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*Editors*

# Stripe Rust

Springer

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# Preface

Stripe rust (yellow rust) is an old disease of wheat and barley cereals and some grasses. The disease is still an important problem for wheat production throughout the world and even the most important factor limiting wheat production in many regions. Research on stripe rust has been done for more than 130 years since the late nineteenth century, and especially intensive studies have been conducted in the last two to three decades. However, there is no single book focusing on this important disease. This was the incentive for us to start writing such a book specifically on stripe rust about 2 years ago.

We organize the book into seven chapters. Chapter 1 is pretty much an introduction. It briefly addresses the historical aspects of the disease and its research and introduces the distribution and impact of the disease. Chapter 2 focuses on the variations of the pathogen, especially trying to cover both virulence and molecular aspects of pathogen variations. The most recent discovery of the sexual life cycle and its role in the disease epidemic and pathogen variation are discussed. Chapter 3 provides a discussion on the host-pathogen interactions, especially focusing on the recent progress in the molecular mechanisms of the interactions for the stripe rust pathosystem. Chapter 4 presents the epidemiology of the disease. Host, pathogen, and environmental factors determining the pathogen survival and reproduction and the disease development and damage are discussed. Chapter 5 is dedicated to host resistance as it is the most important approach for the control of stripe rust, and tremendous progress has been made in resistance to the disease. In addition to host resistance, nonhost resistance and other sources of resistance are also discussed. Chapter 6 presents the integrated control of the disease from concepts to methods for reducing damage caused by stripe rust. Chapter 7 entitled "Conclusions and Perspectives" summarizes research progress and discusses future perspectives based on our understanding of the existing issues to be addressed and advancing technologies that may help in the research and development of better strategies and techniques for better control of the disease in the future.

There are many thousands of publications on stripe rust. We have tried to include as many publications as possible. However, it is impossible to include all papers and reports on stripe rust, especially those published in languages other than English

and Chinese. We would like to express our regret to those whose papers are missed in this book. We would like to especially thank the scientists who made great contributions to the great body of knowledge on stripe rust. We hope the book will be useful for everyone who is interested in stripe rust and similar diseases. We also welcome any comments and criticisms to this book. We wish more young scientists to dedicate their efforts on studying stripe rust and make great contributions toward more effective control of the destructive disease, protecting the highest potential production of wheat, barley, and cultivated grasses, while reducing the use of fungicides and protecting the environment.

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# Contents

# Chapter 1
# Introduction: History of Research, Symptoms, Taxonomy of the Pathogen, Host Range, Distribution, and Impact of Stripe Rust

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**Abstract** Stripe rust, caused by *Puccinia striiformis*, is a disease on cereal crops wheat and barley, some cultivated grasses and many wild grasses. It is an old disease, but is still economically important. Stripe rust is one of the most destructive diseases of wheat worldwide, and can cause huge yield losses or cost big expenses for chemical control. Although currently not as damaging as stripe rust on wheat, stripe rust of barley can cause significant yield losses in localized barley growing regions. Based on the host species specialization of the fungal pathogen, the species of *P. striiformis* can be separated into different formae speciales, most notably *P. striiformis* f. sp. *tritici* causing stripe rust mostly on wheat and *P. striiformis* f. sp. *hordei* mostly on barley. The rapid evolution of the pathogen create various races or pathotypes that are more specialized on cultivars of cereal crops with different race-specific resistance genes. This introduction chapter presents general aspects on historical perspectives, taxonomy and host range of the pathogen and distribution and impact of the disease, and the following chapters will focus specific aspects of the pathogen and disease.

**Keywords** Alternate host • Auxiliary host • Barley • Formae speciales • Grasses • Host range • Primary host • *Puccinia striiformis* • Stripe rust • Wheat • Yellow rust • Yield loss

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Stripe rust, also called yellow rust, is a disease on cereal crops and grasses. Economically, stripe rust is mostly important on wheat and barley. The disease was recognized several hundred years ago, and it has been intensively studied during the last 120 years. Hassebrauk (1965, 1970) and Hassebrauk and Röbbelen (1974, 1975) wrote a four-part monograph on stripe rust in Germany. Latter, Röbbelen and Sharp (1978) revised the part on host resistance into a monograph in English. Line and Qayoum (1992) wrote a bulletin summarizing virulence, aggressiveness, evolution, and distribution of races of the stripe rust pathogen in North America from 1968–1987. Since then, there has been no any monograph published on stripe rust. So far, there has been no a single book focusing on stripe rust, but covering every major aspects of the research and control of stripe rust. To fill the gap, this book summarizes more than 100-year research, but mostly focusing on the progresses made in the recent decades. The book comprises seven chapters. Chapter 1 covers the introduction on the history, symptomology and effects on plants, distribution and impact of the disease. In this chapter, the taxonomy of the pathogen is also introduced. Chapter 2 focuses on the pathogen variability including variations in virulence, environmental adaptation, and population diversity. This chapter also contains recent findings on genome and functional genomics of the pathogen and discussions on molecular mechanisms of variability. Chapter 3 presents recent findings on host-pathogen interactions using cytological, physiological, and molecular approaches. Interactions to primary and alternate hosts in the context of life cycle of the pathogen are presented in this chapter. The epidemiology of stripe rust is covered in Chap. 4, which also contains how to predict the disease. As resistance is the most important approach to control stripe rust and has been most intensively studied, whole Chap. 5 is dedicated to the topic. The integrated control of stripe rust, including cultural practices and chemical applications, is discussed in Chap. 6. Chapter 7 presents brief conclusions and perspectives on future stripe rust research and management.

## 1.1   The History

Rusts of cereal crops are an old group of plant diseases that may have occurred since the domestication, which perhaps occurred 12,000 years ago (Haldorsen et al. 2011). Based on archaeological evidence, stem rust existed more than 3300 years ago (Kislev 1982). It is likely that stripe rust also existed that early. Because reports before the late ninenteenth century did not distinguish stripe rust from other rusts (Eriksson and Henning 1896; Chester 1946), many of the early reports of rusts were likely stripe rust or combinations with leaf rust and/or stem rust. The severe rust occurred in Italy in 1766 described by Giovanni Targioni Tozzetti (Tozzetti 1767) as "universal over the whole of Italy, and in all the different levels and exposures of its territory" was most likely stripe rust because "as first appearing, it is a bright yellow, soon becoming orange, and finally after days, becoming black" (Goidanich 1943). According to Eriksson and Henning (1896), stripe rust was first described by Gadd and Bjerkander in Europe in 1777, and the first description and naming of the fungus was done by Schmit before 1819.

In China, the earliest record of stripe rust was in "*Ancient Chinese Agricultural Practices*" (齐民要术), an earliest Chinese book written by JIA Sixie (贾思勰) about 1470 years ago on agriculture, horticulture, husbandry, fishery, winery, food and nutrition. In that book and a late book, "*Agricultural Proverbs*" (马首农谚) in 1836, stripe rust was called "jaundice", like a human disease (黄疸 in Chinese) (Li and Zeng 2002). In the former book, stripe rust was related to spring rainy conditions. In India, stripe rust, together with other rusts, was reported in a scientific journal in 1896 (Cunningham and Prain 1896). In Russia, Yachevski (1909) included stripe rust in his book entitled "Rusts of Grain Crops in Russia", containing information on disease distribution, damage caused, environmental conditions favorable for disease development, disease control, and a list of the important rust fungi in Russia.

In the United States, the first clear recognition of stripe rust was in 1915 in Arizona by F Kolpin Ravn, a visiting scientist from Denmark, who was traveling with a United States Department of Agriculture (USDA) crop survey team in the western US (Carleton 1915). Latter, examination of herbarium specimen collected from various locations in the US found that stripe rust, mostly from grasses, occurred at least as early as 1892 in the western US (Humphrey et al. 1924). It is believed that stripe rust very likely occurred on wheat and grasses in California in the 1770s based on old newspapers reporting rusts and the fact that stripe rust is more prevalent than leaf rust and stem rust in California (Smith 1961; Smith and Bowman 1961; Line 2002). In South America, stripe rust was first discovered by Holway on *Hordeum chilense* in Chile in 1919 and on *Agropyron altenuatum* in Ecuador in 1920 (Arthur 1925). The stripe rust was first observed on wheat in 1929 (Rudorf and Job 1931) and on barley for the first time in 1930 (Hirschhorn 1933) in Argentina.

