cereal rusts, caused by obligate and biotrophic fungi in the genus *Puccinia*, are important diseases that threaten world food security. With the recent discovery of alternate hosts for the stripe rust fungus (*Puccinia striiformis*), all cereal rust fungi are now known to be heteroecious, requiring two distinct plant species serving as primary or alternate hosts to complete their sexual life cycle. The roles of the alternate hosts in disease epidemiology and pathogen variation vary greatly from species to species and from region to region because of different climatic and cropping conditions. We focus this review on rust fungi of small grains, mainly stripe rust, stem rust, leaf rust, and crown rust of wheat, barley, oat, rye, and triticale, with emphases on the contributions of alternate hosts to the development and management of rust diseases.

INTRODUCTION

Cereal crops, including maize (*Zea mays* L.), rice (*Oryza sativa* L.), wheat (*Triticum aestivum* L., *Triticum durum* L., etc.), barley (*Hordeum vulgare* L.), oat (*Avena sativa* L.), rye (*Secale cereal* L.), and triticale (× *Triticosecale* Wittmack), are major sources of human food, animal feed, and bioenergy. In terms of 2013 production among grain-producing cereals, maize ranks first, rice second, wheat third, barley fourth, oat seventh, rye eighth, and triticale ninth, with 1,018, 741, 716, 144, 24, 16, and 15 million metric tons, respectively (49). As major staple food sources, cereal crops are essential for almost every country and nearly everyone in the world. Protection of these crops from damage by biotic and abiotic stresses is critical for world food security.

Among various biotic and abiotic stresses, rust pathogens are able to cause the most devastating damage. A severe rust disease can cause more than 90% yield losses in a field (31). Yield losses of multi-millions of tons in a single crop season have been recorded in many countries (31, 68, 74, 76, 100, 123, 138). With the exception of rice, which has no known rust, every cereal crop suffers from two to four rust diseases. Wheat has stripe rust, stem rust, and leaf rust; oat has stem rust and crown rust; barley has stripe rust, stem rust, leaf rust, and crown rust; and rye and triticale also have stripe rust, stem rust, and leaf rust. Similarly, maize has three rust diseases, namely common rust, southern rust, and tropical rust.

All cereal rusts are caused by heteroecious fungi that require two distinct plants to complete their life cycle. In addition to a cereal crop serving as the primary host, a rust fungus also needs an alternate host that cannot be from the grass family to complete the macrocyclic sexual life cycle. The complicated life cycle of the cereal rust fungi consists of five spore stages, with the uredinial, telial, and basidial stages occurring on the primary host and the pycnial and aecial stages occurring on the alternate host. Alternate hosts may play a role in disease epidemics and pathogen variation, but the importance of that role depends on the rust fungus and the climatic and cropping conditions in a region. As limited information about alternate hosts is available for the maize rust fungi, we focus this review on the rust fungi of small-grain cereal crops.

CEREAL RUST PATHOGENS AND THEIR LIFE CYCLE

Common Features of Cereal Rust Fungi

All fungal species causing rust diseases on cereal crops are in a single genus, *Puccinia*. They are obligate and biotrophic parasites, which require living host tissue to grow and reproduce. They all have a macrocyclic heteroecious sexual life cycle with a uredinial stage occurring on cereals and an aecial stage occurring on botanically different plants. In addition to the specificities on different plants by different life stages, each species forms formae speciales specializing on different cereal crops or grasses and forms races specializing on different cultivars of a cereal crop.

Taxonomy. Cereal rust fungi belong to the genus *Puccinia*, family Pucciniaceae, order Pucciniales, class Pucciniomycetes, division Basidiomycota in the kingdom Fungi (65). The following *Puccinia* species cause rusts on cereal crops: *Puccinia striiformis* Erikss. (*Ps*) causes stripe rust; *Puccinia graminis* Pers.:Pers. (*Pg*) causes stem rust; *Puccinia triticina* Erikss. (*Pt*) and *Puccinia recondita* Dietel & Holw. (*Pr*) cause leaf rust on wheat and/or rye; *Puccinia hordei* G.H. Otth (*Ph*) causes leaf rust on barley; and *Puccinia coronata* Corda (*Pc*) causes crown rust. Although these species are generally classified on the basis of morphological characteristics of teliospores and urediniospores (12, 39, 107), alternate hosts are sometimes used to distinguish *Puccinia* species based on the specificity of the different species on different alternate hosts (41, 66).

Primary host: a cereal crop that can be damaged by a heteroecious rust fungus, also known as principal host or uredinial host

Alternate host: a plant, different from a primary host, on which a heteroecious rust fungus must develop to complete its life cycle

Macrocyclic: a life cycle of a rust fungus that comprises aecial, uredinial, telial, basidial, and pycnial stages

Puccinia striiformis (*Ps*): the fungal species causing stripe rust (yellow rust) on cereals and grasses

Puccinia graminis (*Pg*): the fungal species causing stem rust (black rust) on cereals and grasses

Puccinia triticina (*Pt*): the fungal species causing leaf rust (brown rust) on wheat

Puccinia recondita (*Pr*): the fungal species causing leaf rust (brown rust) on rye

Puccinia hordei (*Ph*): the fungal species causing leaf rust on barley

Puccinia coronata (*Pc*): the fungal species causing crown rust on oat (*P. coronata* f. sp. *avenae*; *Pca*) and barley (*P. coronata* f. sp. *hordei*; *Pch*)

Specificity. Cereal rust fungi are considered highly specific to their plant hosts. For each species of the cereal rust fungi, the specificity is generally on different species and genera of cereal crops and grasses for the primary hosts, and similarly on different species and genera of alternate hosts. Different *Puccinia* species can have similar cereal and grass hosts but generally have different alternate hosts. Some of the *Puccinia* species are further separated into formae speciales or varieties based on host specificity and/or morphological characteristics. For example, *P. graminis* f. sp. *tritici* (*Pgt*), *P. graminis* f. sp. *avenae* (*Pga*), and *P. graminis* f. sp. *secalis* (*Pgs*) cause stem rust on wheat/barley, oat, and rye, respectively; *P. striiformis* f. sp. *tritici* (*Pst*) and *P. striiformis* f. sp. *hordei* (*Psh*) cause stripe rust on wheat and barley, respectively; and *P. coronata* var. *avenae* (*Pca*) and *P. coronata* var. *hordei* (*Pch*) cause crown rust on oat and barley, respectively. A large number of races were identified for each of the *Puccinia* species or each forma specialis based on interactions with cultivars of cereal crops, but only limited differences were found in infections among isolates of a pathogen found on alternate hosts (150; X.M. Chen, M.N. Wang, C.J. Xia, unpublished data).

