1

Contributions of Early Scientists to Knowledge of Cereal Rusts

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I. Introduction

Cereal rusts have no doubt been present and evolving during domestication of cereal crops as a major segment of agriculture. Kislev (1982) reported archaeological evidence of *Puccinia graminis* on wheat lemma fragments dated at 1400–1200 B.C. Savile and Urban (1982) reviewed the evolution of cereal rusts relative to human-guided evolution of cereal crops. Ancient observations of cereal diseases and attempts to relate them to specific modern diseases such as rusts, smuts, and mildews were reviewed by Arthur (1929) and Chester (1946). The history of these diseases thus fades into antiquity. However, recognizable references are found in the oldest literature, much of which was summarized by Chester (1946). Arthur (1929) referred to biblical sources and to Grecian and Roman writings. This chapter starts with the recognition of "rust" as a parasitic fungus in 1767.

Recent advancements in understanding are based on preceding work. Thus it is useful to include a history of major contributors who provided the foundation for the current understanding of cereal rusts. We proceed through the intellectual leaders and breakthroughs of the late 1800s and early 1900s and end with those who worked into the mid-1900s with emphasis on researchers who are now deceased. More recent history is found in specific chapters in both volumes of this treatise. Any account of history is not totally objective. Decisions must be made concerning whom and what to cover. Often a person's location had an influence on the impact of the work. Certain works were more widely read and cited because of language, availability, or audience, possibly to the exclusion of other useful but less widely recognized works.

In terms of scholarly contributions, the early detailed descriptions of cereal rusts are those of Fontana (1767) and Targioni Tozzetti (1767), both at Florence, Italy, but published independently. These writings were translated into English and published by the American Phytopathological Society as "Phytopathological Classics."

II. Description and Taxonomy of Cereal Rust Fungi

A. G. TARGIONI TOZZETTI (1712–1783)

The contribution of Giovanni Targioni Tozzetti (1767) is encompassed in a chapter on diseases of plants, which is the fifth and last part of a much broader volume addressed "for the relief of the poor" but largely meteorological and agricultural in nature. Goidànich (1943) described Targioni Tozzetti's "Alimurgia" chapter as "the first treatise on plant pathology, in the sense in which today we would speak of such publications." Targioni Tozzetti described rust as "the terrible scourge . . . to which the fields of the greater part of the temperate zone of the Northern Hemisphere have been subjected . . . even from distant ages. . . ." He further proposed that rust "merits the most serious attention of naturalists for the purpose of investigating the causes of it, and proposing, if it should be possible, some remedy." The year before his publication (1766) was one of severe rust attack "in which the rust was universal over the whole of Italy, and in all the different levels and exposures of its territory." He stated it to be "certain that the rust is a very ancient scourge of the greater part of the country, cultivated by mankind in the old world," and he referred to the scriptures and the writings of Theophrastus in Greece, and Varro, Horace, Virgil, and Pliny in Italy. "The ancient writers . . . were ignorant of the true nature of the rust, but nevertheless noted punctiliously some phenomena and effects."

He found rust to be "little groups or masses . . . situated under the cuticle of wheat." The original tiny spots were reported to amplify and swell speedily, separating cuticle from parenchyma, producing a blister. The rust then becomes visible as a very fine powder. As first appearing, it is a bright yellow, soon becoming orange, and finally after days, becoming black. He found that rust increased as it generated anew on successive days; however, a "bunch . . . does not grow, nor distend more than to its final fullness, which it has attained to cause the cuticle to split." The rust was microscopically examined, and the change from orange, rounded bodies, obtained from young masses, to black, more oblong and pointed bodies, being attached by little stalks, was observed. He reported that each "knot of rust . . . is an internal, very tiny, parasitic plant." He concluded that all of the rusts that he had enumerated formed "a section or family of microscopical parasitic intercutaneous plants."

B. F. FONTANA (1730–1805)

Felice Fontana's contribution was an independent small pamphlet (1767), also motivated by the cereal rust epidemic of 1766. He stated that "On the 10th of June of last year, I discovered that the rust, which had devastated the lands of Tuscany, is a grove of plant parasites that nourish themselves at the expense of the grain." After discussing and discarding the contemporary theories on the nature of the rust, he described "ovules" that were a dark reddish yellow and "nails" with large rounded heads and the appearance of fungi. These two kinds of rust were described in considerable detail from both visual and microscopic observation and carefully illustrated. He discounted the presence of active movement as by an animal and suspected "that the nails are very minute plants that nourish themselves at the expense of the grain." Each form occurred alone, such that the "eggs" always came from reddish spots, and the "nails" from black-rust spots. He concluded that there were two kinds of rust on the grain crop, although the two also occurred together. On extensive, difficult examination, he occasionally observed very delicate stems connected to the "eggs," and concluded that they likewise were plants.

Having established, to his satisfaction, that grain rusts were masses of incalculable numbers of small parasitic plants, Fontana explained their devastating effect on grain yield, due to their absorption of nutritive materials from leaf and stalk tissue. He related severity of damage to the time of attack. He made a plea for additional research on the nature of the disease and on the nature and "economy" of the parasitic plants causing it, because such information would facilitate discovery of control measures.

C. C. H. PERSOON (1755–1837)

Following the major advances in plant taxonomy by Linnaeus from 1735 through 1753 (Reed, 1942), Christiaan Hendrick Persoon (1794), an independent Dutch researcher, made the first significant effort at classification of fungi. With advances in use of the microscope, the major fungal groups as now known could be recognized. Within his classification of 77 genera of fungi, he established three genera of rusts: *Aecidium, Uredo,* and *Puccinia. Puccinia* was taken from earlier work of Micheli (Arthur, 1929) but in a different usage. The genera *Aecidium* and *Uredo* are now designated as "form-genera" and are applied only to aecial or uredial stages for which the full life cycle is not known. Arthur (1929) credited Persoon as the first to recognize the rusts as a distinct group. Thus Persoon provided the first binomial epithets to rusts recognized as such. With complex life cycle relationships not yet established, he gave separate designations for telial, uredial, and aecial states of heteroecious forms such as the cereal rusts, with *Puccinia graminis* Pers., *Uredo linearis* Pers., and *Aecidium berberidis* Pers. being the species names given to the respective forms of the stem rust fungus. The latter names are now relegated as synonyms for the telial designation. Persoon (1801) is the authoritative landmark for Uredinales, Ustilaginales, and Gasteromycetes, and the beginning of accepted nomenclature for the rust fungi and these other groups.

D. L. R. TULASNE (1815–1885)

Louis René Tulasne was a French mycologist who collaborated with his brother Charles, the illustrator of their works. His major classification of the rusts (1854b) was published one year after de Bary's famous "Die Brandpilze," and provided the basis for all subsequent taxonomic treatments of the rust fungi (Arthur, 1929). He categorized the rusts into five groups: Aecidnei, Melampsorei, Phragmidiaceae, Pucciniei, and Cronartiei. The morphology and development of these fungi were studied more thoroughly than before. Tulasne and Tulasne (1847) illustrated and correctly interpreted germination of teliospores and illustrated germ pores on both urediospores and teliospores. Tulasne (1853) was the first to suggest that the rust fungi were basidiomycetous in nature, a concept subsequently further developed by Brefeld. The Tulasne brothers greatly expanded the knowledge of structure of fungi, which provided the basis for subsequent studies of life histories. Tulasne (1854a) himself showed that uredia and telia on wheat stems arise from the same mycelia and are not two distinct species of fungi (Craigie, 1931).