Since the science of plant pathology emerged in the late 1800s and early 1900s, stripe rust has been intensively studied. The first scientific study on stripe rust was done by Jacob Eriksson in Sweden in the early 1890s (Eriksson 1894). This study separated the species of the stripe rust pathogen into five formae speciales based on specialization on different cereal and grass genera. Although Eriksson studied the cytology of rust fungi, he mistakenly considered haustoria as "corpuscules speciaux", a form in which he thought the rust fungus emerged from an invisible "mycoplasm" stage. His concept of "mycoplasma" was challenged by Harry Marshall Ward, who carefully studied cytology of infection by urediniospores, first with *Puccinia dispersa* on *Bromus* spp. (Ward 1904, 1905) and late extended to wheat infected with *P. glumarum* (*P. striiformis*). He provided an extensive set of clear drawings showing appressoria, penetration pegs, substomatal vesicles, infection hyphae, haustoria at several stages of development, and "runner" hyphae beginning to ramify in host tissue. He also showed the number and location of nuclei for each type of fungal cell (Ward 1904). In his study with wheat stripe rust, he included development on an immune cultivar obtained from Biffen. He described "death changes" in the immune host, nowadays more commonly referred as "hypersensitiveness" termed by Stakman (1915). Resistance responses of nonhost species to several rust fungi, including *P. glumarum*, were described histologically by Ward's student, C. M. Gibson (1904), who showed that the fungi usually were able to enter stomata.

The rediscovery of Mendel's laws of segregation and independent assortment of genes stimulated genetic studies on plant disease resistance in the early twentieth century. Working on stripe rust of wheat, Rowland H. Biffen in Cambridge, United Kingdom, was the first to discover the plant resistance to diseases follows Mendel's laws (Biffen 1905). In his first study, Biffen found that stripe rust resistance was controlled by a recessive gene (Biffen 1905). Later, he found that resistance was independent of other plant traits (Biffen 1907). Biffen's results created doubts about the bridging-host theory of Ward (1903). According to the bridging-host theory, a pathogen could gradually adapt to a resistant host by passing through taxonomically intermediate hosts. Within a few years many more examples of Mendelian inheritance of resistance against cereal rusts were found, which eventually brought the debate to the end and scientists generally accepted the concept that Mendel's genetic principles were applicable to resistance against cereal rusts. Biffen's pioneer work with stripe rust led to control of plant diseases, including stripe rust, through breeding for resistant cultivars (Biffen 1931). Since these early studies, intensive research has been conducted on various aspects of stripe rust in various countries to prevent or reduce damage caused by the devastating disease.

## 1.2    Disease Symptoms and Effects on Host Plants

Stripe rust is also called yellow rust. Both names are descriptive for the disease symptoms and pathogen signs. However, it can sometimes cause confusion when "stripe" and "yellow" are used to diagnose the disease from others at a particular time point. Like other diseases, the disease of stripe rust is a process that takes days to months to the fully diseased stage.

Because the disease symptoms and signs on alternate hosts will be presented in Sect. 3.1.3 on infection process on alternate hosts in Chap. 3, here only symptoms on primary hosts (wheat or barley) are presented, which are similar to those on auxiliary hosts (grasses). The development of disease of stripe rust starts when urediniospores of the stripe rust pathogen germinate and germ tubes grow into host tissues. Although could not be seen with naked eyes, host tissues will start a series of changes which usually need to be observed under a microscope, therefore referred as microscopic symptoms. The histological changes will be described in detail in Sect. 3.2 of Chap. 3. Here, only macroscopic changes that can be observed with naked eyes, referred as macroscopic symptoms, will be discussed.

Under controlled conditions, obvious symptoms will not be seen until 6–7 days after inoculation on wheat leaves. The disease first appears as chlorotic patches that are easier to seen when holding an inoculated leaf against a light especially in the early symptom development. The chlorotic system is like many viral diseases or abiotic stress. Depending upon temperatures, uredinia (commonly referred to sori or pustules appears (the rust pathogen sporulation) from chlorotic areas about 11–14 days after inoculation. Uredinia are tiny, elongated, and yellow to orange in color. A uredinium is a fruiting body of rust fungi, from which thousands of urediniospores

are produced. Soon after formation, uredinia erupt to release urediniospores, which cannot be seen with naked eyes, but in mass are yellow to orange powder, which can be collected by tapping off or vacuuming into a tube. Infected leaves can produce urediniospores for many days until the leaves are dried up, or sucked to die. Uredinia can be produced on any parts of wheat plants, including leaf blades and sheathes, young stems, glumes, awns, and young kernels, but most obviously on leaves. Compared to leaf rust and stem rust, the stripe rust fungus is more likely infect glumes, and therefore, the fungus was previously named as *Puccinia glumarum*, and the disease therefore, could be called glume rust in contrast to leaf rust and stem rust. However, to distinguish the three rusts on cereal crops just by plant parts they infect is not always correct as the three fungal species can infect all plant parts above the ground, especially the stripe rust pathogen.

The three rusts of cereal crops can be easily distinguished by the size, shape, color, and arrangement of uredinia. Typical uredinia of both stripe rust and stem rust are elongated and those of leaf rust are round to ovoid. However, stripe rust uredinia are the smallest (0.3–0.5 × 0.5–1.0 mm), those of stem rust are the largest up to several mm in width and several cm in length, and those of leaf rust are in between (up to 1.5 mm in diameter). Uredinia or urediniospore mass of stripe rust are yellow to orange, those of leaf rust are orange red to brown, and those of stem rust are red to red brown. Because uredinia of stripe rust are tiny, uredinial size does not change very much. In contrast, leaf rust and stem rust can have big variations in uredinial sizes depending upon compatible or incompatible interactions between the pathogen and host. Therefore, both stem rust and leaf rust pathogens can produce uredinia as small as or smaller than stripe rust uredinia. As the common name indicates, stripe rust produces uredinia between leaf veins, and therefore, form stripes on adult-plant leaves. In contrast, uredinia of leaf rust and stem rust are randomly distributed and do not form stripes. However, uredinia of stripe rust on seedling leaves are not arranged in stripes, but in clustered patches. On adult-plant leaves, stripes may not be obvious when the leaf surface covered by uredinia. Because infection by the stripe rust fungus is systemic and one-urediniospore infection can produce many uredinia, its uredinia forms stripes on adult-plant and clustered patches on seedlings. In contrast, infection by the leaf rust or stem rust fungus is not systemic, and one-spore infection typically produces one uredinium. Therefore, uredinia are random as infections are random on plant surface. Because of these, it is easy to see infections of one or few uredinia of leaf rust and stem rust, but it is almost always to see a cluster or clusters of uredinia on seedlings and a stripe or stripes of uredinia of stripe rust. Figure 1.1 shows typical systems and signs in a compatible interaction, in which the pathogen is virulent and wheat plants are susceptible.

When host plants are less susceptible or resistant, various symptoms can occur, ranging from tiny flecks without any uredinia to large necrotic patches with or without uredinia on seedlings, or short to long necrotic stripes (up to several cm in length) on adult-plant leaves. When there are no uredinia associated to necrotic patches, the symptoms caused by stripe rust infection can be easily recognized under controlled conditions after inoculation, but can be hard to distinguish from symptoms caused by genetic, physiological or abiotic stresses; or other pathogens

**Fig. 1.1** Typical stripe rust symptoms and signs on wheat leaves in fields. Note the patch of uredinia on the seedling (**a**) and stripes of uredinia on adult-plant leaves (**b**)

at the seedling stage. Taking healthy and unhealthy plants in the same field, rusted plants in nearby fields can add to correct diagnosis. Correct recognition of such necrotic symptoms caused by the stripe rust pathogen on seedlings is less important as the infected plants do not produce spores for secondary infections and generally no control measures are needed. However, if the problem of necrotic patches is caused by other spot disease pathogens, fungicide application may be needed. Further examination of disease symptoms, pathogen isolation, or molecular diagnosis can be helpful. On adult plants, necrotic stripes caused by the stripe rust pathogen can be more easily distinguished from other problems even without uredinia, as stripe rust stripes are rectangular, pale white, and usually with a distinct margin. Most similar symptoms are caused by cereal leaf beetles. However, stripes appear hollow as leaf tissues are eaten by the insects and only leaving the leaf surfaces, and such stripes almost can be seen through. Plants with stripes caused by leaf beetle damage usually have beetles on leaves.

Necrotic patches or stripes with uredinia are easily recognized to be caused by the stripe rust pathogen, rather than other biotic or abiotic stresses. If individual patches or stripes are distinct from each other, uredinia are usually on the margins. In contrast, single uredinia are surrounded by chlorotic or necrosis for leaf and stem rusts. Various ratios of necrotic vs. uredinial areas reflect the level of incomplete

resistance of the host plants against the stripe rust pathogen. Because this is important for phenotypically studying resistance, the scales to qualify or quantify the reactions and intensities of stripe rust will be presented in Fig. 2.1 in Chap. 2 on variability of the stripe rust pathogen.