Obligate parasite. All cereal rust fungi are obligate parasites, which infect, grow, and reproduce only in living plants, although some successful axenic cultures of rust fungi were obtained in the 1960s (110, 139). Like many other obligate microorganisms, the cereal rust fungi infect host plants but do not kill cells immediately. As biotrophic fungi, they get their nutrients by establishing close contact with host cells. Because of the intimate association, it takes several days for disease symptoms to develop. One spore infection does not do much damage, but severe yield losses can be caused by infection of many spores and many cycles during a crop season. If the weather conditions become unfavorable for a rust fungus to infect host plants, the fungus develops teliospores to survive until the conditions become favorable for infection.

Heteroecious and macrocyclic. Cereal rust fungi are heteroecious, requiring botanically very different plants to serve as primary and alternate hosts to complete their sexual life cycle (1, 109). With the recent discovery of alternate hosts for *Ps* (62), all *Puccinia* species infecting small-grain cereals have a macrocyclic life cycle with the following five stages, as illustrated in **Figure 1** using *Pst* as an example (62, 132, 134, 150; J. Zhao, J.N. Yao, M. Jiao, X.M. Chen, Q.M. Han, H.C. Zhang, L.L. Huang, Z.S. Kang, unpublished data). Stage 0 is for pycnia (also called spermogonia) bearing one-celled pycniospores (also called spermatia) and receptive hyphae produced on alternate hosts. Pycniospores and receptive hyphal cells have one nucleus (n). Fertilization of receptive hyphae by pycniospores produces dikaryotic mycelia growing within the host tissue and then produces aecia containing one-celled aeciospores with two nuclei (n+n). The aecial stage is referred to as Stage I. Unable to infect the alternate host, aeciospores are able to infect one or more cereal hosts serving as primary hosts. After aeciospores infect a primary host plant, the rust fungus produces uredinia-bearing urediniospores; this is referred to as Stage II. Similar to aeciospores, urediniospores are one-celled and typically have two nuclei (n+n). Urediniospores can infect the primary host and produce new urediniospores again, which is a complete asexual cycle. This asexual cycle can repeat many times during the host growth season, leading to a severe rust epidemic on the cereal crop. Usually in the late season of cereal crop growth and when weather conditions become unfavorable for urediniospore infection and production, telia-bearing teliospores are produced on a primary host; this is referred to as Stage III. Teliospores of *Puccinia* spp. are two-celled, and each cell contains two nuclei (n+n); the two nuclei later merge into one nucleus (2n) through karyogamy. Teliospores of some species, such as *P. graminis*, have a long dormancy, while those of *P. striiformis* have no dormancy or have a very short dormancy. Teliospores germinate after dormancy is broken. When a teliospore germinates, each cell produces a promycelium (also called basidium) bearing four basidiospores; this is referred to as

Teliospore: thick-walled resting spore in which karyogamy occurs; it germinates to form a promycelium from which haploid basidiospores are produced

Urediniospore: asexual, dikaryotic spore produced in a uredinium of a rust fungus on a primary host

Puccinia graminis **f. sp.** *tritici* **(*Pgt*):** the forma specialis of the fungal species causing stem rust on wheat and barley

Puccinia graminis **f. sp.** *avenae* **(*Pga*):** the forma specialis of the fungal species causing stem rust on oat

Puccinia graminis **f. sp.** *secalis* **(*Pgs*):** the forma specialis of the fungal species causing stem rust on rye
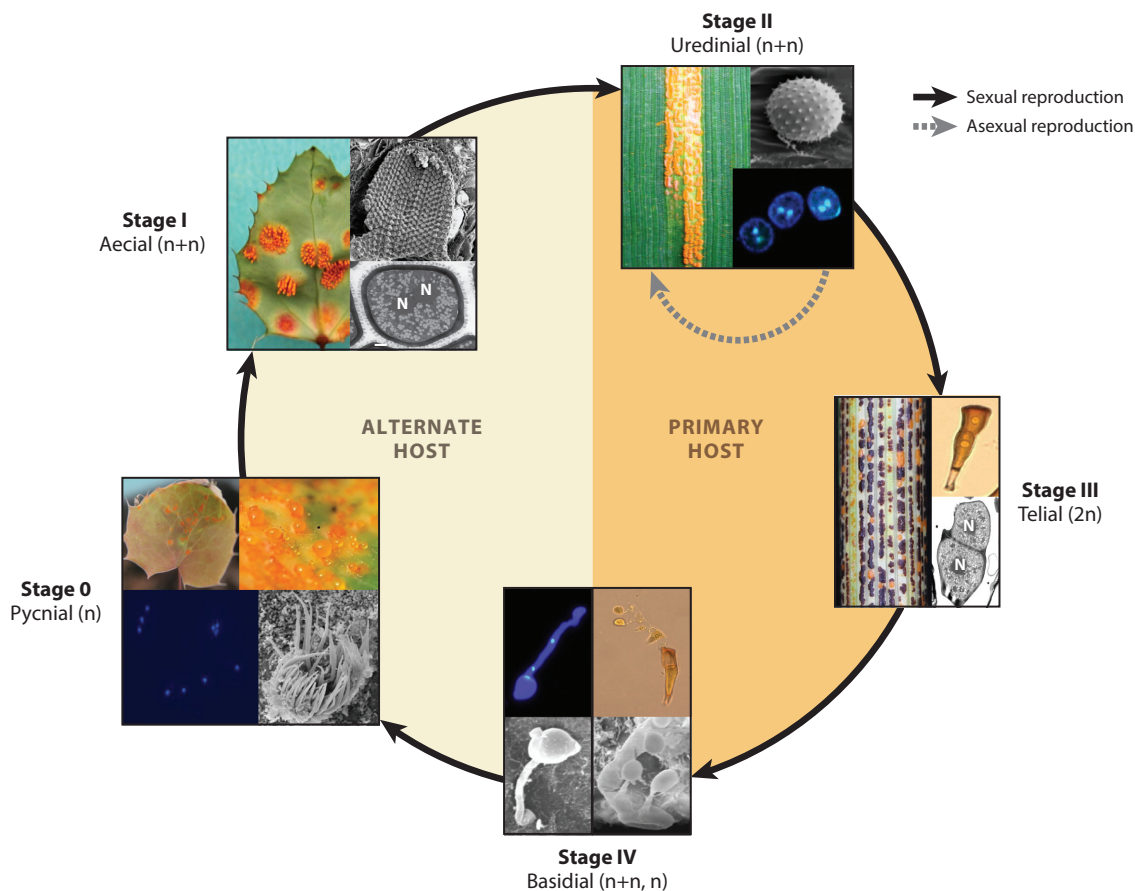
Puccinia striiformis **f. sp.** *tritici* **(*Pst*):** the forma specialis of the fungal species causing stripe rust on wheat

Puccinia striiformis **f. sp.** *hordei* **(*Psh*):** the forma specialis of the fungal species causing stripe rust on barley

Pycniospore: haploid, sexually derived spore (spermatium) formed in a pycnium (spermogonium) of a rust fungus

Figure 1

The complete life cycle of *Puccinia striiformis* f. sp. *tritici*. Stage 0 (*clockwise from left top*): pycnia on a young barberry leaf, nectars on the pycnia, a scanning-electron-microscopy picture showing a pycnium with receptive hyphae and pycniospores, and fluorescent-stained haploid pycniospores. Stage I: aecia on a barberry leaf, a scanning-electron-microscopy picture of an aecial cup containing aeciospores in chains, and an aeciospore with two nuclei (N). Stage II: uredinia in a stripe on an adult leaf of wheat, a urediniospore, and dikaryotic urediniospores. Stage III: black telia and orange uredinia on a wheat leaf sheath, a teliospore with two cells with one nucleus in the top cell and two nuclei in the bottom cell, and a teliospore with one nucleus in each of the two cells. Stage IV (*clockwise from left top*): a teliospore germinating and producing basidiospores, scanning-electron-microscopy pictures showing formation of basidiospores and a germinating basidiospore with an appressorium at the tip of the germ tube and a germinated basidiospore showing two nuclei in the germ tube.