E. J. C. ARTHUR (1850–1942)

Joseph Charles Arthur was the leading American uredinologist, publishing from 1882 until 1936, with many of his publications after his official retirement in 1915. He studied life cycles, relationships, classification, and distribution, and was influential in the development of the rules of botanical nomenclature. Brief reviews of his life and works were published by Kern (1942) and Cummins (1978); both were former students, and the latter was his successor for many years at Purdue University. Arthur described many new species of rust fungi, studied host relations through experimental inoculations, and established life histories of many species of rust fungi. Beginning in 1905 and culminating in his "Manual" in 1934, he modified and updated classification of the Uredinales. His 11 parts of the *North American Flora* on the Uredinales, between 1907 and 1927, were the backbone of this effort (Kern, 1942). His valuable contributions on structures and their importance and on life cycles were often rejected because of objections to his nomenclatural proposals. He abandoned some of his earlier nomenclatural positions when writing his "Manual" near the end of his career (Cummins, 1978). "The Plant Rusts" and "Manual," his two major books, are addressed in Section VIII,I.

Arthur also initiated an extensive herbarium of plant rust specimens, located at Purdue University, and now known as the Arthur Herbarium. Baxter and Kern (1962) credited the original nucleus to collections by Arthur when a student. This herbarium, one of the finest in the world, contains over 100,000 specimens of rust fungi (J. Hennen and J. McCain, personal communication).

Arthur (1905) introduced the terms "pycnium," "aecium," "uredinium," and "telium" to designate the principal spore-bearing structures found in rusts. The corresponding spore forms were designated "pycniospores," "aeciospores," "urediniospores," and "teliospores." These terms avoided confusion with names of form-genera—as for example, the term "uredospore," which had been widely used—and gained wide acceptance in North America. Later, Arthur (1932) changed "uredinium" to "uredium," and he introduced the corresponding term "urediospore." Arthur also emphasized that spore forms in rusts should be designated in relation to the preceding form in the life cycle and not only by morphology. Savile (1968) found this to be unworkable for some rusts, leading him to reject "uredium" in favor of a return to "uredinium," which he also found to be etymologically more appropriate. Although controversies over terminology in rust continue (Cummins, 1978), Arthur's terms—in either the 1905 or 1932 version—predominate in North America.

F. J. ERIKSSON (1848–1931)

Jakob Eriksson (1894), a Swedish pathologist, reported that individual cereal rust fungal species were not homogeneous in their host ranges. This provided for a further "taxonomic" separation within species based on host specificity. This concept was further developed in a major publication on the cereal rusts (Eriksson and Henning, 1896; see Section VII,C). These pathogenically specialized taxa within species were designated *formae speciales*. In a series of publications from 1894 through 1908, Eriksson studied this phenomenon extensively. His work stimulated further studies, and others including Klebahn, Schroeter, Hitchcock and Carleton, Rostrup, and Magnus also soon contributed to the development of this knowledge (Arthur, 1929).

G. E. C. STAKMAN (1885–1979)

Elvin Charles Stakman became a graduate student at the University of Minnesota in 1909 (Christensen, 1979). By this time, Eriksson and others had divided *Puccinia graminis* into *formae speciales*, based on their ability to parasitize various host species. The stability of these was questioned by Ward (1903), who believed that when *Puccinia dispersa* was avirulent on a *Bromus* species, virulence could be derived by culturing the rust on a host taxonomically between the resistant species and the common host of the rust. This bridging-host concept suggested that the *forma specialis* might not be a valid taxonomic division. E. M. Freeman, who had studied with Ward, was Stakman's advisor, and he started Stakman testing the bridging host concept with *P. graminis*. Of 15 wheat cultivars included in the study, not all were susceptible to *P. graminis* f. sp. *tritici* (Stakman, 1914). The work was expanded to a wider host range, and pathogen cultures were obtained from many locations in the United States (Stakman and Piemeisel, 1917b). This widespread sampling led to detection of different phenotypes for pathogenicity within *formae speciales*, and different phenotypes for resistance within host species. Twelve separate forms of *P. graminis* f. sp. *tritici* were found in the United States (Stakman *et al.*, 1919). These studies showed, contrary to the bridging-host theory, that *P. graminis* comprised many stable forms (Stakman *et al.*, 1918). Each form (physiologic race) was a constant identifiable group of individuals within a *forma specialis* of *P. graminis*, based on infection types produced when inoculated to a selected group of hosts. Thus physiological race became a second-level taxon determined by physiological rather than morphological characters. The presence of these forms explained the differences in resistances shown by host cultivars in different locations. The concept placed breeding for host resistance on a firm basis, as consistent results could be obtained when the same pathogen race was used or was present in the natural population. The work on physiologic specialization was continued, with the first key to races published by Stakman and Levine (1922). This key set forth the 12 differential hosts that became the international set for wheat stem rust. It was last updated in 1962 (Stakman *et al.*, 1962) and is still widely used (Roelfs, Chapter 5, this volume). These studies made a tremendous impact throughout all of plant pathology. Variants were rapidly found in other pathogens, and breeding for rust resistance accelerated.

III. Life Cycles and Cytology of Cereal Rust Fungi

A. A. DE BARY (1831–1888)

When Anton de Bary (1853), at age 22, wrote his famous monograph on the "Brandpilze," he regarded the uredial and telial stages of rusts as two distinct fungal species, living communally as a mixture of mycelia within pustules. The "aecidial" forms on alternate hosts were also thought to be independent species, although de Bary recognized that rust in grain occurred near barberry ". . . whether it be because of this in and of itself or because of the Aecidium growing on its leaves."

In successive university positions at Tübingen, Freiburg, Halle, and Strasbourg, de Bary continued to apply his remarkable abilities to observe, experiment with, and interpret plant diseases, publishing his principal works on cereal rusts in 1866 and 1867. He recognized, as had Tulasne (1854a), that uredia and telia were successive stages of a single fungus, and he showed by inoculation experiments that the "aecidial" stages on dicotyledonous species were alternate stages of the cereal rusts. He studied *Puccinia graminis, P. coronata,* and *P. straminis* (*recondita*) on their grass hosts and their respective alternate hosts, Berberis, Rhamnus, and Anchusa. He described germination of urediospores, penetration of gramineous hosts through the stomata, and subsequent development of uredia. de Bary further described germination of teliospores and production of basidiospores. In turn, he described germination of basidiospores on the alternate hosts, development of appressoria, direct penetration of host epidermal cells, and formation of pycnia and aecia. He described pycniospores and later (1884) conjectured that they were sexual fertilizing bodies such that aecia were the product of the presumed fertilization, a concept proven much later by Craigie (Section III,D). de Bary (1867) also showed that aeciospores produce germ tubes that produce appressoria over stomata, then enter the stomata and produce uredia on gramineous hosts. Thus he established the complete succession of spores in macrocyclic rusts as understood today. de Bary introduced the term *heteroiceous* (heterröcisch) for rusts that require more than one host to complete their life cycle.