The infection of the stripe rust pathogen has various effects on its host plants. Because the pathogen is an obligate biotrophic parasite, its growth and reproduction completely rely on the host plants. The stripe rust fungus gets all water and nutrition from host plants. Except that urediniospores can survive for a limited period of time, the fungal parasite also uses host plant as a shelter for survival. It appears that host plants do not get anything good from the parasite, probably except for infection-triggered defense responses that may prevent or reduce infection by more virulent isolates or other pathogens. In general, the stripe rust fungus is viewed as an invader and damager, and host plants suffer from the pathogen damage.

When the stripe rust fungus is growing within the plant tissue, it obtains water and nutrition, directly from the host. When fighting against pathogen infection, host plants need to relocate energy and related nutritional substances for defense. The reduction of energy, nutrition and water slows down the host growth. Once disease symptoms, such as chlorosis and necrosis are developing, especially when the fungus is sporulating, green leaf surface and tissue are reduced, and as a result, plant photosynthesis is greatly reduced. Macroscopically, stripe rust infection reduces the vigor and height of plants; the number of tillers, heads, and kernels; the weight and quality of seed or grain. Economically, stripe rust reduces yield and quality of grain and forage and adds additional costs for crop management. Agriculturally, because the stripe rust pathogen can cause large-scale disease epidemics, the disease is one of the most important diseases on wheat, barley and some grasses. In some regions of the world, it is the most damaging disease.

## 1.3 The Taxonomy of the Pathogen

The stripe rust pathogen, *Puccinia striiformis* Westend., is one of about 4000 species in the genus *Puccinia*, belonging to the family Pucciniaceae, order Pucciniales, class Pucciniomycete, division Basidiomycota of the Fungi kingdom (Kirk et al. 2008). According to Van der Merwe et al. (2008), *P. striiformis* is most closely related to *P. poae-nemoralis* Otth and then to *P. poarum* Nielsen, *P. graminis* Pers. and the *P. recondita* Dietel & Holw. complex including *P. triticina* Erikss. based on partial beta-tubulin sequences. Both *P. poae-nemoralis* and *P. poarum* cause rusts on grasses of the Poaceae family, but they have barberry (*Berberis* spp.) and coltsfoot (*Tussilago farfara*) as alternate hosts, respectively (Stubbs 1986; Cagaś and Marková 1988). Both *P. graminis* and *P. triticina* are important pathogens causing stem rust and leaf rust on wheat, respectively.

The Latin name of the stripe rust fungal species had gone changes of several times before its current *P. striiformis*. The uredinial form of the stripe rust fungus

was first described as *Uredo glumarum* by Schmidt (1827), probably before 1819 according to Eriksson and Henning (1896). The teleomorph of the fungus was described as *Trichobasis glumarum* by Lév. (1849) in 1848, *Puccinia striaeformis* Westend. by Westendorp in 1854, and later by Eriksson (1894) and Eriksson and Henning (1894) as *Puccinia glumarum* Erikss. in 1894. In 1860, Fuckel named the pathogen *Puccinia straminis* (1860), but whether it was stripe rust or leaf rust is unclear. *P. glumarum* had been mostly used in the literature until the 1950s (Hylander et al. 1953). It was Cummins and Stevenson (1956) who correctly applied the name used by Westendorp, with the orthographic correction to *P. striiformis*. According to Liu and Hambleton (2010), *T. glumarum*, even earlier than *P. striaeformis*, is invalid because the combinations were not formally made based on the International Code of Botanical Nomenclature (McNeill et al. 2006). Since the 1950s, *P. striiformis* has been used as a species of fungi causing stripe rust on cereals and grasses with recent separations of the stripe rust fungi on bluegrass (*Poa pratensis*) and orchard grass (*Dactylis glomerata*) as different species, *Puccinia pseudostriiformis* M. Abbasi, Hedjaroude & M. Scholle and *Puccinia striiformoides* M. Abbasi, Hedjaroude & M. Scholle, respectively (2004; Liu and Hambleton 2010). In addition, Liu and Hambleton (2010) described a new species, *Puccinia gansensis* Liu & Hambleton, from a single sample on *Achnatherum inebrians* (called drunken horse grass in China) from Gansu, China. The separation of these four species were based on some morphological traits, which were inconclusive when used individually but conclusive when used in combination, and partial sequences of the internal transcribed spacer (ITS) region and the beta-tubulin gene (Liu and Hambleton 2010). Because the four species formed a strong monophyletic group distinct from other species within *Puccinia*, Liu and Hambleton (2010) proposed a series, *Puccinia* Series *Striiformis* Liu & Hambleton, to include these species within the genus *Puccinia*. The species in this series are characterized by having serial arrangement of uredinia and telia on stripes, moderately obscure urediniospore germ pores compared to *P. recondita* and *P. hordei* with clearer pores and *P. coronata* with more obscure pores, and telial locules that are most often complete compared to *P. recondita* and *P. coronata* with mostly incomplete locules. In the study by Liu and Hambleton (2010), the species of *P.* Series *Striiformis* were mostly close to *P. poae-nemoralis*, and the next close species was *P. coronata*, followed by *P. graminis*, *P. recondita*, and *P. triticina*, generally in consistent with Van der Merwe et al. (2008). For recognition of stripe rust fungi (*P.* Series *Striiformis*), Liu and Hambleton (2010) pointed out that stripes of uredinia or telia are more conspicuous on wide-leaf hosts and less conspicuous on narrow-leaf hosts, and that some leaf rust fungi on grasses may appear in stripes and have yellow uredinia. The separation of different species within the *P.* Series *Striiformis* and the phylogenetic relationships of these species to others species should be further tested with more samples and rust fungal genes using both morphological and molecular techniques.

## 1.4   Host Range and Formae Speciales

Although rust fungi are generally considered to be highly specialized on their plant hosts, some species can have a wide host range. For a cereal rust species, the major cereal crop is generally referred as the primary host because of the economic importance; wild grasses as auxiliary hosts because of sharing same spore stages with the primary host; and non-grass hosts as alternate hosts because they are infected by a different spore stage. Taking the wheat stripe rust fungus (*P. striiformis* f. sp. *tritici*) for example, wheat is the primary hosts; barley and various grasses in the Gramineae family are auxiliary hosts; and barberry (*Berberis* spp.) and mahonia (*Mahonia* spp.) of the Berberidaceae family in the order of Ranunculales are alternate hosts. The various spore stages produced on primary/auxiliary and alternate hosts will be presented in Sect. 3.1.1 of Chap. 3. Here, the focus is on the auxiliary host range of the wheat stripe rust fungus.

Host range of a pathogen is directly related to the crop disease epidemiology and control. Important issues need to be determined, such as how wide the host range is, whether auxiliary hosts are the primary or secondary sources of pathogen inoculum, and how important auxiliary hosts are in pathogen survival and diversity. The determination of host range and at least partially addressing of some of the above issues were done by artificially inoculating typical wheat or barley stripe rust isolates on various grasses and isolates from grasses to cereals under controlled conditions, and/or visually observing rusts on plants of grasses under natural infections. Most studies on the host range of the wheat stripe rust fungus were conducted from the late 1890s and the 1960s.

In North America, scientists paid attention to stripe rust on grasses immediately after wheat stripe rust was discovered in 1915. In the same month (May 1915), AG Johnson observed stripe rust on *Hordeum murinum* near Tehachapi, California (Humphrey et al. 1924). In the same year, stripe rust was found widespread in the western US on *Bromus marginatus*, *Elymus canadensis* and *H. murinum* (Carleton 1915). Hungerford (1923) and Hungerford and Owens (1923) inoculated grasses and cereals to determine the host range of the stripe rust pathogen and made observations in the field. Stripe rust was found on wheat in almost all western states, on barley in eastern Washington and Oregon, central California, and western South Dakota; on rye in northern Idaho, western Oregon and eastern Washington, and on *H. murinum* in California. Stripe rust collections from the US Pacific Northwest infected wheat and 59 grass species. Collections from wheat infected wheat, barley, rye and 48 grass species while collections from 12 other grass species did not infected wheat. These studies indicate that wheat stripe rust has a broad range of hosts and not all stripe rust collections were able to infect wheat. Based on these results, Hungerford and Owens (1923) separate the *P. striiformis* species into varieties and use *P. glumarum* var. *tritici* for the collections able to infect wheat. Hungerford also found that *B. marginatus*, *E. canadensis*, *E. glaucus*, *H. nodosum*, and *H. jubatum* harbored dormant mycelium of the pathogen at low elevations in Oregon (Hungerford 1923). In the studies of Humphrey et al. (1924), stripe rust was

found occurring naturally on 34 grass species plus barley, rye and emmer, spelt and common wheat. In that publication, they listed the hosts of the stripe rust fungus in both Europe and North America, and specifically noted that stripe rust occurred on *Dactylis glomerata* in Europe but not in North America. Stripe rust on *D. glomerata* was not reported in the US until the 1960s (Tollenaar 1967).