Stage IV. Basidiospores are one-celled and each generally contains one nucleus (n), but several *Puccinia* species have been found to contain one, two, or more nuclei (9; J. Zhao, J.N. Yao, M. Jiao, X.M. Chen, Q.M. Han, H.C. Zhang, L.L. Huang, Z.S. Kang, unpublished data). Basidiospores cannot infect primary hosts but can infect alternate hosts to complete the sexual cycle. Different from urediniospore infection, which is through host stromata, basidiospore infection is through direct penetration of host epidermal cells.

Aeciospore:
dikaryotic spore produced in the cup-shaped aecium of a rust fungus on an alternate host

Alternate Hosts of Cereal Rust Fungi

As the alternate hosts for *P. striiformis* have been recently identified (62, 131, 150), all cereal rust fungi have been found to be heteroecious, with the uredinial stage occurring on cereals and grasses

and the aecial stage occurring on other plants. The discovery of plant species as alternate hosts of cereal rust fungi has taken more than three hundred years.

Stem rust. Among the cereal rusts, stem rust (caused by *Pg*) was the first to be recognized as associated to barberry. In 1660, a law enacted in Rouen, France, required the removal of barberry plants (*Berberis* spp.) near grain production fields, long before the identification of the fungal pathogen in 1794 by C.H. Persoon (108). In the United States, local laws against growing barberry were passed in Connecticut 1726, Massachusetts in 1754, and Rhode Island in 1766; and the great Barberry Eradication Campaign lasted more than half of the last century (98). It was de Bary who first proved the heteroecism of *Pg* on cereals and barberry in the 1860s (42). *Mahonia*, a genus very closely related to *Berberis*, is also an alternate host for *Pg*. More than 90 species or varieties of *Berberis*, *Mahonia*, and their hybrids (× *Mahoberberis*) have been found to be susceptible to *Pg* (99). Among the susceptible species, *Berberis vulgaris* is the most important in North America and Europe. There are more than 20 species of *Berberis* and *Mahonia* that have been found to be resistant to stem rust (99). Even for susceptible alternate host plants, only young tissues (two weeks old or fewer) are susceptible. The window of alternate hosts vulnerable to *Ps* infection is much narrower than that of primary hosts.

Crown rusts. It was also de Bary in 1867 who first demonstrated the connection between *Pc* on grasses and on buckthorn when he used sporidia from an unspecified grass to inoculate *Rhamnus frangula* (43). He observed both pycnia and aecia but did not successfully infect oats, rye, or wheat with the aeciospores. In 1875, Nielsen proved the heteroecism of *Pc* by inoculating *Lolium perenne* with aeciospores from *Rhamnus cathartica* and obtaining uredinia, and in 1880, Cornu obtained heavy infection by inoculating oat seedlings with aeciospores from *R. cathartica* and *Rhamnus oleoides* (108). The production of dikaryotic aeciospores by transferring the self-incompatible pycniospores to flexuous hyphae of other pycnia was demonstrated by Craigie in the late 1920s (37, 38). Simons (115) summarized 39 species in 5 genera susceptible to *P. coronata* under controlled conditions, including 35 species belong to *Rhamnus*. Pycnia and aecia were observed on plants of 20 species in four genera infected by *P. coronata* under natural conditions. Among these genera, *Rhamnus* is the most important genus serving as an alternate host for *Pc*.

Leaf rust. In 1914, Tranzschel first indicated *Ornithogalum* spp. as an alternate host for *Ph* (126), which was later confirmed by researchers in many countries. More than 30 species of *Ornithogalum*, together with *Dipcadi serotinum*, have been demonstrated as alternate hosts of *Ph* (40). Anikster (7) successfully infected *Ornithogalum brachystachys*, *Ornithogalum trichophyllum*, *Dipcadi erythraeum*, and *Leopoldia eburnea* with basidiospores derived from *H. vulgare*, *Hordeum spontaneum*, *Hordeum bulbosum*, and *Hordeum murinum*. He observed some levels of specialization of the fungi from the *Hordeum* spp. on the alternate hosts.

Jackson & Mains (57) first reported *Thalictrum* spp. as alternate hosts of *Pt* in 1921. From 1946 to 1980, several other species were reported as alternate hosts of *Pt*. These species include *Isopyrum fumarioides* reported in Siberia (36), *Anchusa* spp. in Portugal (41), and *Clematis* spp. in Italy (114) and the Russian Far East (13). According to d'Oliveira & Samborski (41), the rust fungi on different alternate hosts are different species, with *Pt* infecting *Thalictrum*.

Stripe rust. Alternate hosts of *Ps* were not identified until very recently. The early attempts to find aecial hosts for *Ps* all failed (46, 122, 123, 127), but Mains (80) made the correct speculation, which was proven more than 70 years later, that *Berberis* and *Mahonia* could be alternate hosts of *Ps* because of its relatedness to *Puccinia koeleriae*, *Puccinia arrhenatheri*, and *Puccinia montanensis*.

Basidiospore: uninucleate or binucleate haploid spore produced from a promycelium that resulted from a germinating diploid teliospore

Heteroecism: the necessity of two host species for the completion of the life cycle of certain rust fungi

In 2010, Jin et al. (62) identified a stripe rust fungus by inoculating wheat, barley, oat, rye, and Kentucky bluegrass with aecium-bearing leaf samples collected from naturally infected plants of *Berberis chinensis* and *Berberis koreana* in an arboretum and ornamental plantings of Emerald Caroudel, an interspecific hybrid between *B. koreana* and *Berberis thunbergii* in Minnesota. The rust fungus was the stripe rust fungus *Puccinia pseudostriiformis* (syn. *P. striiformis* f. sp. *poae*), which is found on bluegrass. They also successfully obtained pycnia and aecia by inoculating seedlings of *B. chinensis*, *Berberis holstii*, *B. vulgaris*, and limited aecia on *B. koreana* with germinated teliospores of *Pst*. *B. vulgaris* was successfully confirmed to be susceptible to *Pst* and *Psh*, with all five spore stages produced using a single isolate under controlled conditions (33, 132, 134, 135; X.M. Chen, Y. Lei, M.N. Wang, unpublished data). Moreover, *Mahonia aquifolium* was found to be susceptible to the wheat stripe rust pathogen under controlled conditions (131). In China, inoculation of barberry plants with germinated teliospores of *Pst* identified 28 species of *Berberis* susceptible to the pathogen (64, 136, 150). *P. striiformis* f. sp. *tritici* was identified, although in very low numbers, from aecia collected from naturally infected plants of five species, *Berberis aggregata*, *Berberis brachypoda*, *Berberis polyantha*, *Berberis shensiana*, and *Berberis soulieana* (136, 150). These results show that *P. striiformis* f. sp. *tritici* is able to infect barberry under natural conditions in China. At present, 33 species of *Berberis* and *Mahonia* have been reported to be susceptible to *Pst*.

