Chapter 2

Early Research on the Genetics of *Puccinia graminis* and Stem Rust Resistance in Wheat in Canada and the United States

James A. Kolmer

At the end of the 19th century, spring wheat production in the United States was centered in northern Iowa and southern Minnesota. In Canada, the principal spring wheat growing area was the Red River Valley of southern Manitoba (7). Wheat grown in Minnesota and Manitoba was in demand by wheat millers due to superior grain quality. However, wheat production could be an uncertain proposition as floods, insects, early frost, and disease often ravaged crops. Stem rust, caused by *Puccinia graminis* f. sp. *tritici*, was among the most important diseases. In 1878, a severe stem rust epidemic occurred in Minnesota, Iowa, and Wisconsin (14). Losses were estimated to range between 17-27% in the three states. Severe losses due to stem rust also occurred in Ohio, Indiana, Iowa, Illinois, and Minnesota in 1892 and 1894 (3). The first reported occurrence of stem rust in western Canada dated from 1891 at the Experimental Farm in Brandon, Manitoba (17). Stem rust caused varying amounts of crop loss in Manitoba in 1892, 1896, and from 1900 to 1905. In 1911, stem rust was widespread in western Manitoba and also in Saskatchewan.

The massive stem rust epidemic of 1916 in Manitoba and the mid-western United States was to leave a legacy beyond that of its immediate destruction. It became apparent that a sustainable wheat industry would never be established in western Canada and the north-central United States unless the stem rust problem could be solved. The epidemic of 1916 and those of following years (1923, 1927, 1935, 1937, 1950-1954) provided the stimulus for a remarkable period of stem rust research. The importance of the stem rust situation, the level of research activity, and the long-term significance of the research conducted from 1916 to 1955 has not been equaled in the following years. Much of our current knowledge of plant disease epidemiology, plant disease resistance, and genetics of fungal plant pathogens has its conceptual basis in the research on *P. graminis* that was carried out by a dedicated group of Canadian and United States scientists during this period.

Biological Forms, Bridging Hosts, Physiological Specialization, and Epidemiology of *Puccinia graminis*

BIOLOGICAL FORMS

In the late 19th century, stem rust was considered to be a single homogeneous entity that afflicted cereal crops and other grasses (13). The first division of *Puccinia graminis* into different pathogenic groups was described initially, in 1894, by J. Eriksson, a Swedish plant pathologist (Fig. 2.1). He found that stem rust collected from a cereal host was usually pathogenic to the host from which it was collected or other closely related grasses; however, it could not attack other more distantly related grasses or cereals. For example, stem rust collected from oats was pathogenic to oats but not wheat, rye, or barley. Stem rust from wheat attacked wheat and barley, produced a low level of infection on rye, and was essentially non-pathogenic to oats. Eriksson and Henning divided stem rust into six groups based on host pathogenicity, which they called specialized forms or *formae specialis*: *Puccinia graminis* f. sp. *tritici* -- pathogenic to wheat and barley; *Puccinia graminis* f. sp. *avenae* -- pathogenic to oats; *Puccinia graminis* f. sp. *secalis* -- pathogenic to rye and barley; *Puccinia graminis* f. sp. *agrostis* -- pathogenic to bentgrass; *Puccinia graminis* f. sp. *poae* -- pathogenic to bluegrass; and *Puccinia graminis* f. sp. *airae* -- pathogenic to hairgrass (9).

Bridging Hosts

The division of stem rust into different biologic forms, as *formae specialis* were then referred to, did not necessarily imply that the forms were considered stable. Most workers thought that the forms were not absolutely fixed but had some ability to adapt to other host species by selection or by climatic influences. H.M. Ward (Fig. 2.2), a professor of botany at Cambridge University, developed the concept that the biologic forms of rust could gain pathogenicity to more distantly related hosts. Ward conducted an extensive series of experiments with *Puccinia dispersa* (synonym *P. recondita* f. sp. *secalis*) to test how variation in plant age, temperature, and light affected urediniospore germination. He used urediniospores collected from three sections (*Stenobromus, Libertia, Serrafalcus)* of *Bromus* inoculated to 64 *Bromus* species. During the course of these experiments, he found that some species were infected by urediniospores from other species of *Bromus* that were usually incapable of cross infection. Ward determined that "*Bromus erectus* was apparently infected once out of 37 trials by spores from *B. mollis, B. sterilis* 4 times out of 90 trials by spores from *B. mollis* . . . ." Ward concluded "that although it is generally true that adapted races of *P. dispersa* are restricted to groups of closely related allied species (*formae specialis*) there do occur *sp.* which serve as intermediaries in the passage of the fungus from one section of the genus to another. I propose to call these intermediary species of *Bromus*, 'bridgeing species.'" He went on to add "there seems no longer room for uncertainty as to the existense of the intermediacy or 'brideging species' [by which the] phenomenon of adaptative parasitism occurs by passage of the fungus from species of one circle of alliance to those of another. . ." (35).

The bridging host theory became the accepted wisdom among mycologists and plant pathologists at the turn of the century. This theory, if rigorously shown to be correct, would have had broad implications for plant pathology and the breeding of rust-resistant cereal crops. If the host range of rust fungi could be modified by culturing urediniospores on certain hosts, then breeding for stable rust resistance in any cereal crop would be rendered nearly impossible. At that time, it was already known that *Puccinia graminis* was

Fig. 2.1. J. Eriksson (Courtesy of Hunt Institute for Botanical Documentation, Carnegie Mellon University, Pittsburgh, PA.)

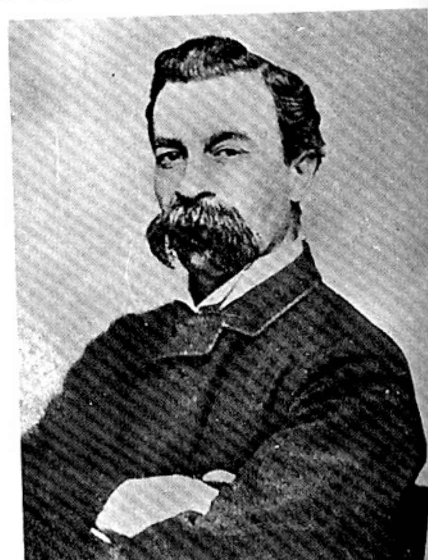

Fig. 2.2. H.M. Ward (Courtesy of the Cereal Research Centre, Winnipeg.)

pathogenic to over 50 species of wild grasses which could potentially serve as bridging hosts, thus allowing stem rust from rye or oats to gain pathogenicity to wheat. In essence, it would have been necessary to breed for resistance to nearly all forms of stem rust, not just the form found on wheat. The bridging host theory which proposed plasticity of host range in stem rust would also practically negate Eriksson's concept of *formae specialis*.