B. H. M. WARD (1854–1906)

Harry Marshall Ward, working at Cambridge University, and once a student of de Bary, undertook studies of *Puccinia dispersa* on *Bromus* spp., including a careful cytological investigation of infection by urediospores (Ward, 1904). He was particularly interested in formation of haustoria, because he believed that Eriksson had mistaken haustoria for "*corpuscules speciaux,*" a form in which Eriksson thought the rust fungus emerged from an invisible "mycoplasm" stage. Ward 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. The number and location of nuclei were shown for each type of fungal cell.

Ward (1905) extended his studies to wheat infected with *P. glumarum* (*striiformis*), including development on an immune cultivar obtained from Biffen. He described "death changes" in the immune host, what Stakman (1915) later termed "hypersensitiveness." Ward surmised that host cell death resulted from either starvation or poisoning and that ". . . the hyphae attack the cells too vigorously at the outset." Resistance responses of nonhost species to several rust fungi, including *P. graminis* and *P. glumarum* (*striiformis*), were described cytologically by Ward's student, C. M. Gibson (1904), who showed that the fungi usually were able to enter stomata, although several failures to enter were recorded.

C. V. G. TRANSHEL (1868–1942)

Vladimir Genrikhovich Transhel was influenced by M. S. Voronin, 30 years his senior and regarded as the founder of Russian mycology, who in turn had been a student of de Bary. Most of Transhel's career was at Leningrad (St. Petersburg), where he described and curated mycological collections. He also wrote theoretical compositions including "Rust Fungi in their Relation to the Systematics of Vascular Plants" (1927), "'Fischer's Law' and 'Transhel's Method' in Rust Fungi" (1934a), and "Alternate Hosts of Grain Rusts and their Distribution in the USSR" (1934b). He summarized 50 years of his studies in "Conspectus" (1939), his most comprehensive work (Section VII,K). Like Arthur in the United States, he established a major herbarium of rust fungi, which is actively maintained in the Institute of Botany in Leningrad.

Transhel is best known for his life-cycle studies, which he continued from earlier research by Voronin. He proved the relationships of numerous heteroecious rusts and determined host specialization of many species. Of particular interest is Transhel's method or law, proposed in 1904 (Kuprevich and Transhel, 1957). This is a method of prediction stating that on finding morphological similarity between the telial stages of a presumed heteroecious rust on one host and a microcyclic species on an unrelated host, the aecial host of the heteroecious rust will likely be the same as, or related to, the host of the microform. He explained this relationship on an evolutionary basis; that is, although aecia and uredia are lost from the life cycle, basidiospores can infect only the previous aecial host; thus for a microcyclic species to complete its life cycle and survive without aecia, telia are now required on the previous aecial host. This "law" led to the concept of correlated species and later the broadening of its definition by Cummins (1959) to include endocyclic species.

In Transhel's correlative taxonomic studies with rusts and hosts, he reported that primitive Uredinales parasitize ferns, whereas more highly differentiated rust species attack advanced plant families such as Leguminosae and Rosaceae. He also found that rusts may distinguish groups of hosts more readily than taxonomists, thus assisting in taxonomic studies of higher plants (Transhel, 1936). Transhel's ideas in relation to evolution of cereal rusts are discussed further in Wahl, Chapter 2, this volume.

D. J. H. CRAIGIE (1887–)

After years of speculation by uredinologists about sex in the rust fungi and the function of pycnia and pycniospores, John Hubert Craigie (1927a,b), at the Canadian Dominion Rust Research Laboratory, found that pycnia are in fact sexual structures and that the rust fungi studied are heterothallic but not dioecious. With cytological support from subsequent workers (Andrus, 1931; Allen, 1930), his research showed that pycniospores are functional male gametes. [Harder (Chapter 11, this volume) describes the sexual function of pycniospores.]

The cytological basis for Craigie's discovery had been set by Sappin-Trouffy (1896), whose studies under Dangeard's direction showed that pycniospores and the hyphae from which they originate are uninucleate, but that aeciospores and urediospores are binucleate, as are the cells of immature teliospores (Craigie, 1931). Sappin-Trouffy showed that conjugate nuclei fuse during maturation of teliospores and that two divisions, one a reduction, occur in the basidium (Arthur, 1929). This was considered a sexual process. Blackman (1904) demonstrated the origin of the binucleate condition at the base of the aecium, but the source of the nuclei involved in dikaryotization was not known.

Craigie's research solved the final enigma of sex in the rusts and ended years of controversy revolving around this gap in understanding rust life cycles. It opened the vista for subsequent cytological and genetic studies. A more thorough treatise was published later (Craigie, 1931), with an extensive literature review on the problem and the history of previous developments as well as a comprehensive presentation of the details of his experiments. Green *et al.* (1980) provided a biography.

E. R. F. ALLEN (1879–1963)

Ruth F. Allen, United States Department of Agriculture and University of California, published two series of cytological investigations of cereal rusts. The first described development of infection structures and uredia in cereal hosts; the second showed stages of infection and development of pycnia and aecia in alternate hosts. These studies were characterized by excellent comprehensive descriptions, presented in both words and drawings.

Allen's work on uredial development was directed largely toward comparisons of resistant and susceptible wheats (e.g., Allen, 1924, 1926, 1927). For *Puccinia graminis* and *P. triticina* (*recondita*), fungal development was followed through formation of appressoria, substomatal vesicles, infection hyphae, haustoria, and intercellular hyphae. The number of nuclei per fungal cell was clearly documented through each developmental stage. Responses of chloroplasts, nuclei, and cytoplasm in host cells were shown in both susceptible and resistant hosts. The collapse and death of host cells as part of the resistance response was shown. These descriptions remain the basic reference work for cereal rust cytologists and physiologists, especially those concerned with compatibility and incompatibility.

Following Craigie's discovery of heterothallism in rusts in 1927, Allen (e.g., 1930, 1932, 1934) used her cytological expertise to describe development of pycnia and aecia in cereal rusts, including work with *P. graminis, P. triticina* (*recondita*), *P. coronata,* and *P. sorghi.* She described the development of germ tubes and appressoria from basidiospores, the penetration of the leaf, the development of hyphae within the leaf, and the formation of pycnia and aecia. She showed pycniospores fused with paraphyses of the pycnium, provided evidence that pycniospores fuse with "receptive hyphae" emerging from the leaf surface, and that pycniospores could germinate and invade leaf tissues, the latter two phenomena disputed by Buller (Section VII,H).