During the late 1910s–1930s, Canadian scientists also reported stripe rust on grasses in addition to wheat. Fraser found stripe rust on *H. jubatum* near Edmonton in 1918, and later the disease was observed on grasses and wheat in Alberta from Edmonton to the southern border with the US, British Columbia and Saskatchewan (Fraser and Conners 1925; Johnson and Newton 1928; Sanford and Broadfoot 1929; Newton and Johnson 1936). The host range included *Agropyron*, *Elymus* and *Hordeum* species of grasses as well as wheat and barley (Newton and Johnson 1936). The disease was found most common on the native grass species. Collections from *H. jubatum* infected wheat and *Agropyron* species.

More species were added to the list of the host range for the stripe rust pathogen in the 1960s. In the US 126 species of grasses in 20 genera were susceptible to wheat stripe rust (Line 2002). The most important genera were *Aegilops*, *Agropyron*, *Bromus*, *Elymus*, *Hordeum*, *Secale* and *Triticum*. Based on collections of 40 years in California, Tollenaar and Houston (1966) pointed out that stripe rust occurred on grasses in the San Francisco area, the coastal mountains and valleys from San Francisco to the Oregon border, and the Sierra Nevadas mountain range. They found stripe rust on wild *Hordeum*, *Elymus* and *Sitanion* species in the Sierra Nevadas at high altitudes during the summer, and logically concluded that winds could carry the urediniospores from grasses in the mountains to the fall-planted wheat fields in the valleys. In the state of Washington, Hendrix and associates did intensive studies on stripe rust on grasses and how grass stripe rust is related to epidemics on wheat. Hendrix et al. (1965) found stripe rust on grass species *Agropyron bakeri*, *A. reparium*, *A. spicatum* (now known as *Pseudoroegneria spicata*), *Bromus carinatus*, *B. pumpellianus*, *B. sitchensis*, *B. marginatus*, *Hordeum jubatum*, *Sitanion hystrix* and *Poa nemoralis* in the mountains surrounding the Columbia Basin of the Pacific Northwest. They concluded that stripe rust on grasses at high elevations was probably a source of inoculum for the wheat at the low elevations. In contrast, Shaner and Powelson (1971, 1973) believed that grasses were not very important as sources of stripe rust on wheat in Oregon based on their epidemiological studies from 1961 to 1968. Similarly, Sharp and Hehn (1963) concluded that grasses were not an important source of stripe rust of wheat in a study of the fungal survival on winter wheat in Montana.

Dietz and Hendrix (1962) inoculated randomly selected 948 grass lines with a wheat stripe rust isolate in a greenhouse at Pullman, Washington. They observed stripe rust on 372 lines representing 105 species in 16 genera. Tu (1967) selected susceptible grasses reported by Dietz and Hendrix (1962) and studied the behavior of stripe rust on grasses during the summer. Selected grasses were artificially inoculated in a greenhouse and transplanted to the field during the summers of 1963 and 1964 at Pullman, Washington. Continuous sporulation was observed throughout the summer on *Agropyron caespitosum*, *A. trachycaulum, B. marginatus* and *E. glaucus*.

Sporulation occurred in early and late summer but with a dormant period near mid-summer on *Agropyron brachyphyllum*, *A. caespitosum*, *A. cristatum*, *A. dasystachyum*, *A. intermedium*, *A. spicatum*, *A. sussecundum*, *A. trichophorum*, *Bromus carinatus*, *B. scoparius*, *Elymus crinitus*, *Festuca arundinacea*, *F. rubra*, *Hesperochloa kingie* and *Hordeum bulbosum*. Sporulation was observed on *Alopecurus arundinaceus* and *Hesperochloa kingie* in early summer but the fungus succumbed with the advent of hot weather.

In Europe, stripe rust oversummering was reported on *Agropyron caninum* and *A. repens* at high elevations in Germany (Becker and Hart 1939), but grasses are considered not important in northwestern Europe (Zadoks 1961). As stripe rust was introduced to Australia in late 1970s, studies on host range were conducted in the early 1980s. Holmes and Dennis (1985) found successful infection after inoculating wheat from Australia with urediniospores collected from *Bromus mollis*, *B. unioloides*, *Hordeum hystrix*, *H. leporinum*, *H. marinum*, *H. vulgare*, *Phalaris minor*, *P. paradoxa* and *Triticosecale* (Triticale). It is not clear if these grass species are important for wheat stripe rust epidemics. Natural infection of stripe rust occurs on wild barley grasses in Australia, but the rust pathogen is considered as a different forma specialis (Wellings et al. 2000; Wellings 2011).

Based on Gerechter-Amitai's unpublished data, Wahl et al. (1984) indicated that stripe rust appears sporadically on wheat cultivars and wild grasses belonging to *Triticum dicoccoides*, *Aegilops*, *Hordeum*, and other genera in Israel. Some isolates of the fungus have a host range of over 40 species in 17 genera. The stripe rust isolates from *Ae. kotschyi* and *H. spontaneum* in the arid southern region with average annual rainfall below 100 mm were virulent on wheat.

In China, Prof. Lee Ling in 1945 reported that stripe rust commonly occurred on *Roegneria ciliaris* in the Chengdu Plain and surrounding maintains in the province of Sichuan, but the stripe rust on the grass occurred relatively late, adapted to a relatively high range of temperatures, and relatively low virulent on wheat compared to wheat stripe rust (Li and Zeng 2002). Since then, Chinese scientists found a large number of grass species can be infected by stripe rust. They used the following three criteria to determine grass hosts for wheat stripe rust. First, plants of a species have stripe rust under natural conditions either in cultivated fields or of wildly growing, and the stripe rust isolates from the plants should be able to infect and produce uredinia on common wheat cultivars that are susceptible to wheat stripe rust under artificially inoculation conditions. Second, grass plants in production or experimental fields are infected by stripe rust, and the rust isolates can infect and produce uredinia on common wheat cultivars that are susceptible to wheat stripe rust under artificial inoculation conditions. Third, plants of a grass species can be infected and have uredinia after artificially inoculated with isolates of the wheat stripe rust fungus. A species meets one of the criteria is considered as a host for the wheat stripe rust pathogen. Based on these criteria, a total of 88 species in 16 genera, all in the Poaceae (also called Gramineae) family have been identified as hosts of the wheat stripe rust pathogen (Li and Zeng 2002). The 16 genera are *Aegilops* (23 species), *Agropyron* (8 species), *Aneueolepidum* (2 species), *Bromus* (2 species), *Elymus* (8 species), *Elytrigia* (3 species), *Glyceria* (1 species), *Hordeum* (7 species), *Hystrix* (1

species), *Psathyrostachys* (1 species), *Puccinellia* (1 species), *Roegneria* (12 species), *Secale* (6 species), *Taeniatherm* (1 species), *Thinopyrum* (1 species) and *Triticum* (11 species).

Although Liu and Hambleton (2010) questioned that the early reported stripe rust on some grasses might be other rust species, it is no doubt that the wheat stripe rust pathogen can infect a great large number of grass species. Grass species have different strains or ecotypes that may vary in reaction to stripe rust infection. For example, Dugan et al. (2014) reported lines of basin wild rye (*Leymus cinereus*) either resistant or susceptible to wheat stripe rust. It is almost impossible to include all strains or ecotypes of a grass species in an artificial inoculation study for reactions to stripe rust. Also, the studies of host range for stripe rust have been primarily concentrated in Europe, North America, Israel, China, and Australia. Studies in much of other stripe rust occurring regions in the world have been scarce. More species could be identified as auxiliary hosts of the stripe rust fungus of the cereal species or different stripe rust species.

Not all reported species are equally susceptible to stripe rust. Many of them should be considered opportunistic hosts as they are not sporulating hosts under normal conditions, but can be infected by stripe rust fungus and producing uredinia when weather conditions are extremely favorable for the disease and the inoculum level is extremely high. Because of this reason, stripe rust is more commonly observed on grasses when the disease is severe on cereal crops. So far, no report of stripe rust has been reported on common oat (*Avena sativa*) or wild *Avena* spp. However, the author observed infection of stripe rust on volunteer oat plants near an experimental wheat fields at Pullman, Washington, the USA in 2005 when the weather conditions were extremely favorable for the disease. Even though the reaction of large necrotic stripes with only few uredinia is considered resistant, recovered urediniospores were identified as a typical stripe rust race of *P. striiformis* f. sp. *tritici* in the experimental wheat field. Similarly, rice (*Oryzea sativa*) is a non-host for stripe rust, and no macroscopic symptoms can be observed and cell death of small host tissue can be observed microscopically after inoculated with the stripe rust fungus (Kang and associates, unpublished data). In some rice mutants, the stripe rust fungus is able to form relatively large mat of infectious hyphae and haustoria. On the other hand, some grasses can be even more susceptible than susceptible wheat cultivars. The author observed that stripe rust develops earlier and faster on goat grass plants (*Aegilops cylindrica*) than susceptible wheat lines. To let rust develop fast in experimental fields, goat grass plants are often left from weeding. For example, Fig. 1.2 shows severe stripe rust on goat grass plants in a wheat field. Between host and non-host, cereal and grass species have a relatively continuous variation in their ability to interact with the stripe rust fungus. The variability within the stripe rust fungal species at the cultivar level of a host species (such as wheat or barley), reflected by different races or pathotypes, will be discussed in Sect. 2.1.4 of Chap. 2 on pathogen variability. Here, variability within a fungal species at the host genera level, reflected by formae speciales, will be discussed below.