A rigorous evaluation of the bridging host theory was the means by which E.C. Stakman would make the first of many significant contributions to stem rust research and the emerging field of plant pathology (Fig. 2.3). In 1909, Stakman, then a high school teacher at Argyle, Minnesota, was offered by E.M. Freeman (Fig. 2.4), the first head of the Plant Pathology Section at the University of Minnesota, an opportunity to undertake graduate research in plant pathology at St. Paul, Minnesota (4). Freeman, a disciple of the bridging host theory, did postgraduate studies with Ward, and his research was cited extensively in Ward's 1903 paper (35). Stakman accepted Freeman's offer and completed his M.A. degree in 1910, working on aspects of spore germination in smut fungi. Stakman's Ph.D. research dealt with the parasitic ability of stem rust forms on wheat, barley, rye, and oats to infect hosts other than the original host. In this work, he found no evidence to support the bridging host theory. He completed his doctoral studies in 1913 and succeeded Freeman as plant pathology section head. Stakman continued his research on the host range of biologic forms of *Puccinia graminis*. With the assistance of F.J. Piemeisel, he undertook an extensive study to determine what *formae specialis* of stem rust were present on various grass hosts and to ascertain if rust from these wild hosts contributed to the stem rust epidemics that were then occurring on wheat. As an example, the *tritici, secalis,* and *compacti* forms were found on *Hordeum jubatum,* the wild barley which is found commonly in the northern plains. It was determined that the *tritici* and *secalis* forms also both occurred on *Elymus canadensis* and *Secale cereale.* Stakman and Piemeisel were able to separate the two forms by culturing urediniospores collected from *Elymus* on wheat for a number of generations and by further culturing the *Secale* rust collections on *Secale*. At the end of the experiment, the rust maintained on wheat was largely non-pathogenic to rye, and the rust maintained on rye was non-pathogenic to

Fig. 2.3. E.C. Stakman (Courtesy of the University of Minnesota Archives.)

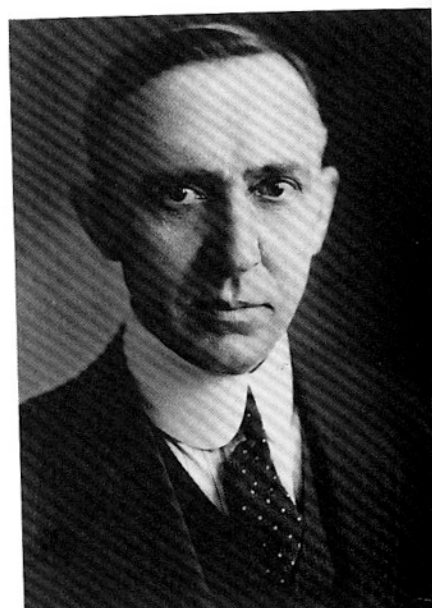

Fig. 2.4. E.M. Freeman (Courtesy of the Department of Plant Pathology, University of Minnesota.)

wheat. Stakman and Piemeisel concluded that the forms of *Puccinia graminis* that attack cereals occur on many wild grasses (33). In addition to stability of biologic forms, they recognized that the results had important implications for overwintering and dissemination of stem rust.

In the course of these same studies from 1915 to 1918, Stakman also specifically addressed the bridging host theory. He may have been inspired by the results from his previous research which failed to support this paradigm. Stakman, working with Peimeisel and M. Levine, used hosts that were equally susceptible to the *tritici* and *secalis* forms in attempts to change their pathogenicity (34). Species of *Hordeum, Elymus, Agropyron,* and *Bromus* were investigated as possible bridging hosts for these two stem rust forms. Each rust collection was increased and maintained on hosts of different cereals for several uredinial generations in order to separate and purify any different forms that might be present in the collection, much like Stakman had done earlier with the *tritici* and *secalis* forms on *Elymus* and *Secale*. The purified collections were then maintained by successive transfer of uredinia on the potential bridging hosts for a period of two to three years. Urediniospores of the *secalis* form were maintained on barley for three years and then tested for pathogenicity on over 2,000 wheat plants. There was no increase in pathogenicity of the *secalis* form to wheat. Similarly, the *tritici* form was cultured for more than two years on barley, but did not increase in pathogenicity to rye. There was simply no evidence to support the bridging host theory. The pathogenicity of the purified collections was unaltered by culturing on common, or bridging, hosts. Stakman surmised that the previous results of Ward and Freeman must have been due to contamination of two or more forms on one host plant. To see if this were possible, wheat was inoculated with the *secalis* form, and the plants were placed on a greenhouse bench for ten days, after which no stem rust uredinia were visible. Stakman then transferred spores that had not germinated from the wheat plants to rye where infections occurred on a large number of plants. A sufficient number of spores of the *secalis* form must have retained viability on the wheat plants in order to subsequently infect the rye plants. In essence, the bridging host theory had been based on mixtures of different forms in the original stem rust collections. Stakman et al. demonstrated that the biologic forms of

Puccinia graminis were analogous to pure lines, and their host ranges were unaffected by host selection or climatic factors (34).

Physiological Specialization

The next level of specialization in stem rust was to be found within the different biologic forms. As part of their studies examining host range of biologic forms that were published from 1917 to 1918, Stakman and Piemeisel isolated stem rust from club wheat in the Pacific Northwest that was non-pathogenic to the common bread wheats (32). At the time, the stem rust from club wheat was referred to as *P. graminis* f. sp. *compactii*, essentially treating it as another biologic form. Stakman later referred to this as the first example of physiologic specialization within *P. graminis* f. sp. *tritici* (4).