F. M. NEWTON (1887–1971)

Margaret Newton teamed with Thorvaldur Johnson and A. M. Brown at the Canadian Dominion Rust Research Laboratory to pioneer genetic studies on *Puccinia graminis* in the period immediately following Craigie's discovery of heterothallism and the function of pycnia. This research group monitored the occurrence of races of the fungus as a practical follow-up of Stakman's earlier research. They found occasional color mutants. Subsequently, they pursued the sexual cycle of the fungus and studied the genetics of uredial pathogenicity and spore color following hybridization on the barberry (Newton *et al.*, 1930a,b). This effort produced knowledge on inheritance of pathogenicity, as described by race designation, along with contemporary studies in the United States (Stakman *et al.*, 1930) and Australia (Waterhouse, 1929a). It provided the genetic information to parallel the cytological research pursued concurrently by Allen (1930). When combined with host plant genetics, this was a stepping stone to the classical interorganismal genetics of Flor (1946) in the next decade (Section VIII).

A major treatise on pathological specialization, race distribution, and hybridization of *Puccinia graminis* f. sp. *tritici* was published by Newton and Johnson (1932). They pointed out that as long as the rust fungus remained in the uredial stage, permanent changes in pathogenicity were rarely encountered. In contrast, on completing the life cycle on barberry, races were found usually to be heterozygous for pathogenicity, segregating and recombining into new races. For the most part, hybridizing followed Mendelian laws, although some cytoplasmic influences were evident. Similar studies were continued for some years by this research group and particularly by Johnson following Newton's retirement in 1945.

IV. Epidemiology of Cereal Rusts

A. E. C. STAKMAN (1885–1979)

In addition to his studies on pathogenic specialization (Section II,G), Stakman became interested in sources of inoculum for the vast epidemics of stem rust in North America in 1904 and again in 1916. With the finding of the second biologic form of *P. graminis* f. sp. *tritici* in 1916 (Stakman and Piemeisel, 1917a), there were detectable markers in the pathogen. This assisted in the identification of sources of inoculum (Stakman and Hoerner, 1918). Starting in 1917, Stakman and co-workers began a study of the epidemiology of wheat stem rust. Methods of conducting field surveys, collecting samples, trapping spores, and following spore movement were developed and spread worldwide by Stakman, his co-workers, and students. These studies continued for 36 years under his guidance.

Studies elsewhere indicated the involvement of barberry as a source of inoculum. Although others had major roles (H. L. Bolley deserves special mention), Stakman personally led a campaign to eradicate susceptible *Berberis* and *Mahonia* species as a source of inoculum of *P. graminis.* This campaign involved administrative, scientific, and publicity phases. Stakman *et al.* (1934) utilized Canadian, Australian, and American research on sexuality and variation to support barberry eradication. The effects of this program have been summarized by Roelfs (1982).

Studies were also initiated on movement of urediospores from the southern United States and Mexico. Spore traps were designed and exposed from aircraft and ground stations (Stakman *et al.*, 1923). Urediospores were abundant at altitudes up to 3333 m and were present in trace amounts to 5000 m. Spore numbers trapped were related to ground disease severities. The results of 30 year's study were summarized by Stakman and Harrar (1957).

Additionally, extensive annual field surveys were conducted to monitor disease severity and prevalence and to obtain collections for identification of physiological races (Stakman *et al.*, 1929). This information was used in selection of parents for breeding resistant cultivars (Harrar *et al.*, 1944). The effect of temperature on epidemics was analyzed (Stakman and Lambert, 1928). Histories were developed for individual annual epidemics (e.g., Stakman *et al.*, 1925; Stakman, 1935) and comparisons made between years (Stakman and Harrar, 1957). The history of development and spread of important pathogenic races was studied (Stakman and Cassell, 1938; Stakman, 1950). These long-term studies revealed relationships linking severity of stem rust epidemics with dates of disease onset (Hamilton and Stakman, 1967). These studies became the largest collection of epidemiological information obtained on a single plant disease.

B. K. C. MEHTA (1892–1950)

Karamchand Mehta became interested in cereal rust epidemiology at Cambridge in the early 1920s (Mehta, 1923). He shortly initiated experiments on the annual recurrence of rusts on wheat and barley in India (Mehta, 1933). During the next decade, Mehta determined that *Berberis* and *Thalictrum* spp. occurring in the hills of India did not have a significant role in the life cycle of rust in India (Mehta, 1929, 1933, 1940). He further found that intense summer heat (>38°C daily maximum lasting for weeks) destroyed rust in the plains where wheat is grown (Mehta, 1929). Mehta used extensive field surveys throughout India and Nepal to determine that rusts survive the summers in the Himalaya mountains of the north and the Nilgiri and Pulney hills in southern India (Mehta, 1929). Inoculum had to be blown from these areas to the wheat-growing regions (Mehta, 1952). Mehta's contributions were reviewed by Prasada (1950). The "green revolution" has created a renewed interest in epidemiology of the cereal rusts in India (see Nagarajan and Joshi, Chapter 12, Vol. II).

C. K. S. CHESTER (1906–1969)

Kenneth Starr Chester was an active researcher on cereal rust epidemiology in Oklahoma from 1937–1948, a relatively short period. His influence on epidemiology, however, was significant. He summarized great volumes of previous work including much from eastern Europe (Chester, 1946; Chester *et al.*, 1951). The conclusions presented by Chester were not always those widely held by his contemporaries, but by 1960 his work was widely respected and cited. His pleas for crop loss measurements (Chester, 1950) are only now receiving attention.

Chester's research involved the development of the "critical month" theory (Chester, 1946). This theory states that final severity of wheat leaf rust on fall-sown wheat is primarily determined during the spring 30-day period in which the daily mean temperature average is approximately 10°C (Chester, 1942, 1943, 1944). In Oklahoma this is the month of March, but it would be earlier farther south and later northward. In contrast, little correlation was found between the amount of leaf rust that developed in the fall and that occurring in the later spring. Little pathogen increase occurred until mean temperatures reached 10°C. The temperature and moisture during the 30-day period (critical month) immediately after winter when the normal mean temperature was 10°C were the most vital to disease development. Following this period little correlation was found between weather and final disease severity, because the daily mean temperatures were generally in the range that allowed pathogen development, and the interyear variation in weather did not significantly affect rust development. Thus the interyear variation of this later period was of no forecasting value. The rust prediction system developed by Chester was used successfully in Oklahoma for more than 30 years.

V. Resistance to Cereal Rusts

A. R. H. BIFFEN (1874–1949)

The rediscovery in 1901 of Mendel's laws of segregation and independent assortment of genes stimulated genetic evaluation of plant disease resistance data. The first report was by Rowland Harry Biffen (1905) at Cambridge. He crossed the stripe rust susceptible wheat cultivar Red King with the resistant Rivet. His F_1 plants were susceptible, and in the F_2 generation he found 195 infected plants and 64 rust-free plants—fulfilling a 3:1 prediction of Mendelian genetics, with susceptibility being dominant. (Observations earlier in disease development gave three categories in a 1:2:1 ratio, indicating incomplete dominance.) Resistance and susceptibility were also independent of other plant characters (Biffen, 1907).

