

# Role of *Berberis* spp. as alternate hosts in generating new races of *Puccinia graminis* and *P. striiformis*

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**Abstract** The common barberry and several other *Berberis* spp. serve as the alternate hosts to two important rust pathogens of small grains and grasses, *Puccinia graminis* and *P. striiformis*. Barberry eradication has been practiced for centuries as a means to control stem rust. Diverse virulence variations have been observed in populations of *P. graminis* f. sp. *tritici* that were associated with susceptible barberries in North America. Barberry likely has played a role in generating new races of *P. striiformis* f. sp. *tritici* in some regions in the world. Several North American stem rust races, namely races 56, 15B and QCC, initially originated from barberry, were subsequently responsible for generating large-scale epidemics. Thus, sexual cycles on *Berberis* spp. may generate virulence combinations that could have serious consequences to cereal crop production.

**Keywords** Barberry · Life cycle · Stem rust · Stripe rust · Wheat

## Introduction

The associations of barberry (*Berberis* spp.) with cereal rusts were known long ago as evidenced by a law in a French town in the mid-1600 s requiring the destruction of barberries near grain fields (Zadoks and Bouwman 1985), even though the specific fungal species remains unknown. Many interpreted the pathogen to be *Puccinia graminis* (the causal agent of stem or black rust) after de Bary in 1864 proved heteroecism, i.e. established that stem rust on cereals and aecia on common barberry (*Berberis vulgaris*) were incited by the same fungus, *P. graminis*. This in turn provided the scientific basis for barberry eradication as a means to control stem rust that was practiced by many countries for more than two centuries. Barberry serving as the alternate host of *P. striiformis* (the causal agent of stripe or yellow rust) was discovered only recently (Jin et al. 2010). In light of this finding, it is equally probable that, in some cases stripe rust rather than stem rust, might have been the intended target for control by the destructions of barberries practiced in the 17th and 18th centuries.

## Barberry as a source of genetic variation for *Puccinia graminis* f. sp. *tritici*

The intended purpose of eradicating common barberry plants in the vicinity of grain fields was to

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eliminate initial inoculum of *P. graminis* f. sp. *tritici* (*Pgt*) coming from barberries to grain fields (Stakman 1919) at an earlier date than might be expected from incoming wind-borne urediniospores. The role of barberry in generating new virulence combinations was not known until the concept of sex in rust fungi was established (Craigie 1927), and new races of *Pgt* were obtained in hybridization experiments (Waterhouse 1929; Newton et al. 1930; Stakman et al. 1930). A decade earlier, however, Stakman (1919) suspected that hybridization between strains might be occurring on barberry, generating new races. A careful examination of the effects of barberry eradication on stem rust in the United States by Roelfs (1982) revealed two unintended but remarkable benefits: reduction in the number of races and stabilization of the wheat stem rust population. The population of *Pgt* east of the Rocky Mountains in North America, though historically diverse (Roane et al. 1960) became asexual as a result of barberry eradication. The number of races in the population declined steadily, a trend that continues to this day. In the past decade, a single race (QFCSC) has dominated the *Pgt* population east of the Rocky Mountains, a region with approximately 60 million acres (about 24 million hectares) of wheat and barley grown annually. Most of this area is considered to be conducive for stem rust development.

In contrast to the simple race structure in the asexual population east of the Rocky Mountains, diverse races of *Pgt* were found in the Pacific Northwest region of the United States (Roelfs and Groth 1980; Burdon and Roelfs 1985). These races are presumably a part of a sexual population due to the observed diversity and the presence of aerial infections on *Berberis* spp. in the region. Recent surveys identified an active sexual population in a relatively small area bordering the states of Washington and Idaho where *B. vulgaris*, *Mahonia repens* and *M. aquifolium* are present. Inoculation experiments using aeciospores from these species identified isolates belonging to *P. graminis* f. sp. *tritici* and *P. graminis* f. sp. *secalis*, and isolates that attacked *Elymus glaucus* and ‘Hipoly’ barley (Y. Jin, unpublished) but not wheat. Work is in progress to characterize the host specificity of these isolates. In 2007 a barley field in northeastern Washington was severely infected by *P. graminis*. Analyses of 83 single-pustule isolates derived from a single stem rust sample collected from this field identified 23

races, many of which were further differentiated on a set of supplemental lines consisting of mostly susceptible genotypes (Rouse et al. 2009). In 2009 a total of 16 races were identified from stem rust samples collected from a single wheat field in the Palouse region bordering Washington and Idaho (Y. Jin, unpublished). These races were differentiated by virulence/avirulence on six resistance genes: *Sr5* (line ISr5Ra), *Sr7b* (ISr7bRa), *Sr8a* (ISr8Ra), *Sr9a* (ISr9aRa), *Sr9d* (ISr9dRa), and *SrMcN* (McNair 701). Races of *Pgt* with broad virulence have also been isolated from barberry plants in Russia in recent years (Lekomtseva et al. 2006).