Stakman et al. subsequently showed that the forms of stem rust on club wheat were non-pathogenic to certain spring wheats such as Marquis which had been previously susceptible to all collections of stem rust from wheat. However, some of the collections from club wheat had virulence to the hard red winter wheat Kanred which had been resistant to all previously tested collections from wheat. It was evident that biological specialization could be established only by testing many species and varieties of cereals. There was a strong chance that forms of rust would be found capable of attacking varieties previously considered to be resistant. Twenty-five varieties of *Triticum aestivum* (bread wheat), *T. durum* (durum wheat), *T. compactum* (club wheat), *T. dicoccum* (emmer wheat), and *T. monococcum* (einkorn wheat) were used as differential hosts; none were resistant to all forms of *P. graminis* except for one emmer wheat. In this initial study, four different forms of stem rust on wheat were found in Minnesota, 12 forms being described in total. Stakman et al. also recognized at this early date that the presence of barberry, the alternate host for *P. graminis*, was related to the number of stem rust forms on wheat and that a regional distribution of stem rust forms explained why wheat cultivars could be resistant at one location yet susceptible at another (30).

Stem rust research was also being conducted at federal and university laboratories in eastern and western Canada from 1917-1925. W.P. Fraser was appointed lecturer of biology at McDonald College, McGill University, outside of Montreal in 1912 and, in 1917, was appointed a part-time Officer in Charge of Grain Disease Investigations for all of Canada. Late in 1917, M. Newton began working on stem rust in Fraser's laboratory during her M.Sc. studies at McGill. Fraser gave several collections of stem rust to Newton with a request that she derive single-spore cultures from them. The single-spore isolates differed for virulence to a selection of Marquis wheat. Newton and Fraser independently showed that wheat stem rust was not pathogenically uniform but consisted of many different biological forms that were indistinguishable morphologically but yet differed for pathogenicity on different wheat cultivars. These biological forms came to be called physiological races. In January 1918, Fraser communicated these results to Freeman at Minnesota who confirmed that Stakman and his co-workers had also made a similar discovery. Fraser continued stem rust studies at the Canada Department of Agriculture Laboratory in Saskatoon from 1921-1925. Newton continued her stem rust work with Stakman at the University of Minnesota where she graduated with a Ph.D. in 1922 (17).

Stakman and Levine continued to evaluate different selections of common wheat, durum wheat, and emmer wheats for use in classifying biological forms, or races, of *P. graminis*. The "Stakman" wheat stem rust differentials, as they were called, included the hexaploid club wheat cultivar Little Club; the hexaploid common wheats Marquis, Kanred, and Kota (*Triticum aestivum*); the tetraploid durum wheats Arnautka, Speltz Marz, Mindum, Kubanka, and Acme (*T. turgidum*); the tetraploids White Spring Emmer and Khapli (*T. dicoccum);* and the diploid wheat Einkorn (*T. monococcum*). Infection types of 0 (immune) to 4 (very susceptible) for the biological forms on the differentials were also described. By 1922, 37 races of stem rust were recognized on the "Stakman" differentials (29).

Annual national surveys of physiologic races of wheat stem rust were initiated in both Canada and the United States in 1919 and have continued to this day. In Canada, the wheat stem rust surveys were conducted by Newton and Fraser at the Canada Department of Agriculture laboratory in Saskatoon from 1919 to 1925 (25). After 1926, wheat stem rust research was based at the Dominion Rust Research Laboratory of the Canada Department of Agriculture in Winnipeg. From 1919 to 1930, 41 races of wheat stem rust were identified in Canada. It was apparent, however, that a small number of races were responsible for the major stem rust epidemics that were then occurring in North America since five races accounted for over 75% of the 2,171 isolates sampled in Canada during these years.

EPIDEMIOLOGY OF STEM RUST - THE "PUCCINIA PATHWAY"

The surveys conducted in the United States by Stakman and his co-workers indicated that urediniospores of stem rust which had overwintered in the southern plains states of Texas and Oklahoma could be blown northward in the spring and summer to infect the spring wheats in the northern states (31). This long-distance transport of rust spores from Mexico to the Canadian prairies became known as the "Puccinia pathway." Extensive epidemiological studies that involved exposure of vaseline-coated microscope slides to detect the transport of wind-borne urediniospores were conducted in both the United States and Canada to determine the role of wind-borne spores in the initiation and spread of stem rust epidemics. In areas without local stem rust infections on barberry plants, the presence of urediniospores trapped on the slides one to two weeks before the observance of field infections supplied strong evidence that the infections originated from wind-borne urediniospores. In general, it was found that the first stem rust infections occurred five to ten days after urediniospores were first observed. However, these studies also indicated that infections were occasionally observed before any spores were trapped or that sometimes up to three weeks would pass between the first observance of spores on the slides and the occurrence of stem rust infection in field plots. Environmental factors, such as wind direction and speed, temperature, and relative humidity, were identified as influencing the initiation and spread of stem rust epidemics.

Aerobiology studies were also conducted to determine the prevalence of urediniospores in the atmosphere. Stakman et al. detected urediniospores at 16,000 feet over the midwesterm United States (28). Spores collected at 7,000 feet germinated readily. In flights over Winnipeg and Portage la Prairie, Manitoba, it was shown that the greatest concentration of spores occurred up to 5,000 feet in July and August when stem rust infections were most common in local fields (6). However, at both ground level and high altitude the spore concentrations varied greatly between locations and over time.

During the course of the physiologic race surveys, it was noted that the same stem rust races were the predominant races in both Canada and the United States. This could also be attributed to the long-distance transport of wind-blown urediniospores from the United States southern plains to the northern plains and the Canadian prairie provinces. From 1926 to 1928, race 36 was the most common race each year at between 40-72% of isolates collected in both western Canada and nine states in the Mississippi Valley. Race 21 was the second most common race for each year between 10-31% of isolates in both countries (6). It also become apparent that changes in the predominant stem rust races in the United States would affect the stem rust population in Canada.

The International Rust Conference

A major stem rust epidemic in 1923 in Manitoba, preceded by minor epidemics in 1919 and 1921, was to prompt further action on funding rust research in Canada. In June 1924, H.T. Güssow, the Dominion Botanist, reported before the House of Commons Select Standing Committee on Agriculture and Colonization on the rust situation in Manitoba and of the inadequate funding for research (17). On his recommendations, the House appropriated $50,000 for land and buildings to house a rust research facility.