ECOLOGICAL FACTORS AFFECTING THE ROLE OF ALTERNATE HOSTS

Epidemics of cereal rusts are highly dependent upon environmental conditions, including weather conditions and cropping systems. The environmental conditions are important for disease epidemics caused by urediniospores on cereal crops, but also for rust development and aeciospore production on alternate hosts. The environmental conditions affect survival, infection, growth, and reproduction of the fungi throughout the asexual cycle, but also affect the different stages throughout the sexual cycle, especially teliospore survival, germination, and basidiospore infection of an alternate host. As conditions for germination, infection, and survival of urediniospores or uredinial stage have been well reviewed for *Ps* (30, 76, 96, 111, 112), *Pg* (8, 99, 145), *Pt* (68, 102), and *Pc* (27, 60), we only discuss the weather conditions for teliospore germination to produce basidiospores for infection of alternate hosts, pycniospore production and spermatization, and aeciospore production and infection of cereals.

Humidity and Temperature

Among the weather conditions, humidity is the most important factor for rust development (30) because germination of and infection by any type of spores need dew formation on the plant surface. Although high moisture conditions are generally favorable for rusts, low moisture can allow urediniospores and teliospores to survive for a long period of time, which is especially important for inoculum to carry over to the next crop season and for long-distance dissemination. Temperature is another important factor affecting spore germination and infection, latent period, sporulation, and spore survival of rust fungi (6, 30, 96, 123). Different rust fungi prefer different temperatures for causing epidemics. In general, *Ps* likes low temperature, *Pg* likes high temperature, and the preferences of *Pt* and *Pc* are in between. The adaptation of fungal pathogens to different environments determines the distribution and frequency of rust epidemics.

Stripe rust and stem rust. Under field conditions, infection and sporulation of *Ps* urediniospores can take up to several months if temperatures are mostly between −10°C and 0°C, and teliospore

formation usually does not take place until late in the crop season when temperatures are above 15°C. High temperature and high humidity conditions reduce uredinial formation and survival but increase telial formation. Teliospores can tolerate much higher temperatures than uredini-iospores. Some *Ps* isolates are able to form telia on seedlings of wheat or barley even under the low temperature range (4–20°C) favorable for uredinial formation. In general, *Psh* more readily produce telia than *Pst*. Even among isolates of *Pst*, there are significant differences in the ability to produce telia (A.M. Wan & X.M. Chen, unpublished data). In contrast, *Pgt* telia form much sooner after uredinial formation than those of *Pst*. In the US Pacific Northwest, where stem rust develops in the late crop growth season, telia form just a few days after uredinia appear (134).

Wang & Chen (132) compared germination of teliospores of *Pst* and *Pgt* and found that under saturated moisture conditions, temperatures around 10°C are optimal for *Pst* teliospore germination and basidiospore formation, whereas *Pgt* teliospores and basidiospores germinate best at around 20°C. They also found that *Pgt* basidiospores were produced much faster than the basidiospore formation of *Pst* even at their respective optimal temperatures. The minimum and maximum temperatures for teliospore and basidiospore germination are slightly below 5°C and slightly above 22°C for *Pst* but between 5°C and 10°C and above 30°C for *Pgt* (132, 145).

Teliospores of *Pst* and *Pgt* differ significantly in structure, dormancy, and survival. Telia of *Pst* are submerged under the epidermal layer of wheat tissue and form spherical sori. Teliospores are contained inside the sori and covered by an outside peridial cell layer (132). The two layers from the host plant or the fungus may protect *Pst* teliospores but need to be broken to germinate teliospores. In contrast, *Pgt* telia form tough and thick pseudoparachemata on the surface of wheat tissue, on which teliospores are readily exposed when mature. Without protection by a host epidermal layer or a fungal peridial layer, the exposed *Pgt* teliospores should easily absorb water to germinate. However, a *Pgt* teliospore could not germinate during summer and fall, as it has a long dormancy, whereas *Pst* teliospores have no dormancy or a very short dormancy (132). Thus, *Pst* and *Pgt* utilize very different mechanisms to protect their teliospores from germinating under unsuitable environments, but the protections produce different fates for *Pst* and *Pgt* teliospores.

A four-year field survey in the US Pacific Northwest discovered that *Pst* teliospores can be readily germinated immediately after being produced in fields in July and when the telial sori are forcefully broken (132). The germination rate gradually decreases before winter. After winter, *Pst* telia become degraded and no viable teliospores are available when new leaves of barberry are produced. In contrast, *Pgt* teliospores do not germinate until the following January, and the germination rate reaches its highest in late April and May, nicely catching the formation of new barberry leaves (132). Although it is not clear why *Pst* teliospores are degraded but *Pgt* teliospores are not, wet and fluctuating temperature conditions appear to be favorable for the function of *Pgt* teliospores but not for *Pst* teliospores.

To further determine the effects of humidity and temperatures on *Pst* teliospore survival, Wang & Chen (132) determined the viability of teliospores under different controlled conditions. They found that the germination rate of *Pst* teliospores kept dry and at 22–23°C dropped gradually from 79% in July when fresh to 1% in January, whereas teliospores completely lost viability in three weeks if kept wet at 5°C. The wet condition is detrimental to *Pst* teliospores. On the basis of these results, they speculate that *Pst* teliospores may function in regions where teliospores form late in the fall, the weather is dry during the winter, and long periods of high moisture conditions are possible in the spring, when alternate hosts produce new leaves. Some parts of northwestern China have such conditions. The speculation has been proven by the finding of low infection rates of *Pst* on naturally infected barberry (134, 150). Nevertheless, the role of alternate hosts for stripe rust is not comparable to the important or essential role of alternate hosts to stem rust in many parts of the world.