### Implications of barberry for generating races of *Puccinia graminis* f. sp. *tritici* that have been consequential in North America

Race 56 of *Pgt*, a race responsible for the severe stem rust epidemics in the mid-1930 s in North America, originated from barberry. The race was first found on barberries in Iowa and Nebraska in 1928 (Stakman and Rodenhiser 1958). Race 56 was virulent to Triumph (*SrTmp* +), a winter wheat cultivar developed by a farmer in Oklahoma in the 1920s. Triumph became the predominant genetic background in hard red winter wheat throughout the southern Great Plains because of its early maturity, rust resistance, and high yield. Race 56 also was virulent to Kanred (*Sr5*, a common stem rust resistance gene present in winter wheat on the central Plains during this era) and Ceres (*Sr7b*, *Sr28*), a spring wheat cultivar developed for stem rust resistance that dominated the area in the northern Great Plains. The combination of virulence to these genes enabled race 56 to cause epidemics because it was able to establish and multiply in the southern and central Great Plains, a necessary condition for developing epidemics in the northern Great Plains when barberry was no longer functional as a source of initial inoculum in the region. Epidemiologically, a nearly identical, but more dramatic situation happened two decades later with the epidemics of race 15B. Race 15B was first identified on barberries in Iowa in 1939 and persisted near barberry plants at a low frequency for many years before it caused epidemics in North America in the mid-1950 s (Stakman and Rodenhiser 1958). Although the ability of race 15B to attack Thatcher wheat and durum cultivars carrying *Sr9e*

might have been responsible for inciting epidemics in the northern Great Plains and Prairie Provinces of Canada, it was its ability to attack Triumph wheat that enabled inoculum to build up in the south. Stem rust isolates with virulence to *SrTmp* in North America were rare except in the race 15B lineage and race 56 that originated on barberries.

Between 1989 and 1993, race QCC caused some localized epidemics on barley crops in the northern Great Plains of United States and Prairie Provinces of Canada. This race was first discovered in 1984 in British Columbia (Martens et al. 1989), a Canadian province adjacent to the state of Washington where sexual populations of *Pgt* were known to be present. It is highly likely that QCC originated on barberry because a race with an identical virulence pattern to QCC (i.e. QCCJB) was recently identified from collections near *Berberis* spp. in the Pacific Northwest (Y. Jin, unpublished). Although QCC was avirulent to the majority of wheat cultivars grown in the Great Plains, it was virulent on Karl, a popular winter wheat cultivar grown in the southern and central Great Plains. This race is one of only a few identified in the North American stem rust population that is virulent to *Rpg1* (or T-gene), a gene deployed in nearly every barley cultivar in the northern Great Plains (Steffenson 1992). The combination of sufficient inoculum buildup on susceptible wheat in the south and the ability to attack the barley crop in the north enabled QCC to develop into epidemics. Frequencies of race QCC declined steadily after the removal of the susceptible wheat cultivar in the southern and central Great Plains.

### Has barberry played a role in generating races of *Puccinia striiformis* f. sp. *tritici*?

A previous working assumption that *P. striiformis* f. sp. *tritici* (*Pst*) is asexual, under which interpretations were made in attempts to explain some of the observed variation for virulence, is no longer correct in light of the recent discovery of the alternate host, *Berberis* spp. through laboratory inoculation experiments. We hypothesized that in areas where wheat and stripe rust-susceptible *Berberis* spp. coexist, sexual recombination has likely played an active role in contributing to the variability of *Pst* (Jin et al. 2010). Variation generated via the sexual cycle obviously can provide a more satisfactory

interpretation for the observed virulence and genetic diversity in some of the stripe rust “hot spots” around the world, as in the case of western China (Chen et al. 2009; Duan et al. 2010). *Berberis* spp. are ubiquitous both in their native habitats and as introduced ornamentals in many parts of the world. Although only a few species of *Berberis* have been tested against stripe rust, the known susceptible species, *B. chinensis*, *B. holstii*, *B. vulgaris*, and *B. koreana*, represent several diverse sections in *Berberis* (Ahrendt 1961; Kim et al. 2004), a genus with nearly 500 described species. Thus, more stripe rust susceptible *Berberis* spp. are likely to be found.

### Conclusions

A large number of races of *P. graminis* f. sp. *tritici* were found on or near barberry plants in North America, including those that were consequential in generating large-scale epidemics. It is safe to assume that the unique virulence combinations that equipped these races to overcome different cereal resistance genes in different regions were assembled through the sexual cycle. *Berberis* spp. likely played an active role in generating new races in *P. striiformis* f. sp. *tritici*, although evidence for this is circumstantial at this time. Old and recently emerging evidence continues to be gathered about barberries because they harbor two of the most damaging cereal rusts, *P. graminis* f. sp. *tritici* and *P. striiformis* f. sp. *tritici*. Virulence combinations generated through the sexual cycle on *Berberis* spp., however rare, can have serious and long lasting impacts on cereal crops.

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