Güssow also suggested that a conference with provincial, federal, and university representatives be convened to implement plans for future rust research in Canada (Fig 2.5). Among the attendees, H.M. Tory, W.P. Thompson, and A.H.R. Buller represented the National Research Council; H.T. Güssow, W.P. Fraser, and D.L. Bailey represented the federal department of agriculture; W.R. Motherwell, the Minister of Agriculture, was also present. The President of the University of Manitoba, J.A. McLean, and G.R. Bisby and V.W. Jackson from the Manitoba Agricultural College, also attended. By special invitation, the conferees also included H.L. Bolley from the North Dakota Agricultural Experiment Station; J.G. Dickson from the Department of Plant Pathology, University of Wisconsin; H.K. Hayes from the Department of Agronomy, University of Minnesota; and E.C. Stakman from the Department of Plant Pathology, University of Minnesota. The current status of the cereal rust situation was reviewed by Fraser and Stakman, followed by a synopsis of rust research in both the United States and Canada. Tory, the head of the National Research Council, and Minister Motherwell also addressed the conference. This was followed by a discussion of future research with contributions from the attending scientists. In the last part of the meeting, recommendations were drawn up to insure that the rust research be conducted cooperatively among scientists in both countries. Plans were discussed for studies in epidemiology, physiologic specialization, physiology and ecology, and breeding for rust resistance.

Genetics of *Puccinia graminis*

Discovery of the Function of the Pycnia

In 1926, the facilities of the Dominion Rust Research Laboratory of the Canada Department of Agriculture were completed on the campus of the Manitoba Agricultural College (Fig. 2.6). The "Rust Lab," as it came to be called, was located in Winnipeg partly on the recommendations of H.T. Güssow and A.H.R. Buller, an eminent mycologist in the Department of Botany at the Manitoba Agricultural College (17). The mandate of the Rust Lab was to study the epidemiology and physiologic specialization of cereal rusts and to develop rust-resistant cereal cultivars (Fig. 2.7). I.L. Conners, J.H. Craigie, W.L. Gordon, F.J. Greaney, T. Johnson, and M. Newton, with D.L. Bailey as director, were among the initial team of scientists assembled to work in the Rust Lab (Fig. 2.8).

In 1925, Craigie began to re-examine the life cycle of *P. graminis*. Previously, De Bary had shown that *P. graminis* was heteroecious, i.e. the pycnial and aecial stages on *Berberis* spp., were different stages of the same fungus that produced urediniospores and teliospores on wheat. However, the functional role of the pycnium remained unknown. Germination of pycniospores could not be detected, and this spore stage was incapable of infecting either wheat or barberry. Were the pycnia a "residual" stage of the life cycle that once had a previous function but were now useless, or did they have a

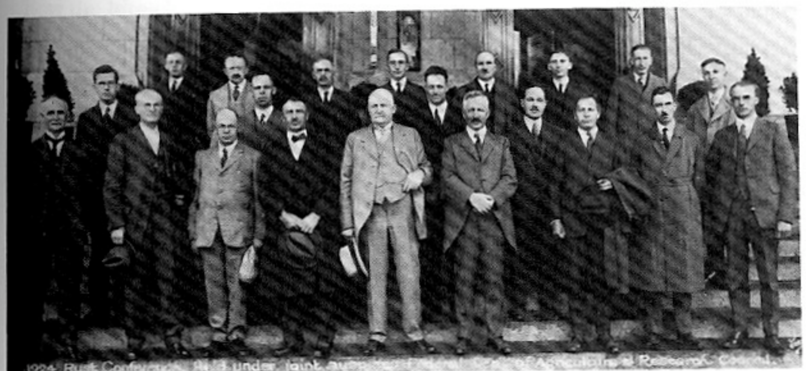

Fig. 2.5. Participants of the International Rust Conference held September 9 and 10, 1924, in Winnipeg, Manitoba. (Courtesy of the Cereal Research Centre, Winnipeg.)

Fig. 2.6. The Dominion Rust Research Laboratory. Cereal rust research was conducted in "The Rust Lab" by Canada Department of Agriculture personnel from 1926 to 1957. (Courtesy of the Cereal Research Centre, Winnipeg.)

Fig. 2.7. Cartoon from the Winnipeg Free Press, April 1929.
(Courtesy of the Cereal Research Centre, Winnipeg.)

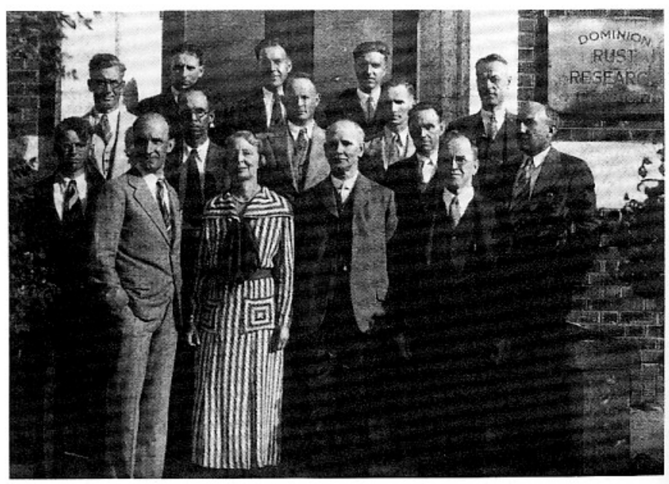

Fig. 2.8. Scientific staff of the Dominion Rust Research Laboratory, Canada Department of Agriculture, Winnipeg, Manitoba, June 1936.
Left to right, first row: Peturson, Hannah, Newton, Buller, Craigie. Second row: Peterson, Waddell, Johnson, Brown, Goulden. Third row: Welsh, Greaney, Machacek, Hagborg, Pope.
(Courtesy of the Cereal Research Centre, Winnipeg.)

role in the sexual process of *P. graminis*? It was also known that pycnia were uninucleate and that aeciospores were binucleate; however, it was not known how the binucleate condition arose in the aecial primordium (17). Craigie was able to demonstrate for both *P. graminis* and *P. helianthi* (sunflower rust) that pycnial infections failed to produce aeciospores unless the pycnial exudates (pycniospores) were intermixed between different pycnia. Thus, both rusts were shown to be heterothallic, i.e. with two mating types. Craigie proved that the pycnia were the functional stage in the life cycle where fertilization occurred in *P. graminis* (5).

Craigie was apparently inspired by Buller, who was a regular visitor to the Rust Lab, and by the actions of flies moving back and forth between pycnia on the barberry plants. This excerpt from Craigie's 1927 paper recalls that "On May 17, Prof A. H. Reginald Buller . . . was in the greenhouse . . . inspecting the experiments in progress. A solitary fly . . . had entered the greenhouse. Prof. Buller directed my attention to the fact that the fly was settling on the sunflower leaves, sipping nectar at the pycnia of one pustule and then flying off to another leaf and sipping the nectar of the pycnia of another pustule, and he at once said: [Buller's words] 'The solution of the problem of the function of the pycnium is an entomological one. Copy the action of the fly. Take (+) pycnospores to (-) pycnia and (-) pycnospores to (+) pycnia, and it may well be that the pycnospores will germinate and bring on the diploid phase of the mycelium'" (5).