Leaf rust and crown rust. *Puccinia triticina* does not produce teliospores readily under greenhouse or growth-chamber conditions (99). In some regions, such as the US Pacific Northwest, *Pt* telia are hard to find even when uredinia are abundant. When formed, teliospores can survive through extremely severe winters. Free moisture is required for teliospore germination and basidiospore formation. The latent period is approximately 14 days after inoculation of alternate host plants with basidiospores under ideal temperature conditions (145). Pycniospores form approximately 7–10 days after basidiospore infection, and aecia emerge 7–10 days later on the abaxial surface of the leaf, generating aeciospores. These results can be obtained under similar moisture and temperature conditions to those for inoculation with and production of urediniospores (102).

Teliospores of *Pc* form readily in the late crop growth season and stay viable after overwintering from October to April (60). Successful inoculation of alternate host plants with teliospores can be reached by keeping inoculated plants for 48–72 h at 15–17°C under near saturated moisture conditions. Pycnia appear 7 days after inoculation at temperatures of 20–24°C, and aeciospores are produced 2 weeks after inoculation. Approximately 9–12 days after inoculation of cereal crops with aeciospores, uredinia can be observed at optimum temperatures.

Phenology of Alternate Hosts

Synchronization between alternate hosts and viable teliospores, together with favorable weather conditions, is vital for infection on alternate hosts and subsequent infection on cereal crops by windborne aeciospores. Alternate hosts of cereal rust fungi belong to herbaceous plants and shrubs with distinct growth habits of evergreen and deciduous types. Only tissue that has been growing for two or fewer weeks, even on susceptible plants, can be infected by *Pg* basidiospores (88). Young fruit can be infected by basidiospores and produce aecia in nature, whereas leaves are resistant. Young fruit and twigs of *Berberis* and *Mahonia* can prolong the period of susceptibility and produce more aeciospores to infect cereals and grasses, in addition to infected leaves.

Viabilities of teliospores of different cereal rust fungi are different. In the US Pacific Northwest, teliospores of *Pst* can germinate under controlled conditions from when they are produced in summer to before winter but become completely degraded before the following May (132). Similarly, teliospores in northwestern China can germinate until the following April (J.F. Qin, Y.Y. Zhao, Q. Li, S.X. Zuo, X.M. Chen, L.L. Huang, J. Zhao, Z.S. Kang, unpublished data). In contrast, *Pgt* teliospores do not germinate until they've gone through a winter, and the germination rate reaches its highest in May when barberry plants have young susceptible leaves for infection (132). In the US Pacific Northwest, the phenology of primary and alternate hosts and different viabilities of teliospores make barberry an important alternate host for stem rust but not for stripe rust (132, 134). This method can be used to determine whether or not alternate hosts are important for rusts in other regions of the world.

Spore Dispersal

Cereal rust fungi generally do not survive in the uredinial stage during hot summers and cold winters. Unfavorable weather conditions can stop rust development and may kill rust fungi. However, rust fungi have developed several abilities to survive the harsh summer and winter environments. In addition to having colored urediniospores and staying dormant in primary host tissue, they can produce darker teliospores, which in general can survive extreme weather conditions, while waiting for favorable conditions to grow and reproduce. More importantly, they can be dispersed by wind to find places favorable for uredinial infection and reproduction. The *Puccinia* pathway in North America and similar pathways on other continents (99, 112, 146) demonstrate the ability of rust fungi to move long distances between regions.

Unlike urediniospores, which can be disseminated by wind over a wide range (from more than 800 km to 8,000 km) (16, 90, 99, 137, 144), basidiospores can survive only a few hours under favorable conditions and are windborne to up to only 270 m (99, 102). Basidiospores cannot travel far because they are colorless, sensitive to UV light, and may not withstand dry conditions. Aeciospores may travel farther than basidiospores as they have color. According to Stakman & Harrar (118), *Pg* aeciospores can be blown by wind up to 2 km at elevations. It is speculated that aeciospores are spread by wind to a distance over hundreds of kilometers, similar to urediniospores, but long-distance dispersal of aeciospores has not been reported (99, 102). Based on field observations, *Pgt* aeciospores can be spread over 500 m but not more than 10 km (X.M. Chen, unpublished data). As pycniospores stick together, as in nectars, they are usually not lifted and carried away by wind. However, pycniospores could be carried by insects for uncertain distances that are completely dependent on migration behaviors of the insects. Because the only function of pycniospores is to fertilize receptive hyphae, not to infect any plants, movement of distances measured in centimeters or meters is adequate for performing their function.

FUNCTIONS OF ALTERNATE HOSTS

Depending on rust fungal species and ecological conditions, an alternate host may have different functions for the disease epidemics and pathogen variations. In general, an alternate host enables a rust pathogen to survive winter, provides inoculum to initiate disease development on cereal crops, generates new races, and diversifies rust populations.

Survive Winter and Provide Initial Inoculum

For some rust fungi, alternate hosts are essential, as the telial stage is the only stage in which the fungi can survive winter. For example, in eastern Siberia, the weather is too cold to grow winter wheat and wheat is sown only in spring. The uredinial stage of *Pt* cannot survive winter. The dormancy of teliospores is broken in spring, and basidiospores infect *I. fumarioides* to produce pycnia and aecia. Aeciospores are the only inoculum source of *Pt* because the windborne urediniospores are not available in spring (21, 22). This wheat-*Isopyrum* system enables *Pt* to survive in this region. In the major wheat-growing regions of the eastern Pacific Northwest of the United States, although winter wheat is a major crop, *Pgt* cannot survive as mycelium in urediniospore-infected leaves, and telia are the only structure to survive winter (132, 134). Because urediniospores rarely spread to other epidemiological regions, aeciospores produced on alternate hosts are the only initial source of inoculum for infection of wheat and barley. Although not the only source of inoculum, alternate hosts provide primary inoculum of *Pgt* to infect wheat and barley crops (54, 98, 117) and of *Pc* (44, 45, 89) in the northern Great Plains.

Produce New Races

New races with combined virulence genes are generated on alternate host plants through sexual reproduction. Stakman et al. (119) studied *Pgt* aecial cultures from natural collections and selfed progenies, and found new races arose through sexual reproduction. Newton & Johnson (92) found new races of *Pga* obtained from aecial collections or uredinial collections near barberry bushes. Wahl et al. (128) identified 24 races of *Pc* from 75 aecial samples on buckthorn in Israel. More races of *Pca* were consistently identified from the north-central spring oat region of the United States than the southern winter oat region from 2001 to 2009, indicating that alternate hosts increase the number of races (26, 27). Wang et al. (134) identified 10 races of *Pgt* from 16 single-uredinium cultures from aecia on barberry bushes in northern Idaho.

Diversify Pathogen Populations

Through sexual reproduction on alternate hosts, rust pathogens become more diverse. In alternate host functioning regions, the number of races is significantly larger than the alternate host eradicated areas. Roelfs & Groth (101) compared virulence phenotypes of *Pgt* populations near barberry bushes from eastern Washington and northern Idaho that reproduced sexually and of populations east of the Rocky Mountains that reproduced asexually. They identified 100 races (23.5%) out of 426 isolates from the sexual population, and 17 races (0.07%) out of 2,377 isolates from asexual population. High genetic diversity in the *Pgt* population in the US Pacific Northwest has also been found in recent years (59, 103, 132). High diversity has also been reported for a sexually produced *Pc* population (4). The large number of rather rare races was collected from alternate hosts, or from cereal and grasses near alternate host plants, indicating that alternate hosts functioned effectively to generate diverse races.