The concept of formae speciales was first proposed by Eriksson (1894) according to specificity on host genera or species. Based on cross-inoculation tests, he

**Fig. 1.2** Stripe rust on goat grass plants (*Aegilops cylindrica*) in a field of wheat without rust

reported five formae speciales within the species of *P. glumarum* (now *P. striiformis*), namely *P. striiformis* f. sp. *tritici* on wheat, f. sp. *hordei* on barley, f. sp. *secales* on rye, f. sp. *elymi* on *Elymus* spp. and f. sp. *agropyron* on *Aropyron* spp. (Eriksson 1894). Latter, four more formae speciales were reported: *P. striiformis* f. sp. *dactylidis* on orchard grass (*Dactylis glomerata*) (Manners 1960; Tollenaar 1967; Zadoks 1961); *P. striiformis* f. sp. *poae* on Kentucky bluegrass (*Poa pratensis*) (Britton and Cummins 1956; Murdoch et al. 1973; Tollenaar 1967; Tollenaar and Houston 1967); and *P. striiformis* f. sp. *leymi* on *Leymus secalinus* (Niu et al. 1991). More recently, the stripe rust fungus infecting barley grass *Hordeum* spp. in Australia was named as *P. striiformis* f. sp. *pseudo-hordei* (Wellings et al. 2000; Wellings 2011). Thus, a total of nine formae speciales of *P. striiformis* have been reported (Table 1.1). Worldwide, most important genera are *Aegilops*, *Agropyron*, *Bromus*, *Elymus*, *Hordeum*, *Leymus* and *Triticum*, and in China, *Roegneria* appears to be an important genus for wheat stripe rust.

The separation of formae speciales based on host specificity is a plant pathological concept. Because they are not taxonomic taxa, formae speciales are not governed by the International Code of Botanic Nomenclature (McNeill et al. 2006). Some of the above mentioned formae speciales have morphological and/or physiological differences. Because of smaller urediniospores than the stripe rust fungus on wheat, the stripe rust fungus on orchard grass was considered by Manners (1960) as a variety, a mycological taxon below species. The stripe rust fungus on bluegrass

**Table 1.1** Formae speciales reported for *Puccinia striiformis*

| *P. striiformis* f. sp. | Hosts | References |
|---|---|---|
| *tritici* | Primarily wheat; some barley and rye varieties; and various grass species | Eriksson (1894) |
| *hordei* | Primarily barley; some wheat varieties; and various grass species | Eriksson (1894) |
| *secales* | Primarily rye | Eriksson (1894) |
| *elymi* | *Elymus* spp. | Eriksson (1894) |
| *agropyron* | *Agropyron* spp. | Eriksson (1894) |
| *dactylidis*[a] | *Dactylis glomerata* | Manners (1960) |
| *poae*[a] | *Poa* spp. | Tollenaar (1967) |
| *leymi* | *Leymus secalinus* | Niu et al. (1991) |
| *pseudo-hordei* | Primarily wild barley (*Hordeum* spp.) and some barley varieties | Wellings (2011) |

[a]Abbasi et al. (2004) named the stripe rust fungus on orchard grass (*D. glomerata*) as species *P. striiformoides* and that on bluegrass (*P. pratensis*) as *P. pseudostriiformis*. The naming of species was supported by some morphological characteristics and partial sequence data of the ITS and beta-tubulin genes

was considered as a forma specialis of *P. striiformis* because no obvious morphological differences were found (Tollenaar 1967). Chen et al. (1995) was the first to use both virulence and molecular markers to separate some of the formae speciales. By cross-inoculation, they find that isolates of bluegrass stripe rust only infected bluegrass isolates, but not any of the tested wheat, barley, and rye accessions, while wheat stripe rust isolates infected mostly wheat accessions, but some barley accessions and similarly barley stripe rust isolates infected mostly barley accession and few wheat accessions. Random amplified polymorphism DNA (RAPD) markers clearly separate isolates of wheat, barley and bluegrass into three groups with wheat stripe rust and barley stripe rust more closely related to each other than to bluegrass stripe rust. Compared to other rust species, *P. graminis*, *P. triticina* and *P. hordei*, the three formae speciales of the stripe rust fungus were more closely related. More recently, as mentioned in Sect. 1.3 above, the stripe rust fungi on bluegrass and orchard grass were recently promoted to different species within Series *P. Striiformis* based on combination of several morphological characteristics and partial sequences of ITS and beta-tubulin. Using SSR markers, Cheng et al. (2014) also found that the stripe rust fungi on bluegrass and orchard grass were much more different from the wheat or barley stripe rust pathogens. Such separations of either formae speciales or species are supported by molecular, morphological and pathogenic data.

However, separations of other *P. striiformis* formae speciales are either still remaining controversial and/or lack of studies. Overlapping host range has been the major reason for the debate whether some of the above mentioned formae speciales may not be consider as separate formae speciales from others, especially between *P. striiformis* f. sp. *tritici* and *P. striiformis* f. sp. *hordei* (Sydow and Sydow 1904; Straib 1935; Newton and Johnson 1936; Fang 1944). In contrast, Zadoks (1961) and

Stubbs (1985) considered the wheat and barley stripe rust fungi as two different formae speciales based on greenhouse and field data. The separation of *P. striiformis* f. sp. *tritici* and f. sp. *hordei* was supported by isozyme variation and RAPD markers (Chen et al. 1995). Simple sequence repeat (SSR) markers also separate isolates of *P. striiformis* f. sp. *tritici* and *P. striiformis* f. sp. *hordei* as two distinct groups (Cheng and Chen 2014). In the US, barley stripe rust (*P. striiformis* f. sp. *hordei*) was introduced in 1991 (Roelfs et al. 1992; Chen et al. 1995). Before the introduction, wheat stripe rust (*P. striiformis* f. sp. *tritici*) had been occasionally found on barley plants but never caused significant damage, but after 1991, barley stripe rust have caused significant yield losses in the western US (Chen et al. 1995; Chen 2004). In the recent years, epidemics caused severe damage on wheat crops when weather conditions were favorable to stripe rust, but in contrast stripe rust on barley were not significant although major barley cultivars were more susceptible to barley stripe rust than major wheat cultivars to wheat stripe rust, and fields of barley and wheat were next to each other. The differences are due to different levels of pathogen inoculum resulted from different cropping systems, regions and acreages in the US Pacific Northwest, as both winter and spring wheat crops are gown in continuous large acreages and mainly just spring barley is grown in much smaller acreages (Chen 2005; Wan and Chen 2012). The field situations clearly show that stripe rust of wheat and stripe rust of barley are two distinct diseases. The separation of the diseases and distinction of the pathogens as different formae speciales are useful for the management of the diseases and also for setting different systems to identify races within each of the formae speciales.

The separation of other formae speciales, namely *P. striiformis* f. sp. *secales*, f. sp. *elymi*, f. sp. *agropyron* and f. sp. *leymi* does not have adequate data. As Stubbs (1985) pointed out, for rye stripe rust, there are no data to support the use of f. sp. *secalis* because rye can be infected by both the wheat and barley form. Worldwide, there have been no many studies or reports of stripe rust of rye since the 1970s, which may correlated with the substantial decrease in rye growing areas. In 1986, 24 million hectares of rye were harvested; but in 1996, only 17 million hectares harvest (Bushuk 2001). About 80% of the rye production is concentrated in few European countries, such as Germany, Poland and Russia. In the US, rye acreage has continually decreased, from 1,154,251 ha in 1941 to 255,466 ha in 1971 and 97,976 ha in 2011 (http://www.nass.usda.gov/Data_and_Statistics/). Rye is mainly grown in the eastern US, and no much rye is grown in the stripe rust more frequently occurring western US. Wildly grown rye plants are widespread in some southern Washington and northern Oregon along roads and hill foots, the author has never seen stripe rust on such rye plants even in the years like 2003, 2005, 2010 and 2011 when stripe rust was severe in wheat fields and the predominant races were all virulent to *Yr9*, a stripe rust resistance gene from rye. In 2004, two stripe rust samples collected from rye plants grown in a germplasm nursery near Corvallis, Oregon was identified as race PST-21, the least virulent race of *P. striiformis* f. sp. *tritici* based on the tests with the wheat cultivar differentials (Chen et al. 2010). In 2010, two samples from rye plants in an experimental field in California were identified as PSTv-36, a typical race identified in wheat fields (Wan and Chen 2014). Samples