The ninth annual meeting of the Canadian Division of the American Phytopathological Society was held in Winnipeg in December 1927. The pre-eminent rust taxonomist of the day, J.C. Arthur of Purdue University, addressed the meeting with his presentation, "Progress in Rust Studies." In his talk, Arthur expressed his pleasure in having an opportunity to visit and "secure first hand information regarding the young, but already famous Dominion Rust Research Laboratory, the only one of its kind in the world, which is making such notable contributions . . . and, in addition, to greet my fellow workers whose signatures are familiar, but whose faces and voices I do not know" (2). Other notable visitors to the Rust Lab at this time were H.L. Bolley, from North Dakota, and H.H. Whetzel, from Cornell University.

Research in genetics of *P. graminis* continued at the Dominion Rust Research Laboratory after Craigie's discovery. Once it was established that *P. graminis* was heterothallic, it became possible to intercross and self isolates of different races of wheat stem rust and thus begin to examine the genetic basis of physiologic specialization. There were many questions about *P. graminis* races that remained: were the physiologic forms heterozygous or homozygous; would different physiologic races hybridize; and did Mendelian factors determine the physiologic races? To address these and other issues, Newton and Johnson, in the late 1920s, began a series of experiments that remain to this day the most thorough and extensive genetic analysis of *P. graminis* (25). A large number of isolates of the common stem rust races were selfed and also intercrossed on barberry, to obtain F_1 and F_2 progeny generations. The recombinant aeciospores and derived urediniospores were tested for segregation of pathogenicity on the stem rust differential hosts (19). Most of the isolates were heterozygous for pathogenicity on the differentials. For example, the selfing of race 53 gave rise to 18 different races among 44 isolates. The F_2 progeny from a cross between an isolate with orange urediniospores and an isolate with grey-brown spores segregated for red (wild type), orange, grey, and white spores in approximately a 9:3:3:1 ratio, indicating that two loci controlled spore color in *P. graminis*. It was apparent that a number of Mendelian factors were involved in determining physiologic specialization since the F_2 progeny from this cross segregated for seven different races. The female parent used in the crosses was also shown to influence the infection type of the progeny isolates. Isolates with an infection type (IT) 3⁻c (small-moderate uredinia with chlorosis) on Marquis and Kota, when used as female parents in crosses, yielded only progeny with the same infection type on these two cultivars. Since progeny from the reciprocal crosses did not have this distinct infection type, the trait was inherited cytoplasmically.

Newton and Johnson also demonstrated that *P. graminis* isolates of the same race could be genetically distinct. A field isolate of race 9, when selfed, produced only race 9 isolates as progeny. The race 9 field isolate was then crossed with an isolate of race 15, and the F_1 progeny were all race 9.

However, the F_2 isolates derived from selfing an F_1 isolate segregated for four different races as well as the cytoplasmically inherited infection type on Marquis and Kota. Because the different isolates of race 9 gave rise to different races after selfing, it was evident that physiologic forms were not the ultimate genetic unit (25).

Johnson and Newton were the first to clearly demonstrate Mendelian inheritance of pathogenicity in a plant pathogenic fungus. An isolate of race 9, which had IT 0, 4, and 4 to the differential cultivars Kanred, Mindum, and Vernal, respectively, was crossed with an isolate of race 36 which had IT 4, 1, and 1 to Kanred, Mindum, and Vernal, respectively. The F_1 isolate had IT 0, 4, and 1 to Kanred, Mindum, and Vernal. The F_2 progeny isolates segregated 96:30 for IT 0 and 4, respectively, on Kanred, which indicated that a single dominant gene controlled avirulence on Kanred; 37:89 for IT 1 and 4, respectively, on Mindum, which indicated that a single recessive gene controlled avirulence to Mindum; and 187:12, respectively, for IT 1 and 4 on Vernal, which indicated that two dominant genes controlled avirulence to Vernal. The four genes that conditioned infection type on the three differentials segregated independently as there were eight races in the F_2 progeny, which agreed with the expected number of 16 F_2 genotypes. Johnson and Newton concluded that the pathogenic properties of races were inherited according to Mendelian laws; genes that conditioned infection type on the differential cultivars could be either dominant or recessive; genes that conditioned virulence segregated independently; and that isolates of the same physiologic race could be genetically distinct (18). The work of Newton and Johnson on the genetics of *P. graminis* provided the first experimental evidence from a plant pathogen for the current paradigm of gene-for-gene relations in host-parasite genetics (10).

Genetics and Breeding of Stem Rust Resistance in Wheat

Marquis, Ceres, Thatcher, and Renown Wheats

Marquis, the first, modern hard red spring wheat bred in North America, was selected from a cross between Red Fife and Hard Red Calcutta in 1903 by Charles Saunders, the Dominion Cerealist at the Central Experimental Farm in Ottawa, and was released as a cultivar in 1910 (17). Relative early maturity with excellent milling and bread-making qualities combined to make Marquis extremely popular. By 1928, over 90% of the hard red spring wheat acreage in Canada was Marquis. However, Marquis was also susceptible to stem rust and leaf rust (*P. triticina*). In the epidemics of 1916 and previous years, all of the bread wheats were susceptible; only the durum wheats had any effective stem rust resistance. In the United States and somewhat in Canada, durum wheats had largely replaced Marquis from 1917 to 1923 because of stem rust (4). However, in 1923, stem rust isolates in the race 11-32 complex were found on durum wheats. A stem rust-resistant wheat cultivar was needed to replace Marquis and the durum wheats.

L.R. Waldron, at the North Dakota Agricultural Experiment Station in Fargo, crossed Marquis with Kota in 1918. Kota was resistant [later determined to be conditioned by gene *Sr7b* (24)] to some of the common stem rust races. In 1926, a stem rust-resistant selection from this cross was released as Ceres wheat. Ceres was grown in the United States and Canada and had a moderate level of stem rust resistance until 1935 when it suffered heavy losses. Stem rust race 56 had been increasing in frequency from 1928 to 1935 when it caused severe yield losses on Ceres (19).