IMPORTANCE OF ALTERNATE HOSTS

Although the susceptibility of an alternate host can be proven under controlled conditions, whether it functions in nature is determined by several factors. First, the teliospore must germinate at the time when susceptible tissues of alternate hosts are available. Second, the vulnerable stage of alternate host plants must encounter germinating teliospores. Third, the green and susceptible cereal plants must be available within the distance of aeciospores during the time of aecial formation on alternate hosts. Fourth, the weather conditions must be suitable for the infection of alternate and primary hosts by basidiospores and aeciospores, respectively. These conditions include the means of spore dispersing between primary and alternate hosts and temperature and moisture conditions for spore germination, infection, and development. Only when the above factors take place in the right time and space can alternate hosts play a critical or important role in the rust epidemics.

Alternate Hosts for Stem Rust and Stripe Rusts

Barberry plays an important or even essential role for stem rust in northern Europe, Canada, and the northern United States (54, 92, 93, 98, 99, 117, 132, 146). In North America, before barberry eradication, barberry bushes were an important source of *Pg* inoculum on wheat, barley, rye, and oat in the north-central states of the United States and in Canada and can still be a source of early inoculum for *Pga* from Pennsylvania to southern Ontario and for *Pgt* in the Pacific Northwest (58, 99, 132). In Europe, barberry was responsible for local or regional epidemics in Bavaria, France, Ireland, Spain, Yugoslavia, and Switzerland as well as the alpine and subalpine flood plains (146). In Denmark, barberry was used as hedge shrub in field separations, which led to stem rust epidemics within the following years, and the barberry eradication law was established in 1904 (146). In Sweden, aeciospores of both *Pga* and *Pgs* were detected from barberry bushes using molecular markers. However, aeciospores play an important role for oat stem rust epidemics but not for rye stem rust epidemics (17, 19). In contrast, barberry is not important in the southern United States (98), South America (72), Australia (77), India (84–87), the Russian Far East (13), and South America (11, 14), but it is important for *Pgt* and *Pga* in Tajikistan (18).

In some countries or regions, the role of barberry in stem rust is not clear. For example, in New Zealand, Allen (5) reported that the native barberry species was resistant to stem rust, but recent surveys show that susceptible *Berberis* species exist in this region (129). In Africa, aeciospores from naturally infected *B. holstii* plants were inoculated on cereal hosts but failed to infect these hosts because of nonviable spores; however, some aecia were identified as *Pgt* using molecular markers

(75). In China, early studies indicated that barberry did not function as an alternate host for *Pgt* in Hebei Province (149). Although *Berberis amurensis* was found to be an alternate host for *Pgt*, it did not have any effect on epidemics of stem rust in the middle part of northeastern China, a major epidemiological zone of the country for stem rust (148). However, recent studies have shown that new *Pgt* races were recovered from aeciospores on *Berberis* spp. in a natural infection in northwestern China (151). In a recent study of barberry plants in Kenya, Azerbaijan, Georgia, India, Iran, Kazakhstan, Nepal, and Turkey, aecial infections were observed on barberry, but the role of barberry in stem rust epidemics was unclear (95). More research is needed in these countries to clarify the role of barberry in stem rust and stripe rust epidemics.

For stripe rust, barberry is not as important as for stem rust worldwide. In the US Pacific Northwest, barberry is essential for stem rust, but does not play a role for stripe rust (132, 134). Barberry possibly serves as an alternate host for stripe rust in Pakistan and the Himalayan region (2, 3) and for stripe rust in China (136, 150). In western Asia and eastern Africa, barberry plants have been found, but their association with stripe rust epidemics has not been confirmed (58, 62). So far, the only evidence of natural infection of barberry by *Pst* has been obtained in China but at a very low frequency (136, 150), and more studies are needed to determine the connection of stripe rust on barberry and on wheat.

Alternate Hosts for Crown Rust

Buckthorn (*Rhamnus* spp.) plays an important role for crown rust in Europe, Canada, and the northern United States (115). Aeciospores on common buckthorn (*R. cathartica*) are important inoculum for crown rusts of both oat and barley in the northern Great Plains of the United States (60, 89, 116) and for oat crown rust in Denmark (24, 56) and Ireland (83). The species functions as an alternate host in small scale for crown rust in spring oat in the Czech Republic (67), and occasionally functions as an alternate host in Siberia, depending on the winter and spring weather conditions (115). Other *Rhamnus* species are susceptible to *Pc*, but their role is less important than *R. cathartica* (89, 115, 116, 128).

The role of buckthorn in crown rust varies greatly depending on the climatic conditions and cropping systems in different regions. In cold northern climates, such as Siberia, where the ure-dinial stage cannot overwinter, crown rust on oats is completely associated with the rust on buck-thorn (116). In northern Europe, Canada, and the north-central United States, the uredinial stage of *Pc* does not overwinter and aeciospores on *Rhamnus* are the primary inoculum, but windborne urediniospores can come from the south (116, 122). In the Middle East, *Rhamnus* plants harbor diverse races but not the source for initial inoculum (128). Oat crown rust regularly undergoes sexual reproduction on common buckthorn, which is responsible for the virulence diversity of crown rust in North America, in much of the northern United States and eastern Canada (26, 27, 70, 71). Crown rust on barley has been reported in Nebraska, Minnesota, Wisconsin, North Dakota, and South Dakota, and Manitoba and Saskatchewan in Canada. *R. cathartica* is an important source for starting local barley crown rust infection (61).

Alternate Hosts for Leaf Rust

Alternate hosts of leaf rust are generally regarded as unimportant in epidemics and not functioning in most regions (23, 36, 104), except in eastern Siberia (36) and the marginal areas of Morocco durum wheat–growing regions (47, 48). In North America, alternate hosts are considered unim-portant in leaf rust epidemics, although aeciospores pathogenic to wheat have been isolated from *Thalictrum dioicum* (73) and *Thalictrum dasycarpum* (23, 142, 143). In Japan, Yamada et al. (141)

found aecia on *Thalictrum thunbergii* near wheat fields, but they thought it not an important inoculum source. Other researchers found that *Thalictrum speciosissimum* was infected by *Pt* in Portugal (10, 41). Pycnial and aecial infections of *Pt* on *Thalictrum* spp. have been observed in northeastern Kazakhstan (69), but their connection with wheat leaf rust epidemics is unknown. In India, Mehta (85) claimed that *Thalictrum* plants are rare in the Indian plains, and they have never been found to be infected by *Pt* (85). In Europe, *Thalictrum* is regarded as the primary alternate host of *Pt*. Sexual stages of *Pt* can be induced on *T. speciosissimum* in the Czech Republic and Slovakia, but none of the native *Thalictrum* species have been found to host *Pt* in fields (15). In South America, several *Thalictrum* species exist, but they do not function as alternate hosts for *Pt* (36).