from Triticale varieties were identified as *P. striiformis* f. sp. *tritici* races predominant in wheat fields. These observations indicate that stripe rust on rye is either of the same *tritici* forma specialis or the true secales forma specialis reported by Eriksson (1894) and Eriksson and Henning (1896) in Europe does not exist in the US. Hovmøller et al. (2011) reported a new *P. striiformis* race, which became widespread in Denmark and Sweden in 2008 and 2009 and was frequently sampled from cultivated triticale (x Triticosecale). In addition to triticale, the race could also infect several cultivars of spring wheat, barley and rye. The crossing genera host range is common. In the US, stripe rust samples collected from grass species, mainly of genera *Aegilops*, *Agropyron*, *Hordeum*, *Bromus*, *Elymus* and *Leymus*, were mostly identified as *P. striiformis* f. sp. *tritici* and sometimes as *P. striiformis* f. sp. *hordei* races, mostly predominant in wheat or barley fields and sometimes as least virulent races unable to infect wheat cultivars grown in fields. Like barley can be mainly infected by *P. striiformis* f. sp. *hordei* and occasionally infected by *P. striiformis* f. sp. *tritici*, it is possible that some of the grass species may have their mostly adapted formae speciales and also can be sometime infected by less adapted formae speciales. Not all formae speciales exist in the regions where grasses are either native or introduced.

Stripe rust on grasses can contribute to the disease on cereal crops in several ways. (1) Urediniospores from grasses may initiate epidemics on cereal crops. As speculated by Tollenaar and Houston (1967), stripe rust on the high elevations of the Sierra Nevada may initiate the disease on wheat in the fall in the valleys in California. This speculation is challenged by the fact that stripe rust can survive summer in the Sacramento Valley of California on wheat plants grown as cover crops in irrigated orchards (Line 1976). Although it may not be always the case for stripe rust from grasses to initiate the disease on cereal crops, this is possible in some years or some regions in the world. As discussed above, super susceptible grasses, like *Ae. cylindrical*, may provide spores to infect wheat plants in the same field or adjacent fields. (2) Urediniospores from grasses add to the inoculum pressure. When races are able to infect cereal cultivars grown in the region, spores produced on grasses during the disease season definitely increase inoculum load to cereal fields, speeding up the disease development and causing more damage. (3) Grasses may serve as green bridges for the pathogen survival. Susceptible grasses add more possibilities for the stripe rust fungus to survive the hot or cold periods. The role of providing host tissue for the pathogen to survive varies among grass species. As discussed above, when inoculated with wheat stripe rust, some grass species (such as *Elymus glaucus* and *Bromus marginatus*) showed continuous sporulation throughout the summer (Tu 1967). some grasses (such as *Agropyron trichophorum* and *Bromus carinatus*) had sporulation in early and late summer but with a dormant period near mid-summer and some other grass species (such as *Alopecurus arundinaceus* and *Hesperochloa kingie*) had sporulation in early summer but the fungus succumbed with the advent of hot weather (Tu 1967). (4) Grasses provide reservoirs for the stripe rust fungus to maintain diversity and keep mutants. In regions where stripe rust of cereal crops is a production problem, resistant cultivars are grown. Even cultivars that are susceptible to races occurring on wheat crops often have resistance against previous

races or new mutants unable to reproduce on wheat cultivars. These races or variants may be able to grown on grasses. As discussed earlier, least virulent races are often collected from grasses. The diverse populations on grasses that may provide new virulent races able to attack cereal cultivars may come from grasses. As previous studies with stripe rust on grasses only deal with very few represent isolates, stripe rust populations on grasses have not been adequately studied. (5) Grasses provide common hosts for somatic hybridization between different formae speciales or isolates. In a recent study using virulence tests, Cheng et al. (2014) found that isolates from grasses, especially wild barley grasses, were able to infect both wheat and barley cultivars. Using SSR markers, these grass isolates were found to be hybrids between wheat and barley isolates.

From the evolutionary standpoint, long before cereals came into existence, stripe rust may have existed on grasses and the rust has become adapted on cereals since crops are grown. Understanding the rust evolution on grasses will help us to understand the mechanisms of the pathogen variation. Based on research results so far for the stripe rust pathogen, it is no doubt that grasses as auxiliary hosts play more roles to the diseases of stripe rust on wheat and barley and the variations of the pathogens than the alternate hosts of *Berberis* spp. and *Mahonia* spp. As grasses are a rich source of resistance, understanding the various interactions among the stripe rust pathogen and its primary and auxiliary hosts will lead to more efficient exploration and utilization of resistance genes from grasses into cereal crops.

## 1.5    Distribution and Impact of the Disease

### 1.5.1    Wheat Stripe Rust

Through checking the literature before 2005, this author found that wheat stripe rust was reported in more than 60 countries (Chen 2005). By conducting an international survey, Wellings (2011) compiled a list and map showing that stripe rust occurred also in more than 60 countries in 2000–2009. Although stripe rust varies in frequency of occurrence and significance of damage, almost every country with significant production of wheat has stripe rust as a problem. Based on the survey, wheat stripe rust epidemics can be widespread in all wheat producing areas, very frequent (in 2 or more out of 5 years), and cause 5–10% yield losses in Australia, New Zealand, China, India, Nepal, Pakistan, Uzbekistan, Yemen, Ethiopia, Kenya, the United Kindom, Chile, Peru, Ecuador, Colombia, Mexico and the US (Fig. 1.3).

Because stripe rust can infect wheat plants starting from one-leaf stage throughout the plant growth season, the disease is able to cause 100% yield loss on highly susceptible wheat cultivars. More than 90% yield loss was evident on a susceptible check in an experimental field near Pullman, Washington, the USA in 2011 (Chen 2014). Worldwide, many devastating wheat stripe rust epidemics have been recorded in the literature.
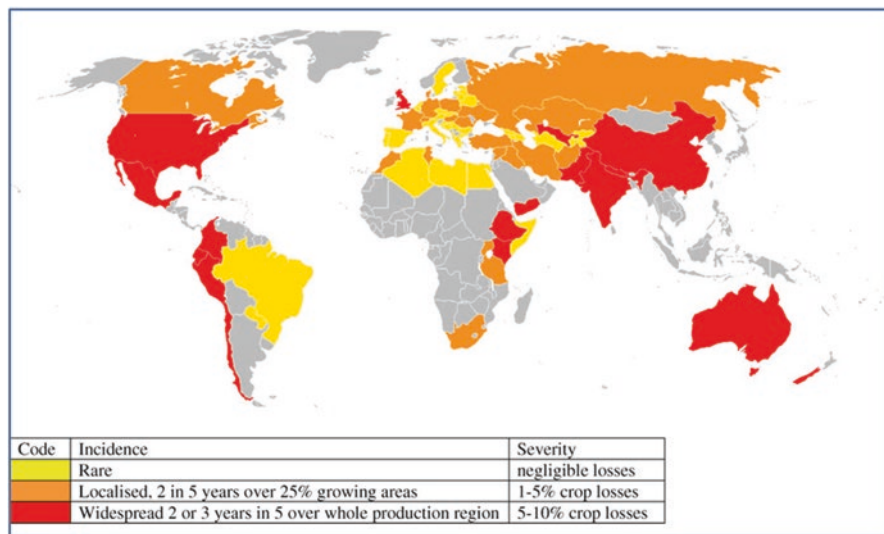
**Fig. 1.3** Wheat stripe rust (*Puccinia striiformis* f. sp. *tritici*) in wheat producing nations for the period 2000–2009

In East Asia, stripe rust has been reported in China, Korea and Japan (Stubbs 1985), but there are not many studies on stripe rust in Korea and Japan. In 2011, the author heard from a colleague of Korea origin that significant wheat rust occurred in South Korea, but it is not clear if the rust was stripe rust. Stripe rust is one of the most important diseases, if not the most important, of wheat in China. The disease is a potential problem throughout wheat growing regions of the country except the far northeast spring wheat growing region. The disease is more frequent and severe in the northwestern and southwestern regions, and often damages the major wheat growing regions along the Yellow and Huai river regions. The 1939–1940 epidemics of stripe rust in Fujian and Sichuan provinces caused 10–15% and 60% of wheat yield losses, respectively (Li and Zeng 2002). In central Shaanxi, severe wheat stripe rust epidemics occurred in 1942, 1946, 1948 and 1949. In the 1950s and 60s, countrywide epidemics occurred in 1950, 1956, 1958, 1960, 1962 and 1964, affecting 222,000–888,667 ha. The extremely widespread epidemics in 1950 and 1964 caused wheat yield losses of 6.0–3.2 million tons, respectively (Li and Zeng 2000). From 1972 to 1983, moderate and severe stripe rust epidemics occurred in 9 out of the 12 years. The 1975 epidemic spread from the northwest and southwest provinces to the east coast, affecting 285,000 ha and causing yield loss of 1.0 million tons. The epidemic in 1990 affected 652,330 ha and caused yield loss of 1.83 million tons (Li and Zeng 2002). In 2002, stripe rust occurred on 6.6 million ha in 11 provinces, and the epidemic caused 1.31 million tons of yield loss and fungicide application on 6.2 million ha (Wan et al. 2004).