The discovery of discrete, heritable differences created doubts about the bridging-host theory of Ward (1903), which held that 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 were found. However, the confusion resulting from the occurrence of physiologic races of pathogens, polygenic inheritance, varying effects of the environment on disease, and the bridging-host theory resulted in a continuing debate for several years before agreement was reached that Mendel's genetic principles were applicable to resistance against cereal rusts.

Biffen (1931) further reported that when resistance is intermediate and not clearly defined, the distinct classification of progenies becomes impracticable. He concluded that the details of inheritance are not so important, the significant result being that resistant lines are obtained, following segregation, in a stable form in later generations.

B. H. K. HAYES (1884–1972)

Three sources of resistance to cereal rusts have been of such great long-term value that they deserve mention. Perhaps other sources of resistance may subsequently be added to this list. Initial wheat breeding in Minnesota for stem rust resistance, led by Herbert Kendall Hayes, supplied a 1914 cross between Marquis hard red spring wheat and resistant Iumillo durum (Hayes *et al.*, 1920). Marquillo was selected in 1918 as a resistant hard red spring wheat and distributed in 1928. This cultivar did not become important, but in the next breeding cycle a sib selection was crossed with a Marquis/Kanred derivative in 1921. This cross was made to study the genetics of resistance when the parents were known to possess different types of resistance (Hayes *et al.*, 1925). Thatcher wheat was selected from this "double cross" in 1925 and released in 1934 (Hayes *et al.*, 1936). Although not yet in widespread use, Thatcher was spectacularly effective against the 1935 stem rust epidemic and provided valuable protection in 1937. Thatcher has *Sr5, 9g, 12, 16,* and at least two additional recessive genes, a combination that continues to provide useful resistance 55 years after the release of Marquillo (Nazareno and Roelfs, 1981).

Thatcher was an important parent in subsequent North American cultivars, Mida, Rushmore, Pembina, Justin, Chris, Era, Fortuna, Manitou, Waldron, Olaf, Sinton, Neepawa, and Marshall among many others, essentially all of the North American hard red spring wheats for many years. In the CIMMYT (Centro Internacional de Mejoramiento de Maiz y Trigo) program, Thatcher occurs in the pedigrees of Ciano 67, Yaqui 48, Penjamo 62, and through these lines in many others. The Australian cultivars Eagle, Gatcher, Mersey, Summit, Tarsa, and Zenith all have a Thatcher parentage.

C. E. S. MCFADDEN (1891–1956)

In 1915, shortly after the first Iumillo durum cross, Edgar S. McFadden found an emmer wheat to be resistant to stem rust. This emmer (designated Yaroslav) was also crossed to Marquis. A selection subsequently named Hope was made in 1923 on the McFadden farm near Webster, South Dakota (McFadden, 1925), and increased and released in 1927 (McFadden, 1930). Like Marquillo, Hope was not itself a successful cultivar. However, Hope and a sib selection H-44 were probably the widest used sources of stem rust resistance in the world. Hope possesses *Sr2, 7b, 9d,* and *17.* The adult plant resistance *Sr2* is still effective worldwide except under special circumstances at high inoculum densities (Sunderwirth and Roelfs, 1980; Roelfs, Chapter 1, Vol. II). Hope was back-crossed to Thatcher in Minnesota, and a selection with combined resistance named Newthatch was also widely used as a parent (Ausemus *et al.*, 1944). Important Hope and H-44 derivatives include Rival, Regent, Pilot, Mida, Rushmore, Selkirk, Renown, Pembina, Justin, Centurk, Scout, Genwari, Hopps, and numerous others. The present North American hard red spring wheats largely include a parentage of Thatcher and/or Hope or H-44, combined with additional genes for stem rust resistance.

D. I. BECKMAN (1896–1971)

In 1925, at the Veranopolis Experiment Station in Brazil, a cross was made by Iwar Beckman between two local wheat cultivars, Polysu and Alfredo Chaves 6121. These two locally grown cultivars had survived through the many diseases and soil problems common in Rio Grande de Sul. Lines from this hybrid were taken by Beckman to San Luis Gonzaga in 1926 and then to Bage in 1929. During a stripe rust epidemic, plants of this cross were unaffected. Beckman named several selections from this cross in 1934: Frondoso, Fronteira, and Surpreza.

To add earlier maturity he crossed Fronteira with Mentana, resulting in the cultivar Frontana. Unpublished reports do not indicate leaf rust resistance to be a major selection factor; however, resistance evidently was transferred from Alfredo Chaves 6121 to its offspring (Beckman, 1954). These cultivars, particularly Frontana, have been a major source of leaf rust resistance. *Lr13* from Frontana is utilized worldwide and is known to be an important part of the leaf rust resistance of the cultivars Chris, Era, and Columbus. Surpreza is a parent of Redcoat, the North American soft red winter wheat, and Frondoso of the Atlas cultivars.

E. W. L. WATERHOUSE (1887–1969)

Walter Lawry Waterhouse initiated research on cereal rusts in Australia in 1919 (Watson and Frankel, 1972). He started by collecting urediospores from as many sources as possible (Waterhouse, 1929b). This led to an interest in variation for virulence in the cereal rust pathogens. He established that passage of *Puccinia graminis* through barberry resulted in variation among aeciospores (Waterhouse, 1929a). He showed that within races of *P. triticina* (*recondita*), identified on the international differential series, additional variation could be identified using other sources of resistance (Waterhouse, 1929b). This demonstrated that races were not necessarily homogeneous units but "packages" of similar pathogenic characteristics as determined by a designated host series. Waterhouse also documented the effect of temperature on race determinations (Waterhouse, 1929b). His early experiences with variation in the pathogen populations provided the background that allowed Waterhouse and associates later to determine the effect of resistant cultivars on the frequency and distribution of combinations of virulence (Waterhouse, 1935; Watson and Waterhouse, 1949). He very early moved into breeding for resistance (Waterhouse, 1930). During the period of his activity, Australian cultivars progressed from very susceptible, to those possessing single gene resistance that was overcome in time, to cultivars with several genes for resistance that have remained effective (Watson and Waterhouse, 1949).

VI. Physiology of Cereal Rusts

Changes in host plant physiology as a consequence of rust in cereals were reviewed by Chester (1946), who emphasized that rust increases transpiration of cereals, adding to stress under conditions of limited water supply. From available studies of respiration, photosynthesis, and related processes in rusted cereals, Chester concluded that ". . . the effect of reduced photosynthesis is increased by its association with accelerated rates of respiration. . . . Meanwhile, the economical utilization of the products of photosynthesis is impaired by the disruption of normal translocation and amylase activities." These conclusions remain valid today (Bushnell, Chapter 15, this volume; Durbin, Chapter 16, this volume).