With races virulent to Ceres in the stem rust population, it was once again imperative to have a bread wheat adapted to the northern United States and the Canadian prairie provinces that had stem rust resistance. However, all of the bread wheat cultivars were susceptible to some of the stem rust races that had been characterized at that time. W.P. Thompson, of the University of Saskatchewan (and later president of the University), noted in his plots during the 1916 epidemic that one emmer and one durum wheat were resistant to stem rust (17). Thompson crossed the common bread wheats which are hexploid (AABBDD) with the tetraploid (AABB) durum and emmer wheats. Thompson was among the first to study the chromosome incompatibilities which often resulted in sterility in these crosses and also noted that rust-resistant progeny tended to have agronomic characteristics and grain quality of the emmer and durum parents. If stem rust resistance was to be transferred from the tetraploid wheats to the hexaploid bread wheats, it would be necessary to break the negative association between rust resistance and bread wheat grain quality.

H.K. Hayes, a wheat breeder and later head of the Department of Agronomy and Plant Genetics at the University of Minnesota, working with Stakman tested the standard stem rust differentials for resistance to the common races to determine which might be useful as resistant parents (15). In seedling tests, the red winter wheat Kanred was shown to be very resistant to 14 of 21 races that were tested. Iumillo durum was resistant in seedling tests to all of the races. Thus, Kanred and Iumillo were chosen as parents, and both were crossed with Marquis. The F_3 families of Kanred x Marquis segregated in a 1:2:1 ratio for homozygous resistant, segregating, and homozygous susceptible families (1). This indicated that a single gene [later determined to be *Sr5* (24)] conditioned stem rust resistance in Kanred. Progeny lines with the Kanred resistance and spring wheat habit of Marquis were selected for further crossing. Over 1000 F_3 families of Iumillio x Marquis were evaluated for field rust resistance and grain quality, and only a few recombinant rust-resistant families with acceptable bread wheat grain quality were advanced to F_6 for further crossing (15). A cross was then made between a Kanred/Marquis line and an Iumillo/Marquis line in order to combine the specific seedling resistance of Kanred with the general field resistance of Iumillo. The 250 F_3 lines from the double cross segregated in a ratio of 15 susceptible:1 resistant ratio for field stem rust resistance which indicated that the Iumillo resistance was conditioned by two recessive genes (16). Resistant lines were further selected from the double cross, and in 1935, the cultivar Thatcher was released by the Minnesota Agricultural Experiment Station. Thatcher, which combined high levels of stem rust resistance with excellent grain quality and agronomic characteristics, quickly became the predominant spring wheat cultivar in both the United States and Canada.

Another very important source of stem rust resistance came from the tetraploid wheats. E.S. McFadden in South Dakota crossed Yaroslav emmer wheat with Marquis and was able to recover lines with bread wheat grain quality along with the stem rust resistance from the emmer (23). The cultivar Hope and the breeding line H-44-24a, both having a high level of field stem rust resistance, were derived from this cross. Although Hope was never a popular cultivar, H-44-24a was used by Goulden et al. at the Dominion Rust Laboratory as a parent in crosses with Marquis (12). The F_3 lines from H-44-24a x Marquis segregated in a 3 susceptible:1 resistant ratio for field stem rust resistance, which indicated that a single recessive gene conditioned resistance in H-44-24a. The resistance originally derived from Yaroslav emmer was later designated as *Sr2* (24). At Winnipeg, wheat breeders C.H. Goulden, K.W. Neatby, and R.F. Peterson used H-44-24a as a resistant parent in crosses with Marquis and Reward (Reward = Marquis/Prelude) (17). The cultivar Renown, the first stem and leaf rust-resistant wheat developed by the Dominion Rust Research Laboratory, was selected from a H-44-24a x Marquis cross and was released in western Canada in 1937 (Fig 2.9).

Race 15B, Selkirk Wheat, and Sr6

The cultivars Thatcher and Renown and the new wheats Regent and Redman were resistant to stem rust from the time of their release until 1949. Johnson referred to this period as "The Years of Immunity" (17). The slight amount of stem rust infections that occurred were insignificant and were not associated with the appearance of new races. However, Thatcher was susceptible to leaf rust, and starting in 1943, leaf rust severities began to increase on Renown and its derivatives. Testing of the leaf rust isolates on differential cultivars revealed that new races with virulence to the H-44-24a leaf rust resistance had become common. In the absence of heavy stem rust infection, the importance of leaf rust on yield losses became apparent.

In 1939, an isolate of stem rust race 15B was found near Fort Dodge, Iowa (27). The detection of this race was highly significant since it was virulent to the Thatcher resistance and particularly virulent to the H-44-24a resistance. In the United States from 1940 to 1949, race 15B occurred at very low levels in uredinial collections made from wheat. However, race 15B was collected every year at levels up to 5% of isolates in aecial collections from barberry. In Winnipeg, wheat breeders and rust pathologists realized that if race 15B ever became common in Canada, it would cause serious damage to cultivars with the H-44-24a resistance. An isolate of race 15B was obtained from the University of Minnesota in 1945 (race 15B was not

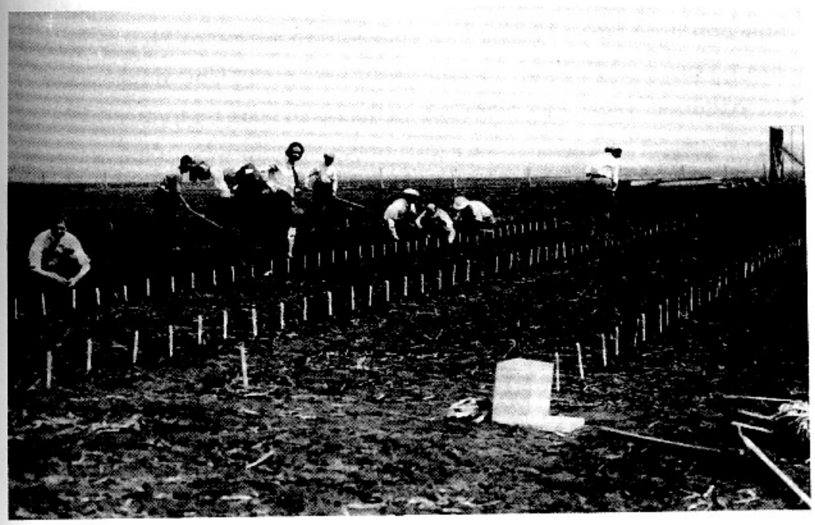

Fig. 2.9. Seeding of rust plots in Winnipeg. Field plot work was a more formal occasion in the 1930s. M. Newton is facing the camera. (Courtesy of the Cereal Research Centre, Winnipeg.)

detected in Canada until 1946) and thus began the search for a wheat line with resistance to this race.