In South Asia, stripe rust of wheat is important in the northern areas of India, Pakistan, and Nepal, in southeast Afghanistan, and at the higher elevations in the south (Saari and Prescott 1985). Severe epidemics have occurred about once in every 10 years. Losses of 100% can occur in fields of susceptible cultivars. In the Indian subcontinent, stripe rust oversummers throughout the Himalaya, Hindukush and Sulaiman mountain ranges and in the northwestern Frontier Province, but the largest amounts are in the mountains and valleys of Indus and its tributaries (Nagarajan and Joshi 1985). The disease occurs along the foothills of Himalaya in Jammu and Kashmir, Punjab, Haryana, Himachal Pradesh, and western Uttar Pradesh in early January. In India, primary infections occur near Jammu, Gurdaspur, Pathankot, Ropar, and Jagadhari, where the Tawi, Ravi, Beas, Satluj, and Jamuna rivers enter the plains, respectively. Urediniospores are spread by katabatic wind to the foothills. From such secondary foci, disease spreads gradually during February into the adjoining plains. In Nepal, wheat stripe rust is a dominant disease in the hilly areas, sometimes with losses of 100% (Karki 1980). In Pakistan, wheat is grown in about 8 million ha and stripe rust can attack 70% of the wheat acreage (Anonymous 2006; Aquino et al. 2002). Stripe rust is important in the foothills in the north and also occurs in the central regions and western upland areas (Hassan 1968). The disease is a more serious problem in the Northwest of Pakistan (Chatrath et al. 2007). Since 1948, 13 epidemics have occurred, of which the severe epidemics in 1978, 1997, 1998 and 2005 resulted in losses of 244, 33 and 100 million US dollars, respectively (Hafiz 1986; Duveiller et al. 2007). In Afghanistan, stripe rust is the most important rust disease in wheat, with losses up to 90% in epidemic years (Ghaffor 1970). In Southeast Asia, stripe rust occurs in Bangladesh and Burma, but has not been reported in Thailand, Cambodia, Laos, Vietnam, Sri Lanka, Singapore, Malaysia, Indonesia and the Philippines.

In Central and West Asia, stripe rust of wheat is the most important rust disease especially in Tajikistan, Kyrgyzstan, Kazakhstan, Uzbekistan, Azerbaijan, Iran, Iraq, Syria and Turkey. In Lebanon, Jordan, Israel, Saudi Arabia, Yemen Arab Republic, and Yemen Peoples Democratic Republic, stripe rust regularly appears on wheat and/or barley and can become serious (Stubbs 1985). The most recent epidemic occurred in 2010 throughout Central and West Asia. The 2010 epidemic caused wheat yield loss between 20 and 70% in various countries (http://www.icarda.org/striperust2014/wp-content/uploads/2014/01/Strategies_to_reduce.pdf). The epidemic was so devastating on major wheat cultivars that Syria made an unusual request of help from the US for stripe rust resistant wheat germplasm in that year. In Turkey, stripe rust caused wheat yield losses of 26.5% in 1992, 1.2 million tons (568 million $US) in 1996 and 10 million $US in 2010 (http://www.slideshare.net/bgri/2013-bgrisession31solh). In Iran, stripe rust is important in all wheat-growing regions, particularly along the Caspian Sea where epidemics occur once every 3–4 years (Niemann et al. 1968; Khazra and Bamdadian 1974). Wheat yield loss caused by stripe rust was estimated as 2.5 million tons ($258 million $US) in 1992–1994; in 2007 and 2009, 2 million ha were infected; and in 2010, 650,000 ha were sprayed with fungicides to control stripe rust (http://www.slideshare.net/bgri/2013-bgrisession31solh). In Iraq, stripe rust is a serious wheat disease in the

mountainous area in Kurdistan (Stubbs 1985). In Uzbekistan, stripe rust epidemics caused 35% yield loss (worthy 135 million $US) in 1998 and 30% yield loss in 2010.

In Europe, stripe rust epidemics have been reported in varying frequencies in all wheat-growing countries (Hassebrauk 1965; Stubbs 1985; Zadoks and Bouwman 1985). A well-known subarea with a high risk of epidemics comprises the countries of northwest Europe, namely, England, the Netherlands, Belgium, northern France, and northern Germany (Stubbs 1985). Priestley and Bayles (1988) estimated losses in susceptible winter wheats due to stripe rust and leaf rust as £83 million in the United Kingdom in the 1980s. In Italy, stripe rust does not develop to a damage level, but widespread and severe stripe rust occurred on wheat throughout the wheat growing areas in the country in 2014 (M. Maccaferri, personal communication). In eastern Europe, stripe rust sometimes causes significant damage in Poland, Czech Republic, Hungary, Ukraine and Russia. In Russia, stripe rust is one of the major diseases of wheat in the North Caucasus region and its importance has increased in the recent years (S. Sanin, personal communication).

In Africa, stripe rust is a major disease in Ethiopia and Kenya in the east, Morocco and Tunisia in the north, and South Africa in the south. Epidemics sometimes occur and cause damage in Egypt (Mohamed 1963; Abdel-Hak et al. 1972). The disease occasionally occurs in Uganda, Tanzania, Zambia, Malawi and Madagascar (Stubbs 1985). In East Africa, stripe rust infecting wheat and barley in the highlands is a serious problem, particularly in Ethiopia (Wodageneh 1974; Ciccarone 1947) and in Kenya (Martens and Oggema 1972). In Ethiopia, a stripe rust epidemic in wheat occurred in 1983 (Stubbs 1985), and the epidemic in 2010 caused 67–100% yield loss on commercial wheat cultivars (ICARDA 2011). In South Africa, stripe rust of wheat was first reported in 1996 (Pretorius et al. 1997). Since the initial detection in Western Cape, the disease has spread to all wheat growing regions in the country. The 1996 widespread epidemic provided the foothold for stripe rust in South Africa, resulting in epidemics in the central and western Free State in 1997, the eastern Free State in 1998 and all summer rainfall wheat growing areas in 2002. Based on farm and experimental data, stripe rust can reduce yield by more than 50% and hectolitre mass by 14%. The 1998 epidemic on ca. 42,000 ha winter wheat in the eastern Free State resulted in losses of ZAR 12 million (Pretorius 2004).

In Australiasia, stripe rust of wheat was first detected in Victoria, Australia in 1979 and spread to New Zealand in 1980 ((O'Brien et al. 1980; Beresford 1982). Stripe rust is able to cause yield loss of up to 84% in susceptible cultivars (Murray et al. 1995). Severe epidemics occurred in Australia between 1983 and 1984. In 1983, $A8 million was used for chemical application to control the stripe rust epidemic (Wellings and Luig 1984). The disease was restricted in eastern Australia until 2002 when it was first detected and developed quickly in western Australia. During the severe 2003 epidemic in eastern Australia, fungicide control cost in 2003 was estimated in excess of $A40 million (Wellings and Kandel 2004). Brennan and Murray (1988) estimated the potential national cost in susceptible cultivars as $A168 million annually, and control strategies primarily with resistant cultivars at a value of $A139 million. In New Zealand, yield losses in susceptible cultivars are as high as 60% (Beresford 1982).

In South America, stripe rust was first discovered by Holway on *H. chilense* in Chile in 1919 and 1 year later on *A. altenuatum* in Ecuador (Arthur 1925). The disease on wheat was first observed in Argentina in 1929 (Rudorf and Job 1931). In 1930, stripe rust was also observed on barley for the first time (Hirschhorn 1933), but the stripe rust infections on barley as mentioned in literature may have been caused by the form attacking wheat until 1975, when the form specifically infecting barley was found in Colombia (Stubbs 1985). In the Andean zone and in central Chile, stripe rust is a major disease on wheat. In Argentina, Uruguay, and, to a much lesser extent, in Brazil and Paraguay, stripe rust appears regularly in wheat but seldom reaches epidemic levels (Grillo 1937; Marchionatto 1931; Stubbs et al. 1974).