A. G. GASSNER (1881–1955)

As part of their comprehensive program to develop methods of rust control, Gustav Gassner and colleagues at the Braunschweig Technische Hochschule investigated the mineral nutrition of cereals in relation to rust development. They found that high levels of nitrogen favored rust development, whereas high levels of potassium tended to reduce it (Gassner and Hassebrauk, 1931, 1933). Rust development was correlated with capacity of leaves to assimilate CO_2 (Gassner and Goeze, 1932). Increasing the concentration of CO_2 in air to above normal concentrations enhanced CO_2 assimilation and in turn stimulated rust development (Gassner and Straib, 1929). Gassner and Franke (1938) determined the amount of protein and soluble nitrogen in leaf and stripe rusted wheat, showing that disease usually retarded loss of nitrogen compounds from wheat leaves. Gassner also showed that rust development varied with leaf position on adult cereal plants and with the age of leaves and plants (Gassner, 1932; Gassner and Kirchhoff, 1934).

B. S. DICKINSON (1898–)

Sydney Dickinson (e.g., 1949, 1971, 1977), Cambridge University, pioneered the study of cereal rust fungi on artificial membranes, showing that membrane surfaces stimulated formation of infection structures by germinating spores. He manufactured membranes from nitrocellulose and other materials, using carefully prescribed formulations to obtain the most effective membranes. Several developmental phenomena were observed, including zigzag growth of germ tubes and differentiation of structures resembling appressoria, substomatal vesicles, infection hyphae, and haustoria. This work clearly implicated the effect of leaf surfaces on fungal differentiation and led to ongoing efforts to understand the mechanisms involved (Staples and Macko, Chapter 9, this volume). Furthermore, Dickinson (1949) demonstrated that infection structures must be produced before leaf-colonizing hyphae can grow, a finding instrumental in the culture of *Puccinia graminis* on artificial media (Williams, Chapter 13, this volume).

C. P. J. ALLEN (1914–1976)

Paul James Allen (e.g., 1953, 1954, 1959), University of Wisconsin, wrote a series of influential reviews on the physiological aspects of plant disease. He had earlier determined rates of respiration and photosynthesis in powdery mildew of wheat and was interested in the causes of metabolic change in host tissues. His theory that a toxin uncoupled phosphorylation from respiration (Allen, 1953) stimulated research into the causes of respiratory change in powdery mildews and rusts. Later, Allen (1966) acknowledged that the toxin hypothesis was untenable and that the respiratory changes were akin to "wound" or "developed" respiration involving extensive cellular adjustment and new protein synthesis.

Allen also contributed to our understanding of germination of urediospores and differentiation of infection structures. He demonstrated that urediospores contained a self-inhibitor of germination, and that substances in spore extracts could induce differentiation of infection structures (Allen, 1955, 1957, 1976). This provided the foundation for work by others on spore and germling physiology (Staples and Macko, Chapter 9, this volume).

VII. Books and A Newsletter of Special Significance

Books of special importance to the cereal rusts are listed in Table I. Several of these, of course, are broader in scope than the cereal rusts. As evidenced by the citations in the present volumes, there is a further vast literature on cereal and other rust fungi. If, in addition to listing books, one chose to include comprehensive bulletins, or publications on local flora, the list would include many more entries from all over the world, in most written languages. Authors of several more general texts not listed here have used one or more of the cereal rusts as a vehicle in discussing epidemiology, genetics of pathogens, disease resistance, or other relevant topics. Except for the more recent listings,

Table I

Selected Books and a Newsletter of Major Worldwide Importance on the Cereal or Plant Rusts

Author(s)	Date	Title
de Bary, A.	1884	Comparative Morphology and Biology of the Fungi, Mycetozoa, and Bacteria
Plowright, C. B.	1889	A Monograph of the British Uredineae and Ustilagineae with an Account of their Biology Including the Methods of Observing the Germination of their Spores and of their Experimental Culture
Eriksson, J., and Henning, E. J.	1896	Die Getreideroste. Ihre Geschichte und Nature sowie Massregeln gegen Dieselben
Klebahn, H.	1904	Die wirtswechselnden Rostpilze. Versuch einer Gesamtdarstellung ihrer biologischen Verhältnisse
McAlpine, D.	1906	The Rusts of Australia. Their Structure, Nature, and Classification
Yachevski, A. A.	1909	[Rusts of Grain Crops in Russia]
Grove, W. B.	1913	The British Rust Fungi (Uredinales). Their Biology and Classification
Buller, A. H. R.	1924	Researches on Fungi, Vol. III
	1950	Researches on Fungi, Vol. VII
Arthur, J. C.	1929	The Plant Rusts (Uredinales)
	1934	Manual of the Rusts in United States and Canada
Lehmann, E., Kummer, H., and Dannenmann, H.	1937	Der Schwarzrost, seine Geschichte, seine Biologie und seine Bekämpfung in Verbindung mit der Berberitzenfrage
Transhel, V. G.	1939	[Conspectus of the Rust Fungi of the USSR]
Naumov, N. A.	1939	[The Rusts of Grain Crops in the USSR]
Chester, K. S.	1946	The Nature and Prevention of the Cereal Rusts as Exemplified in the Leaf Rust of Wheat
Vallega, J., Cenoz, H. P., and Tessi, J.L.	1956–1967	Robigo (A Newsletter)
Cummins, G. B.	1971	The Rust Fungi of Cereals, Grasses, and Bamboos
Kvostova, V. V., and Shumnyi, V. K.	1978	[Resistance of Wheat to Leaf Rust. Genetic Diversity of the Fungus and the Host Plant]
Littlefield, L. J., and Heath, M. C.	1979	Ultrastructure of Rust Fungi
Littlefield, L. J.	1981	Biology of the Plant Rusts, An Introduction
Scott, K. J., and Chakravorty, A. K., eds.	1982	The Rust Fungi

not considered "historical" at this time, the publications in Table I and their authors are reviewed here.

A. DE BARY, A. (1884) COMPARATIVE MORPHOLOGY AND BIOLOGY OF THE FUNGI, MYCETOZOA, AND BACTERIA

de Bary (Section III,A) brought together the mycological knowledge of his time in this book, perhaps the single most important mycological publication of all time. It was translated into English in 1887. Included among his comprehensive descriptions of structure and development were the cereal rust fungi, principally from his own studies of 1866–1867.

de Bary discussed the nature of parasitism and introduced the term "obligate parasites" for organisms such as rusts ". . . to which a parasitic life is indispensable for the attainment of their full development" including "strictly obligate parasites . . . which as far as we know, live only as parasites. . . ." He wisely cautioned that the definition ". . . hold(s) good in the natural, and . . . the spontaneous course of things. . . . Artificial conditions may in some cases be established which may result for example, in the development of a spontaneously and strictly parasitic fungus in a way not parasitic. . . ." Thus he anticipated culture of rusts on artificial media but believed this should not alter their classification as obligate parasites (see Williams, Chapter 13, this volume).

B. PLOWRIGHT, C. B. (1889) A MONOGRAPH OF THE BRITISH UREDINEAE AND USTILAGINEAE

Building on the work of Tulasne, de Bary, and others, Charles Bagge Plowright (1849–1910) presented descriptions and life histories of the known British rust and smut fungi. He discussed major structural and developmental features of urediospores, teliospores, pycniospores, aeciospores, and mycelia, including figures of germinating urediospores and teliospores of cereal rusts. He described the methods he used to study spore germination and to inoculate plants without contamination by unwanted rust spores. He reviewed the many reports indicating that barberry was associated with cereal rust and included the complete text of "The Barberry Law of Massachusetts" of 1764. He discussed the available evidence regarding the role of pycniospores and described their apparent budding, concluding incorrectly that they more likely functioned as conidia than as sexual organs.