Several other plant species have also been reported to serve as aecial hosts of *Pt* in nature, but the reports rarely claim that leaf rust epidemics are caused by these aecial hosts (10, 13, 28, 51, 114, 125). However, *Anchusa italica* likely provides inoculum for leaf rust on durum wheat in Portugal, Morocco, and Spain (10, 41, 47, 48).

The alternate hosts of the leaf rust on rye (*Pr*) and barley (*Ph*) are *Lycopsis arvensis* and *Ornithogalum* spp., respectively. *L. arvensis* functions as an alternate host for *Pr* in central Europe (the Czech Republic and Poland), and *Ornithogalum* spp. provide initial inoculum for *Ph* in the Mediterranean region (Israel and Greece) (10).

ALTERNATE HOSTS AS PLATFORMS FOR STUDYING THE GENETICS OF HOST-PATHOGEN INTERACTIONS

Alternate hosts are important for studying the genetics of the cereal rust pathogens. Through self-crossing or intercrossing between isolates or between formae speciales of a rust species, the genetics of various traits of rust fungi have been studied, particularly avirulence and virulence. Although other biological traits associated with pathogenicity were also reported, such as latency, lesion size, spore production rate, sporulation duration, spore color, telial formation, and other biological traits, we summarize the studies on avirulence and virulence.

Inheritance of Avirulence/Virulence

The rust-cereal pathosystems follow the gene-for-gene concept established by Flor (50). A resistant reaction is observed on an incompatible interaction when a rust isolate carrying an avirulence gene encounters a plant possessing a corresponding resistance gene. A susceptible reaction is observed when either an avirulence gene or a resistance gene does not function or is absent in a compatible interaction. Understanding the genetics of avirulence is important for interpreting the nature of host resistance and fungal pathogenicity. Most life stages of rust fungi on cereal hosts are dikaryotic, as in diploid plants. Through meiosis, basidiospores are produced and their infection on an alternate host produces haploid gametes, pycniospores, and receptive hyphae. Thus, the inheritance of a rust fungal trait is similar to that of a higher plant trait following the Mendelian genetics laws. The genetic analysis of pathogenicity has been intensively studied for *Pg*, *Pc*, and *Pt* using segregating populations. However, the genetic studies of *Ps* have just started, as its alternate hosts have been only recently discovered (62, 131, 150).

Earlier literature on pathogenicity genetics of cereal rust fungi is reviewed by several researchers (81, 82, 116). Although avirulence can be either dominant or recessive, most avirulence genes in *Pgt*, *Pga*, *Pt*, and *Pc* are dominant and controlled by single loci (52, 91, 94, 120, 121, 147). For *Pst*, Wang et al. (133) found that avirulences to seven *Yr* genes (*Yr6*, *Yr7*, *Yr8*, *Yr19*, *YrExp2*, and *YrTye*) in race PST-127 were dominant and controlled by single genes; Tian et al. (124) found

that three avirulences (to *Yr6*, *Yr43*, and *YrSP*) were dominant and controlled by single genes in the Chinese isolate Pinglan 17–7.

However, some avirulences are recessive. Statler & Jin (121) reported that three avirulence genes in *Pt* were recessive. Other researchers reported recessive avirulences in *Pga* (52, 53, 82) and *Pc* (20). In *Pst*, avirulences to *Yr17* and *YrExp1* in the US race PST-127 are controlled by single recessive genes (133). In the Chinese isolate Pinglan 17–7, avirulences to *Yr27* and *Yr28* are reported to be controlled by single recessive genes (124).

Some individual avirulence phenotypes are determined by two genes. For example, Statler (120) showed that the avirulences/virulences of *Pt* on *Lr* genes (*Lr3*, *Lr11*, *Lr16*, *Lr21*, *Lr26*, and *Lr30*) segregated at a ratio of 15:1, indicating two independent dominant genes. Avirulences controlled by two independent dominant genes in *Pt* were also reported in other studies (105, 106, 121). In *Pgt*, the avirulence to *Sr* (*Sr* fleck) (147) and the avirulence to wheat cultivar Vernal are controlled by two independent dominant genes (63). For *Pst*, avirulence to *Yr44* is controlled by two independent dominant genes and avirulences to *Yr43* and an unknown *Yr* gene are controlled by two recessive genes (7 avirulent:9 virulent) in PST-127 (133).

Another inheritance pattern of avirulence in some rust fungi is controlled by an interaction of two complementary genes, with one gene dominant for avirulence loci and another gene dominant for suppression of avirulence, such as avirulence in *Pgt* (147), *Pt* (55), and *Pc* (20). In these cases, the phenotype ratio of avirulence:virulence is 3:13. For *Pst*, Tian et al. (124) reported that avirulences to *Yr4*, *Yr32*, and *Yr44* in Pinglan 17–7 were controlled by two recessive complementary genes (1 avirulent for every 15 virulent).

Some virulence phenotypes are significantly different in reciprocal crosses, and the cytoplasm of the maternal parent influences virulence expression. The *Pgt* virulence to the resistance in wheat cultivar Marquis is maternally inherited (63), whereas the inheritance of avirulence to *Pg-3* is controlled by an extra chromosome (53).

Linked avirulence genes have been documented for *Pt* (106, 120), *Pgt* (147), and *Pst* (124). The avirulence loci *AvrTU* and *AvrT10* of *Pgt* are 9 cM away (147). The *Pt* genes for virulence to *Lr2a* and *Lr2c* are allelic and linked with the gene for virulence to *Lr29*, approximately 14 cM away (120). For *Pst*, two pairs (*Avr6-Avr44* and *avr4-avr32*) of avirulence genes are linked in a selfed progeny population of the Chinese isolate Pinglan 17–7 (124).

Molecular Mapping

Constrained by the limited traits available in rust fungi, mapping rust fungal genes has long been hampered. Molecular techniques have greatly increased the available markers in rust fungi for constructing linkage maps. Zambino et al. (147) constructed the first *Pgt* linkage map. They crossed two US isolates and developed an F_2 population consisting of 81 progeny isolates. Using RAPD (random amplified polymorphic DNA) and AFLP (amplified fragment length polymorphism) markers, they established seven genetic linkage groups containing eight avirulence genes and 52 molecular markers. The map distance of the closest markers to the eight avirulence genes ranged from 5 cM to 14 cM. In a linkage group for *Pst* constructed with 10 markers and 8 avirulence loci, four virulence genes (*avr4*, *avr32*, *avr44*, and *avr27*) are linked in a chromosome region between SSR (single sequence repeat) markers SUNIPst10-06 and SUNIPst15-30 and avirulence genes *Avr6* and *Avr43* are linked with a genetic distance of 7.4 cM (124).