The problem posed by the presence of race 15B was eventually solved by an international effort to find different wheat cultivars that were resistant to this race. Extensive screening of wheat cultivars and lines began at various locations in the United States, Canada, and also at the Rockefeller Foundation-Mexican Government Cooperative Agricultural Research and Production Program in Mexico [currently known as Centro Mejormiento de Maize y Trigo (CIMMYT)]. Breeding programs in the United States and Mexico utilized wheat lines from Kenya that were resistant to race 15B.

The source of resistance to race 15B in the Winnipeg breeding program came about by a combination of serendipity and keen foresight. In the fall of 1930, J. McMurachy was having lunch with his daughter Helen in a field of badly rusted Garnet wheat that he was harvesting near McConnell, Manitoba (17). While eating, McMurachy noticed two stalks of wheat that were not infected with stem rust and gave the seed from the plants to Helen for safekeeping. Approximately 70-80 kernels were obtained from the two plants. However, in the following spring when McMurachy went to plant the seed for increase, he found that only 11 kernels remained because mice had eaten most of the sample during the winter. McMurachy planted the remaining seed, regularly irrigated the plot, and was able to obtain an ink bottle full of kernels in the fall. McMurachy continued to increase the selection every year and, by 1935, had sufficient seed to plant six acres. This selection of wheat was very resistant to stem rust and yielded 35 bushels to the acre when wheat in the adjacent fields was not worth harvesting due to stem rust. Eventually, news of this rust-resistant wheat reached the Rust Lab in Winnipeg, and McMurachy personally delivered 10 lbs. of seed to be used for further testing. The variety McMurachy, as the selection came to be called, had very good seedling and adult-plant resistance to all the known races of stem rust; however, it had poor milling and baking qualities, and the agronomic characteristics made it unsuitable for production in Manitoba. The selection by itself would not be useful as a cultivar, but could be used as a stem rust-resistant parent. In 1939, McMurachy wheat was crossed with the leaf rust-resistant cultivar Exchange, which had been obtained from Purdue

University. The wheat line RL 2265 which had both stem and leaf rust resistance was selected from this cross.

When the search for resistance to race 15B began, it was already known that McMurachy was resistant to all other stem rust races, and it had been used as a parent in the crossing program. In 1945, RL 2265 was crossed and backcrossed to the new cultivar Redman, a derivative of Renown, to develop a wheat cultivar with resistance to race 15B and acceptable agronomic and grain quality characteristics.

In the summer of 1950 in the north-central United States, stem rust pustules began appearing on wheat cultivars that previously had been resistant. These varieties included the bread wheats and the durum wheats. The infections were subsequently shown to be caused by race 15B which occurred at 27% of isolates in the United States in 1950 (27). Before 1950, race 15B had been present at very low levels. The lateness of the rust epidemic on the spring wheats in 1950 allowed race 15B to become established on the winter wheats in the southern plains states. It was immediately obvious that this stem rust race would cause serious damage to all of the currently grown wheat cultivars, bread wheats and durum wheats alike. As a result, a wheat stem rust conference was held in St. Paul, Minnesota, in November 1950. The purpose of the conference was to summarize the information available on race 15B, make plans for the dissemination of new information and breeding materials, and develop plans to further strengthen the international cooperative programs in stem rust research. At the conference, it was decided to organize on a regional and international basis a special collection of wheat lines to supplement the regional nurseries. This collection was to be used for selecting stem and leaf rust resistance material and was grown at various locations in the United States, Canada, and Latin America. H.A. Rodenhiser of the USDA at Beltsville, Maryland, also reported that a collection of 740 wheat lines had been planted in the spring of that year at locations in South America, Mexico, and Texas, to evaluate the entries for stem rust resistance. This collection was the start of the International Spring Wheat Rust Nursery. Further wheat stem rust conferences were held in Winnipeg in 1953 and Mexico City in 1956.

At Winnipeg, the most promising material with resistance to race 15B was from the RL 2265 x Redman^3 crosses, which had resistance to race 15B derived from McMurachy. In the fall of 1952, the derived line C.T. 181 was determined to have acceptable milling and baking qualities and agronomic attributes that would make it suitable for production in Manitoba. This line also had better stem rust resistance than McMurachy or Redman, good leaf rust resistance, as well as resistance to bunt and loose smut.

Race 15B continued to increase in frequency and caused the most severe yield losses in wheat since the 1935 epidemic. By 1953, 63% of the stem rust isolates in the United States were race 15B. The loss in Minnesota durum wheats due to stem rust was 75% and 10% loss in bread wheats (27). Forty million bushels of wheat were lost due to stem rust in Manitoba in 1953. It became critical to have a cultivar with resistance to race 15B. A rapid seed increase of C.T. 186 (a selection of C.T. 181) was undertaken in cooperation with the U.S. Department of Agriculture. In the fall of 1952, 150 acres of C.T. 186 were sown at locations in California and Arizona. From this crop, 5,000 bushels were harvested in the spring of 1953 and were then planted for increase in western Canada. C.T. 186 was licensed under the name Selkirk and was accepted for cultivar status in 1953. The resistance gene in Selkirk was later designated as *Sr6* (24). Selkirk also had *Sr2*, which was derived from Redman. By the spring of 1954, enough seed of Selkirk was available to sow 170,000 acres in Manitoba.

In the spring of 1954, conditions were nearly perfect for a stem rust epidemic in the northern plains: the vast majority of wheat cultivars were susceptible to race 15B; the crops were planted late due to a wet spring; extensive infections of stem and leaf rust were present in the Kansas winter wheats; and strong southerly winds in May and June deposited rust on the young wheat plants in Manitoba and Saskatchewan (17). The stem rust epidemic of 1954 in Canada and the United States was of unequalled destruction. In Manitoba alone, losses were estimated at 150 million bushels. Because Selkirk was resistant to both stem and leaf rust, the small amount of it that was planted yielded 35 bushels per acre. The cultivar Lee, resistant to leaf rust but susceptible to stem rust, yielded 21 bushels; Thatcher, which was susceptible to stem rust race 15B under high inoculum conditions and was also leaf rust susceptible, yielded only 14 bushels. As a result, by 1956, Selkirk was the dominant cultivar in the rust area of Manitoba, eastern Saskatchewan, and in Minnesota and North Dakota. Selkirk provided excellent resistance to stem rust for the next ten years, even though stem rust races were found that had virulence to the Selkirk resistance. These races never increased to damaging levels during the time Selkirk was widely grown. Eventually, Selkirk was replaced in Canada and the United States in the 1960s by cultivars with better leaf rust resistance, higher yield, and superior grain quality. In Mexico, the wheat cultivar Kentana 48 was released by the Rockefeller Foundation in 1948. Although this cultivar was not specifically bred for resistance to race 15B, it had *Sr6* which was derived from Kenya C9906. Chapingo 52 and Bajio 53 were later CIMMYT wheats with stem rust resistance derived from Kentana 48. In the Minnesota breeding program, the first wheat cultivar that had *Sr6* was Chris (named after J.J. Christensen, former department head of Plant Pathology), with the resistance derived from Kenya 58.