C. ERIKSSON, J., AND HENNING, E. J. (1896) DIE GETREIDEROSTE

Two years following his exposition of *formae speciales* within the cereal rust fungi, Jakob Eriksson (Section II,F) joined with Ernst Johan Henning in this major reference work on cereal rusts. This book reviewed history, etiology, infection processes, and geography of occurrence of six cereal rust species, and included fine colored illustrations. Possibly the main long-term contribution was the detailing of *formae speciales* within the context of a thorough presentation on cereal rusts. They proposed four *formae speciales* within *P. graminis,* two within *P. dispersa* (*recondita*), and three within *P. glumarum* (*striiformis*). They referenced a wide range of foreign authors including Arthur, Bolley, Cobb, de Bary, Dietel, and McAlpine, as well as many of Eriksson's own previous publications. Later on, Eriksson authored several other books including a general plant pathology text in German, the second edition of which was translated into English (1930). Cereal rusts accounted for 30 pages of this text.

D. KLEBAHN, H. (1904) DIE WIRTWECHSELNDEN ROSTPILZE

The earliest publication of Henrich Klebahn on rusts concerned blister rust of pine. His interests in rust fungi, however, gradually focused on heteroecious species and their biology, culminating 17 years later in his book "The Rust Fungi with Alternating Hosts, a Presentation of their Biological Relations." The general portion of the book comprises a discussion of the concepts of heteroecism, mycoplasma, specialization, and sexuality, as well as of environmental requirements for spore distribution, spore germination, and infection. In the specialized section of the book Klebahn discussed the cereal rusts and their nearest relatives. Included were *Puccinia graminis, P. dispersa* (now *P. recondita* f. sp. *secalis* and f. sp. *tritici*), and near relatives (including *P. hordei*), *P. glumarum* (*P. striiformis*), *P. coronata,* and many other rusts attacking both Gramineae and nongrass hosts. For *P. graminis,* Klebahn reviewed the relationship of barberry to stem rust. Otherwise, he provided a listing of the associated aecial, uredial, and telial hosts as given in the literature for each rust. This was the major presentation of heteroecism in the rust fungi of its day.

E. MCALPINE, D. (1906) THE RUSTS OF AUSTRALIA

Daniel McAlpine (1849–1932) was contemporary with Eriksson, Plowright, Arthur, and Klebahn. He provided the Australian arm of the worldwide expansion of knowledge of plant rusts in the late nineteenth and early twentieth centuries. His primary contribution was the well-known "Rusts of Australia." This was the third of five major books that McAlpine authored, and it followed numerous of his previous research papers of which he cited 36.

His book is divided into two parts: a general discussion and description of the rust fungi, followed by a systematic arrangement of all of the rust species known to occur in Australia. At the end of the first part, a chapter is included on rust in wheat in Australia. A unique observation is that barberry had not been infected by *Puccinia graminis* in Australia either naturally or artificially, although teliospores were readily germinated. He included discussion and speculation on the epidemiology and control of stem rust of wheat. He concluded that the only effective means of control were to cultivate the most rust-resisting plants, to choose early-maturing cultivars, and to sow early. Like Eriksson and Henning's text of a decade earlier, McAlpine included illustrative color plates as well as photomicrographs of spores.

F. YACHEVSKI, A. A. (1909) (RUSTS OF GRAIN CROPS IN RUSSIA)

Artur Arturovich Yachevski (1863–1932) was a mycologist at the Leningrad institute where Voronin, Transhel, and Naumov also worked. He was prominent early in forest pathology, having written the first large handbook on that topic in Russia in 1897. His "Fundamentals of Mycology," a large general text, appeared in 1933 after his death. However, he wrote a series of articles on various plant rusts and a book entitled "Rusts of Grain Crops in Russia" (1909). This volume contained information on disease distribution, damage caused, environmental conditions favorable for disease development, disease control, and a list of the important rust fungi in Russia. The principal pathogens covered were *Puccinia graminis*, *P. dispersa* (*recondita*), *P. triticina* (*recondita*), *P. glumarum* (*striiformis*), *P. simplex* (*hordei*), *P. coronifera* (*coronata*), and *P. maydis*. Yachevski was particularly reputed for his opinion that the selection of resistant cultivars was the basic method for controlling rust.

G. GROVE, W. B. (1913) THE BRITISH RUST FUNGI (UREDINALES)

This text by William Bywater Grove (1848–1938) was published 24 years after Plowright's monograph, with the author's purpose to update knowledge of the Uredinales in a major British text. He pointed out that great progress in elucidating the biology of rust fungi had been made in the intervening years. He addressed life histories, sexuality, specialization, and classification. The general part is followed by a systematic portion that includes species found in Britain. With Biffen's studies on genetics of resistance now available and the Mendelian nature of resistance determined, Grove made a strong case for the likelihood of the pycniospores being male gametes in his discussion of sexuality. He pointed out that because of the minute specialization of the rusts, a host "variety may be immune to one rust while susceptible to another, or may even be immune in one country but susceptible to the same rust in a different climate."

H. BULLER, A. H. R. (1924, 1950) RESEARCHES ON FUNGI, VOLS. III AND VII

A. H. Reginald Buller (1874–1944), at the University of Manitoba, devoted two major parts of his seven-volume "Researches on Fungi" to rust fungi. In Volume III (1924), he described basidiospore and aeciospore discharge in *P. graminis*. He documented the timing of events in basidiospore growth and discharge, including the formation of a water droplet at the base of the basidiospore prior to discharge, and the distance traveled by discharged spores. He speculated about mechanisms of discharge and compared discharge phenomena in rusts and Hymenomycetes, pointing out many similarities. In Volume VII (1950), published posthumously, Buller presented what was then known of the sexual process in the Uredinales. Here, he reviewed historical aspects of pycnial development and function. He described the fusion between pycniospores and the flexuous hyphae of the pycnium, showing pycniospores of *P. coronata* fused to flexuous hyphae, and he defended the flexuous hypha as the only structure that can fuse with pycniospores. Proto-aecia were described in detail, including their transition into aecia following dikaryotization. He marshaled the available evidence that fungal nuclei migrate through septal pores, deducing that cells at the base of preformed proto-aecia are dikaryotized by nuclei migrating from flexuous hyphae.

Buller speculated about the role of insects in movement of pycniospores from one pycnium to another. As had Plowright (1889) earlier, he took special interest in the content and probable function of pycnial nectar as an insect attractant. He recounted (1950) how he demonstrated to Craigie that flies move from pycnium to pycnium, which led to Craigie's discovery of heterothallism in rusts.