In recent years, as more and more rust fungal genomes have been sequenced, many SSR and SNP (single nucleotide polymorphism) markers have been developed and used in genetic studies of rust fungi (29, 35, 78, 140). Comparing 4,219 ESTs (expressed sequence tags) of *Pst* to the genome sequences of *Pgt*, Ma et al. (79) grouped 1,432 of the genes into 237 supercontigs using

the *Pgt* genome as a reference. The physical relationships of some of the ESTs were confirmed by PCR (polymerase chain reaction) amplification of the *Pst* bacterial artificial chromosome clones. The application of these markers in rust genetics dramatically increases the intensity of genetic and physical maps, which are useful for map-based cloning of *Pst* avirulence genes.

Determination of Homozygous and Heterozygous Virulences

Investigating the heterozygosity in rust fungi is useful to predict virulence changes in rust populations. The change from avirulence to virulence at a heterozygous locus happens more rapidly than that at a homozygous avirulence locus. The long-lasting resistance conferred by *Lr21* in wheat is attributed to the homozygous status of its avirulence gene (120, 121). The genes in *Pst* for avirulences to resistance genes *Yr5* and *Yr15* in wheat have been found to be dominant and homozygous in isolates from North America (133), Europe (97), and China (124), which may explain the wide effectiveness of these genes in many countries (113; A.M. Wan & X.M. Chen, unpublished data). In the United States, the *Pst* population reproduces asexually (34, 132). A segregating population has been developed on barberry from selfing PST-127, a predominant race since 2007. This representative isolate showed homozygous loci for avirulences to *Yr5*, *Yr10*, *Yr15*, *Yr24*, *YrSP*, *YrTr1*, *Yr32*, *Yr45*, and *Yr53*, which are either resistant to all *Pst* races or have low frequencies of corresponding virulence genes in the United States (130). The effectiveness of some of these resistance genes is likely associated with the homozygous status of the avirulence genes. With the segregating analysis on homozygosity of more avirulence gene loci, the durability of the rust resistance genes would be predicted; thus, combinations of resistance genes with corresponding avirulence genes at their homozygous states in the rust fungal population could be selected for developing wheat cultivars with long-lasting resistance.

CONCLUDING REMARKS

All rust fungi on small-grain cereals have proven to be heteroecious, requiring both primary and alternate hosts to complete their life cycle, including the stripe rust fungus that has been recently found to have *Berberis* and *Mahonia* species as alternate hosts. Alternate hosts function in helping the pathogen survive adverse environments and providing inoculum to infect cereals, generating new races, and diversifying pathogen populations. Climatic conditions and phenology of alternate and primary hosts have large but different effects on the roles of alternate hosts to different rust pathogens, and thus the roles of alternate hosts to different rusts vary greatly and also vary significantly for different regions even for the same rust. More studies are needed to determine the roles of alternate hosts for all rust pathogens in different regions of the world, especially for the stripe rust pathogen. The current knowledge implies that eradication of alternate host plants works best in regions where alternate hosts are essential for the disease or provide primary inoculum, such as barberry for stem rust in the northern United States (98). In regions where alternate hosts provide supplementary inoculum, eradication may be less effective or not effective. In regions where alternate hosts are native and major members of plantations, like barberry in northwestern China, eradication may not be feasible and ecologically sound, and fungicide application on alternate host plants around cereal fields may be helpful in reducing inoculum or races. Nevertheless, developing cereal cultivars with durable resistance is the best approach to control rusts, no matter whether alternate hosts are important or not (30, 32). However, surveying rust pathogens on alternate hosts should be conducted together with surveying cereal crops to identify new virulence genes and races. Genetic characterization of avirulences/virulences of pathogen populations on alternate hosts are useful for selecting combinations of resistance genes for developing cultivars with long-lasting resistance.

SUMMARY POINTS

1. With the discovery of *Berberis* and *Mahonia* species as alternate hosts for *P. striiformis*, rust fungi on small-grain cereal crops are now known to be heteroecious, with five spore stages in their macrocyclic life cycle.

2. Under natural conditions, alternate hosts may provide initial inoculum for starting rust epidemics or additional inoculum for intensifying infection of cereal crops, generating new races, and diversifying pathogen populations.

3. Climatic conditions and host phenology greatly affect aeciospore production on alternate hosts, infection of cereal crops, and teliospore survival and germination to produce basidiospores for infecting alternate hosts.

4. Owing to the differences in telial structure and teliospore dormancy as well as the ability of teliospores to survive different environments, different rust fungi play different roles in disease epidemiology and pathogen variation, and the roles of the same rust fungus can be significantly different in different regions.

5. In general, alternate hosts of the stem rust and crown rust fungi are more important than those of the leaf rust and stripe rust fungi.

6. Eradication of alternate hosts works better in regions where alternate hosts are essential for the rust epidemics or are the primary source of inoculum; however, eradication of alternate hosts may be less effective in regions where alternate hosts are not the primary source of inoculum and may not be feasible or ecologically sound in regions where alternate hosts are ecologically important.

7. Whether alternate hosts are important or not, developing and growing cultivars of cereal crops with durable resistance is the most effective, economic, easy-to-use, and environmentally friendly approach to controlling rust diseases.

8. Alternate hosts are an important platform for genetic characterization of rust fungi, especially their avirulence/virulence genes, and presence/absence and homozygous/heterozygous status of avirulence/virulence genes are useful for choosing combinations of resistance genes to develop cultivars with relatively long-lasting resistance.

FUTURE ISSUES

1. More studies should be conducted to determine the infection frequencies of rust fungi on alternate hosts as well as the connections between rusts on cereal crops and alternate hosts in various regions of the world, especially for the stripe rust fungus.

2. In addition to cereal crops and alternate hosts, the rust fungi also infect a wide range of related wild grass species generally referred to as auxiliary hosts. The roles of auxiliary hosts in rust epidemiology and pathogen variation should be studied in comparison with alternate hosts.

3. The relative importance of sexual and asexual recombination in generating new races and diversifying pathogen populations needs to be studied for different rust fungi and in different regions in the world.

4. The five spore stages and their different functions as well as the infection processes on different plants by different spores are fascinating. Basic studies are needed to identify genetic, physiological, and biochemical mechanisms of the various stages of the pathogen and disease life cycles as well as the interactions of the pathogen with different hosts.

5. Alternate hosts are great platforms for genetic studies of cereal rust fungi. More studies should be conducted using alternate hosts to identify, map, and clone genes for important traits of rust fungi, especially those related to pathogenicity.

6. Dikaryotic urediniospores have been used for genomic sequencing, as large amounts of spores can be relatively easily obtained. However, the genomic sequences are hard to assemble, as the genomes in the two nuclei are highly variable. This issue could be solved by sequencing genomic DNA from pycniospores of a single haploid pycnium. A sequencing technique using a limited amount of DNA is needed for this purpose.

DISCLOSURE STATEMENT

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