In North America, stripe rust is a major disease of wheat in Mexico and the US, and a less frequent problem in Canada. In Mexico, wheat is grown annually on about 586,000 ha (Huerta-Espino and Singh 2000), mainly under irrigation in the northwest state of Sonora and in the El Bajio region, both lowland areas (http://www.siap.sagarpa.gob.mx). Yield losses of 60% have been recorded in common wheat crops in those areas. In the US, stripe rust was found in states west of the Rocky Mountains, often referred as western US when discuss stripe rust distributions (Line 2002; Chen 2005; Chen et al. 2010; Wan and Chen 2014), including California, Arizona, western New Mexico, western Colorado, Utah, Nevada, western Wyoming, western Montana, Idaho, Oregon and Washington, before the early 1930s. Because stripe rust was not observed in states east of the Rocky Mountains (referred as the eastern US), for more than 25 years, the eastern limit of stripe rust was considered to be the Black Hills of South Dakota in the US, and similarly, Whitewood of Saskatchewan was considered as the eastern limit for stripe rust distribution in Canada (Line 2002). In 1941, McFadden found a small amount of stripe rust in a wheat nursery at College Station, Texas (Humphrey 1941), which was the first time when stripe rust was found in the eastern US. Stripe rust was found as a hot spot at Denton, in 1953 and as a large hot spot at Prairie View in Texas in 1956 (Futrell and Atkins 1954, 1957). Stripe rust became widespread in the Great Plains in 1957. It spread from south and central Texas to Oklahoma, Kansas, Nebraska, South Dakota and Wyoming, but no reports of stripe rust in the spring-wheat region of the northern Great Plains (Daly et al. 1957; Young and Browder 1957; Pady et al. 1957; Pady and Johnston 1958). Stripe rust occurred in the Great Plains again in 1958, spreading from Texas to Oklahoma, Kansas, Nebraska, Wyoming, Minnesota, South Dakota and North Dakota, close to the Canadian border (Bridgmon and Kolp 1958; Davison 1958; Futrell et al. 1959; Gough et al. 1959; Hennen and Komanetsky 1959; Miller and Christensen 1959; Pady and Johnston 1959a, b; Rosen et al. 1959). The epidemic of stripe rust in the Great Plains was attributed to the increase of wheat production and use of new cultivar (Lerma Rojo) in the states of Coahuila, Nuevo Leon and Tamaulipas in Mexico, where stripe rust had occurred in the high elevations for many years (Rodriguez 1946; LeBeau et al. 1956). Although the distribution of stripe rust was much expanded in the 1950s, the disease was not found in eastern states of the US. During the 1960s and 1970s, stripe rust was not a problem in the wheat-growing regions east of the Rocky Mountains, and in the 1980s and 1990s the disease occasionally occurred in the south-central states

(Texas, Louisiana and Arkansas) causing yield losses (Line and Qayoum 1992; Line 2002). However, in 2000, stripe rust occurred in 16 states east of the Rocky Mountains, including Alabama, Arkansas, Colorado, Georgia, Indiana, Kansas, Louisiana, Michigan, Minnesota, Mississippi, North Dakota, Oklahoma, South Dakota, Texas, and Virginia; and caused 7% yield loss in Arkansas (Chen et al. 2002). In 2003, stripe rust occurred much severer in the eastern US, and the disease was first found in Florida and samples were also received from Ontario, Canada (Blount et al. 2005; Chen 2005). In 2005 and 2010, stripe rust was wide-spread, basically covering all wheat growing states in the continental US (Chen 2007; Wan and Chen 2014). In 2005, a leaf sample showing few stripe of necrotic reaction was obtained, but in 2010, stripe rust developed to significant levels in wheat variety trial nurseries in the state of New York. So far, wheat stripe rust has occurred in almost every state, except Alaska, Hawaii, Maine and New Hampshire. However, bluegrass stripe rust was reported in Hawaii (Nurdoch et al. 1973).

In the US, cereal yield losses caused by rusts have been estimated since 1918 (http://www.ars.usda.gov/main/docs.htm?docid=10123). Although stripe rust started to be reported since 1915, estimation of yield losses had not been done until 1958. The lack of yield loss estimates is due to several reasons, including the lack of yield loss studies from the middle 1910s to 1930s, the lack of stripe rust research from the 1930s to the late 1950s, and relatively insignificance of stripe rust due to resistance in diverse cultivars before the late 1950s (Line 2002). The increase of stripe rust in the late 1950s and especially the early 1960s revived stripe rust research. The first yield loss of wheat due to stripe rust was reported in 1958, estimated as 7967 tons, about 4.0% of the total yield in the State of Washington. In 1959, the yield loss due to stripe rust, also just in Washington, was estimated to be 232,466 tons at 10% of the total yield in the state. In 1961, an extreme severe epidemic of wheat stripe rust occurred throughout the entire PNW (Line 2002). Yield loss in the state of Washington was estimated by Dr. J. Walter Hendrix as 7.5 million bushels (204,300 tons, $15 million) in 1960 and 15 million bushels (408,600 tons, $30,000,000) in 1961 (Line 2002). The 1961 epidemic also caused growers in the state of Oregon $15,000,000 (Shaner and Powelson 1971). Dr. George W. Bruehl believed that Hendrix was conservative in his estimates of losses (http://plantpath. wsu.edu/wp-content/uploads/2012/10/History.pdf). According to Bruehl, stripe rust was more as a curiosity than as a real problem in Washington in the middle of 1950s. The release of Omar, a winter club wheat variety of superb quality, smut resistance, and high yield changed everything. By 1960 Omar occupied 67.5% of the wheat acreage of the entire US Pacific Northwest. It was highly susceptible to stripe rust. He witnessed rust spores blew from the earlier areas south and west of the Palouse (around Pullman, Washington and Moscow, Idaho), in a sense a repetition of the smut spore shower phenomenon described by early smut pathologists. Since then, severe stripe rust epidemics has been recorded in the US, but mostly in the Pacific Northwest and California, until 2000, when stripe rust started to cause national scale epidemics (Chen et al. 2002, 2010; Chen 2005, 2007). Because of the huge wheat acreage, yield losses are much bigger whenever stripe rust is severe in the Great Plains. Based on the yield loss data compiled by the USDA-ARS Cereal

Disease Laboratory (http://www.ars.usda.gov/main/docs.htm?docid=10123), from 1958 to 2016, stripe rust caused yield losses of 1,165,823,500 bushels (31,757,032 tons), of which 362,220,900 bushels (9,866,897 tons) were lost from 1958 to 1999 and 803,602,600 bushels (21,890,135 tons) from 2000 to 2016. Table 1.2 lists the severe epidemics caused at least 1.0% yield loss in the nation or at least 5% yield loss in a single state on either winter or spring wheat crop from 1958 to 2016.

### 1.5.2   Barley Stripe Rust

Barley can be infected by both *P. striiformis* f. sp. *tritici* and *P. striiformis* f. sp. *hordei*, but epidemics are primarily caused by the latter form. Because of this, the distribution and impact of barley stripe rust discussed here are mostly caused by *P. striiformis* f. sp. *hordei*. Barley stripe rust occurs in Africa, Asia, and Europe for a long time. In these continents, barley stripe rust is generally important in countries where wheat stripe rust is important. The barley form had not been reported in the new hemisphere (South and North America) before 1976, and so far has not been reported in Australasia. Compared to wheat stripe rust, stripe rust causes relatively small scale damages, although yield losses can be high in localized regions, due to relatively small barley producing areas, primarily spring barley crops, and relatively short growth season throughout the world. According to the World Food and Agriculture Organization (FAO, http://www.fao.org), wheat is grown in 210–240 million ha, whereas barley is grown only about 56–80 million ha in the world annually over the last several decades. Compared to wheat, barley is grown in similar climates, but usually in the more marginal production environments where limited moisture and poorer soils prevail (Saari and Prescott 1985), which reduces the vulnerability of barley to stripe rust. Therefore, barley stripe rust appears not as important as wheat stripe rust, and as a consequence barley stripe rust has not received as intensive studies as wheat stripe rust.

In China, barley stripe rust is most damaging in the barley growing areas in the southwest such as Yunnan province and the Tibet Autonomous region (Wang 1992; Wang et al. 1989a, b). Although yield loss data are not available, some barley cultivars are highly susceptible in fields for stripe rust in Tibet (Wang 1992; Wang et al. 2002a; T. Wang, personal communication). In a trip to Yunnan in 2011, Dr. Timothy Murray at Washington State University observed very severe stripe rust in barley fields in Xianggelila, Yunnan Province. In contrast, when tested with wheat stripe rust, 101 out of 104 Chinese barley cultivars and lines were highly resistant to all 30 tested races of *P. striiformis* f. sp. *tritici* (Sui et al. 2010). In Japan, stripe rust was known in the 1890s and occurred from Kyushu in the south to Hokkaido in the north (Ito 1909; Hemmi 1934). Epidemics were recorded in 1950–1956 on both wheat and barley (Kajiwara 1964; Kajiwara et al. 1964). Since then, there have been no available reports of stripe rust on either barley or wheat in Japan. Barley stripe rust occurred in India, Burma, Bangladesh, Nepal, Pakistan, Iran and Saudi Arabia (Stubbs 1985).