I. ARTHUR, J. C. (1929) THE PLANT RUSTS (UREDINALES); (1934) MANUAL OF THE RUSTS IN UNITED STATES AND CANADA

In addition to innumerable research reports throughout his long lifetime (Section II,E), Arthur's most widely recognized contributions are two major books. "The Plant Rusts" (1929) is a treatise on the overall biology of this group of fungi, in collaboration with six of his former students and associates, and "Manual of the Rusts in United States and Canada" (1934), an exhaustive taxonomic presentation. The latter has for many decades been the primary authoritative source for taxonomic and nomenclatural treatment of the rust fungi in North America. "The Plant Rusts" is the most comprehensive presentation of the biology of the rust fungi with discussion and integration of prior literature. More recent texts have served to supplement and update rather than to replace it. Arthur's manual is so comprehensive that Cummins (1962), who illustrated the original edition in 1934, chose to have it reprinted in 1962 without revision, adding only a 24-page supplement.

J. LEHMANN, E., KUMMER, H., AND DANNENMANN, H. (1937) DER SCHWARZROST

This book summarized most of the worldwide literature on *P. graminis* available in 1937 and is the only widely circulated monograph on this important plant pathogen. It was an important source of information for readers of German for many years. Lehmann and Kummer had previously published jointly and independently a series of articles on barberry distribution, effect of barberry on stem rust occurrence, and control of stem rust through barberry eradication in 1934 and 1935 (Lehmann *et al.*, 1937). Their book had an extensive content with emphasis on the history of understanding of the disease and its biology, relation to barberry, resistance and pathogenicity, epidemiology, distribution, losses, and control. There was a thorough review of literature except for that from Russia, represented only by English and German language articles. This text and Chester's subsequent book (1946) on leaf rust have been the only book-length works devoted to individual rusts of cereals, although several excellent pamphlet-length treatises are available.

K. TRANSHEL, V. G. (1939) (CONSPECTUS OF THE RUST FUNGI OF THE USSR)

This review by Transhel (Section III,C) summarized a lifetime of rust research. Kuprevich (Kuprevich and Transhel, 1957) stressed the great importance of this publication in the study of rust fungi in the Soviet Union. It provided an exhaustive list of rust fungi with critical notes, keys, hosts, areas of occurrence, and fungal and host indices. It also included a presentation of the morphology, taxonomy, geographical distribution, and biology of the rust fungi. Much of this information was abbreviated and updated under the authorship of Kuprevich and Transhel (1957), 15 years after the death of Transhel, and was subsequently translated into English. It provides a historical review of investigations of the rust fungi in the Soviet Union. Like the earlier texts of McAlpine (1906), Grove (1913), and Arthur (1929, 1934), it has an extensive general discussion of the biology of rust fungi plus a detailed systematic part, providing the Russian counterpart to these other major texts on rust fungi.

L. NAUMOV, N. A. (1939) (THE RUSTS OF GRAIN CROPS IN THE USSR)

Nikolai Aleksandrovich Naumov (1888–1959) was a mycologist in the research institute at Leningrad that was the professional home of A. A. Yachevski, V. G. Transhel, and many other important Russian mycologists and plant pathologists. Like his associates, he published numerous articles on the mycoflora of Russia. He was intensively involved in the epidemiology of cereal rusts, with several titles relating environmental conditions to rust development. During the 1920s and 1930s numerous articles by various authors on cereal rusts were published in Russia. In 1939 Naumov brought this information together in a monograph on "The Rusts of Grain Crops in the USSR." This appears to be the first such compilation since the similar title by Yachevski 30 years earlier, and was published the same year as Transhel's more broadly oriented "Conspectus." The book covered current information on biology, ecology, physiological specialization, losses incurred, and control measures. Foreign literature was reviewed, and much of the information was from outside the Soviet Union. Included among the pathogens discussed were *P. graminis, P. triticina* (*recondita*), *P. glumarum* (*striiformis*), *P. dispersa* (*recondita*), *P. coronifera* (*coronata*), and *P. anomala* (*hordei*).

M. CHESTER, K. S. (1946) THE NATURE AND PREVENTION OF THE CEREAL RUSTS

Chester was head of the Department of Plant Pathology at the present Oklahoma State University when he conducted his research on leaf rust of wheat (Section IV,C). This interest provided the impetus for a worldwide search of the literature on the cereal rusts. He used this information and his considerable language and writing abilities to compile a monograph on leaf rust of wheat (1946). This book comprehensively presented the current state of knowledge, to which Chester frequently added his opinions, which often differed from conventional views. Time has generally proven Chester right. A major contribution was the broad review for the first time in an English-language text of the Russian literature. After leaving Oklahoma for Battelle Memorial Institute, Chester also coauthored a summary report on stem rust of wheat (Chester *et al.*, 1951).

N. VALLEGA, J. (1956–1967) ROBIGO (A NEWSLETTER)

José Vallega (1909–1978), like Chester, was a relatively recent contributor to cereal rust research. His importance in the context of this section was the development of an international publication "Robigo," which compiled "cereal rust news from everybody to everybody." Vallega began his research on races of cereal rusts in 1934 at the Instituto de Fitotechnia de Santa Cataline of the University of La Plata in Argentina (Eide, 1978). He later became interested in breeding for resistance and then in genetics of resistance (Villar, 1979). These experiences led him to establish the international Robigo for exchange of information on the cereal rusts. This newsletter was published from 1956 to 1967, initially with Vallega as responsible editor assisted by Hugo P. Cenoz and Juan L. Tessi. He relinquished this position to his assistants in

1960 to become honorary editor following his move to the Food and Agriculture Organization (FAO) in Rome. He proposed Robigo in 1956 because an investigator confined to a country or region could not efficiently defend crops against a pathogen that had many cultivated and noncultivated hosts worldwide. Therefore, Vallega felt the need for an international work team, with Robigo as its permanent round table to be a place to exchange informally and continually results and ideas even of a preliminary nature. Robigo ended with its nineteenth issue in 1967 following the death of its editor, Hugo P. Cenoz. Today, the Cereal Rusts Bulletin (1973–), published by the European and Mediterranean Cereal Rusts Foundation, and the Proceedings of the European and Mediterranean Cereal Rusts Conferences (every fourth year) have largely become this forum.

VIII. Epilogue—H. H. Flor (1900–)

The classical studies of Harold Henry Flor (1946, 1971) on the genetic interaction of flax and the flax rust fungus (*Melampsora lini*) provide a capstone to the historic contributions outlined in this chapter. Flor's research, of course, was not on a cereal rust, but had its heritage in the earlier studies on cereal rusts and, in turn, provided new vision for further cereal rust research. His "gene-for-gene" theory (see Loegering, Chapter 6, this volume), has been confirmed for the cereal rusts and is the basis for virtually all current research on them.

Flor, a student of E. C. Stakman, worked for the United States Department of Agriculture at North Dakota State University. He worked mostly alone, coming to his theory with great insight only after diligent genetic work.

We view Flor's contribution as the threshold between the early contributors discussed in this chapter and those who came later. His theory set the stage for much that was to come and continues as the dominant force in understanding the cereal rusts.

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