The International Wheat Rust Nursery

The spring wheat rust nursery was continued after the decline of race 15B in North America. The entries in the nursery were initially planted in Mexico, Colombia, Ecuador, Peru, Chile, Argentina, and Brazil. Within a few years, the nursery was also planted at locations in Asia and Africa. In 1955, the United States Congress made a special appropriation for foreign testing and seed increase of cereals. The nurseries were then expanded to include winter wheat, barley, and oats. Standardized methods of evaluating the entries for rust severity and type of response were established in order to present the data from different locations in a uniform manner. Cooperators from across the world were asked to contribute lines which they thought had good rust resistance potential. The spring wheat nursery contained entries from up to 50 different sources, with 38% of the lines originating from breeding programs in the United States and the balance from foreign programs. In 1971, seed of the spring wheat nursery was sent to 64 locations throughout the world. The International Rust Nursery Program served as a direct source of commercial cultivars and rust-resistant parents in many breeding programs and provided a means to increase cooperation among different wheat researchers throughout the world. USDA funding of the program lasted until 1987.

In North America, race 15B began to decline after 1954, and race 56 again became the most common race. The Thatcher resistance conditioned by *Sr12* was once again effective against the prevailing stem rust population. Since Selkirk, the breeding program at Winnipeg developed cultivars such as Canthatch (Thatcher resistance + *Sr7a*), Manitou (Thatcher resistance + *Sr6, Sr7a*), and Neepawa (Thatcher resistance + *Sr7a, Sr9b*). Since 1969, most of the cultivars released have been selected from intercrosses of various Neepawa backcross derivatives. The Thatcher adult-plant resistance, originally derived from Iumillo durum wheat, is still highly effective (21). Dyck determined that the cultivar Roblin had two adult-plant genes for stem rust resistance that were probably derived from Thatcher (8). Liu and Kolmer showed that Pasqua, derived from an intercross of two Neepawa backcross lines, had *Sr6* and also two adult-plant genes that were most likely derived from Thatcher (22). At high levels of disease pressure in inoculated nurseries, the Thatcher adult-plant resistance is not highly effective; however, inoculum levels of stem rust have been low since the epidemics of the 1950s, and there have not been significant losses due to stem rust in the North American hard red spring wheats since that time. Although additional *Sr* genes have been used in recent cultivars, the Thatcher-type stem rust resistance is still important.

The stem rust resistance derived from Yaroslav emmer (*Sr2*) has been used in many breeding programs throughout the world. With the exception of the race 15B epidemics, cultivars with this gene have maintained effective stem rust resistance for many years. The United States wheats Era, Butte, Waldron, and Marshall, along with the Canadian cultivar Pembina, were derived from wheats with *Sr2* and also have Thatcher in their pedigrees. Liu and Kolmer determined that *Sr2* may be present in AC Taber, a recent Canadian cultivar (22). *Sr2* is present in many of the CIMMYT wheats that have been distributed world wide. McIntosh et al. stated that *Sr2* is arguably the most important gene for stem rust resistance and one of the most important disease resistance genes to be used in modern plant breeding (24).

Conclusion

In recent years the stem rust races that occur on wheat in North America have changed very little, and the Thatcher and *Sr2* adult-plant resistance have remained effective. It is virtually impossible to find a single pustule of stem rust on spring wheat cultivars bred for rust resistance from breeding programs in western Canada and the north-central United States. From time to time, introduction of a new stem rust race such as QCC may occur (11). Given the current very low levels of virulence diversity in isolates of *P. graminis* in North America, it is difficult to see how new stem rust races could arise that would be virulent to the resistance in the currently grown spring wheats (20). However, this would be a complacent view, overly influenced by success in the immediate recent years and forgetful of the painful lessons learned in 1935 and again during the race 15B epidemics of the 1950s when it was also thought that the stem rust problem had been solved. Re-establishment of barberry stands in the midwestern United States may yet facilitate sexual recombination in the *P. graminis* population, thus providing a source of new physiological races that could potentially have virulence to the current wheat cultivars grown in Canada and the United States.

In any event, much of our knowledge concerning the epidemiology, genetics, and disease resistance aspects of wheat stem rust dates from research carried out by a remarkable group of scientists from 1915 to 1955. Advances in biotechnology may help us to explore new avenues of research, especially in cloning and sequencing of avirulence and resistance genes. However, much also remains to be done in the traditional areas of the genetics of stem rust resistance in wheat and the genetics of avirulence in *P. graminis* because after all "plant diseases are shifty enemies" (26).

Acknowledgments

In the preparation of this chapter, I had the pleasure of reading a number of original papers and previous summaries regarding this period of stem rust research. There are a few references which I feel merit particular attention,

as I have at times borrowed extensively from them. Clyde Christensen's biography of E.C. Stakman was very useful for providing a framework of Stakman's work in bridging hosts, physiologic specialization, and the early rust surveys (4). A monograph of the physiologic specialization and genetic studies of *P. graminis* conducted by Margaret Newton and Thorvaldur Johnson is an excellent summary of their work to 1932 (25). John Craigie prepared an extensive monograph that summarized the epidemiological studies of *P. graminis* (6). Most of all, I have leaned on Thorvaldur Johnson's *Rust Research in Canada and Related Plant Disease Investigations,* published by the Canada Department of Agriculture in 1961 (17). This monograph is an insightful history of plant pathology research at the Dominion Rust Research Laboratory in Winnipeg. Finally, I thank M. Malyk and Reg Sims for allowing me access to the Buller collection and photographs in the archives of the Agriculture and Agri-Food Canada Cereal Research Centre in Winnipeg.

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