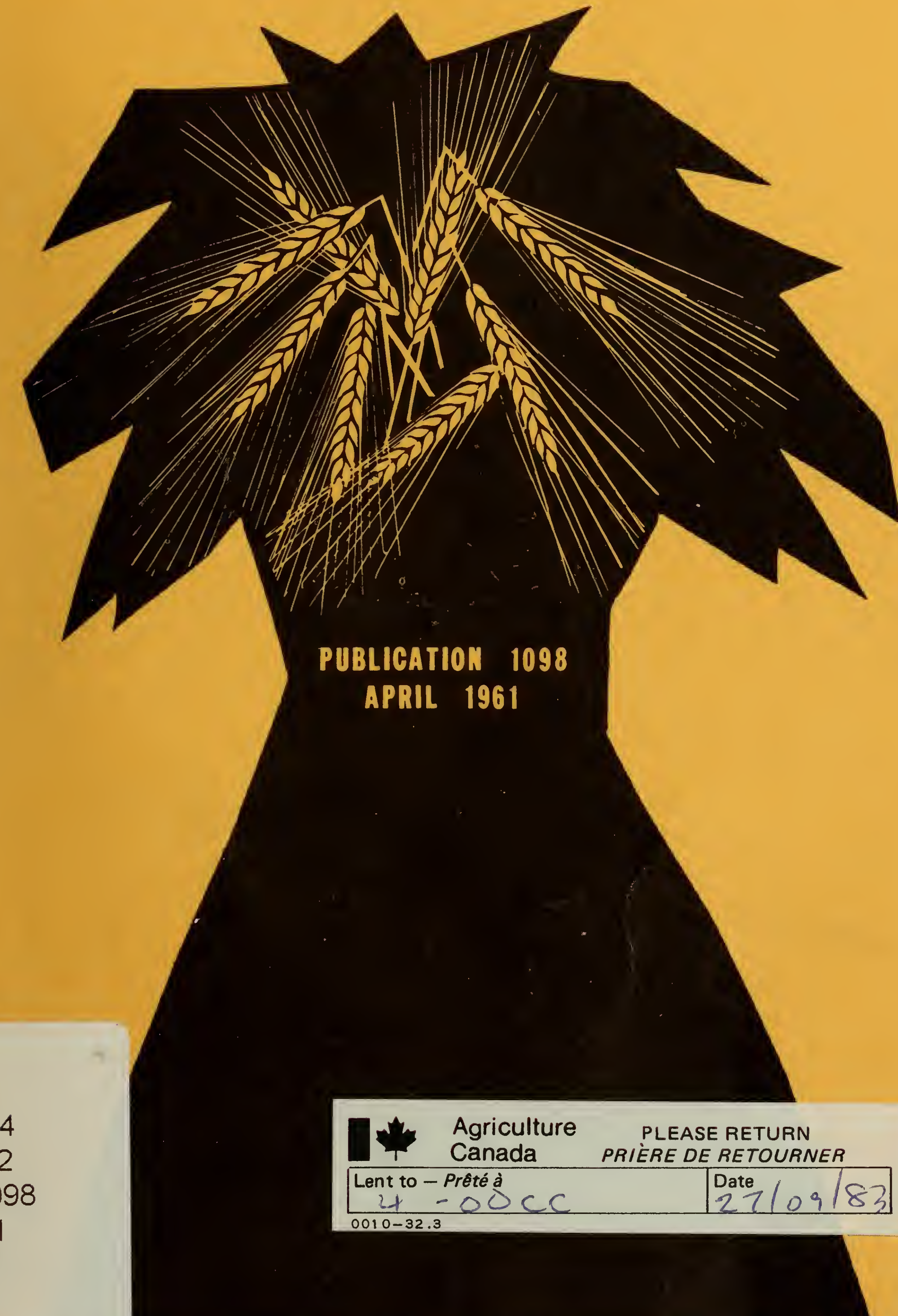
RUST RESEARCH IN CANADA

and Related Plant-Disease Investigations



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RUST RESEARCH IN CANADA

AND RELATED PLANT-DISEASE INVESTIGATIONS

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CEREAL DISEASES IN THE NORTH CENTRAL UNITED STATES IN THE EARLY YEARS

When cereal crops were introduced from Europe and the Mediterranean region to North America most of the disease organisms that affected them in their homeland were brought along with them. On the new continent these crops were, therefore, exposed to their accustomed diseases in a new environment and were, moreover, exposed to other disease organisms that they may not have encountered previously. These hazards were little realized by the early growers of grain who simply planted their seed and hoped for a good crop.

The soils and the climate of the Mississippi Valley proved ideally suited to the growing of wheat. By 1839 the center of wheat growing in the United States had shifted westward across the Allegheny Mountains to southwestern Pennsylvania (Reitz, 1954). By 1859 the concentration of wheat production was in western Ohio and a decade later had shifted westward to Indiana. By 1879 Illinois had become the center, and by the end of the century the center of wheat production was considered to be in northern Iowa and southern Minnesota. This westward movement of wheat cultivation continued uninterruptedly until about 1920, when northern Kansas came to be considered the pivotal area of wheat production in the United States.

The westward displacement of the center of grain growing to the open plains was paralleled by an ever-increasing concentration of the wheat crop. Wheat fields were no longer few and far between but came to occupy an ever greater proportion of arable land.

Now, it is generally accepted that when the population of the host plant of some parasitic fungus is greatly increased in any given area the parasitic fungus will increase at a much greater rate provided that conditions for its propagation are satisfactory. The environment of the Mississippi Valley proved to be highly congenial to two of the most important fungus enemies of wheat: the rusts and the smuts. In a wheat plant infected by bunt (stinking smut) the grains are converted into 'smut balls', each of which may contain from 3 to 6 million spores. A single spore of the summer stage (urediospore) of stem rust may infect a wheat leaf or stem on which will arise, a fortnight later, a rust pustule containing several hundred thousand spores. With these great potentialities for multiplication the smuts and rusts of grain crops can increase to devastating proportions if conditions favor them and if no effective control measures are devised. During the period of rapid spread of agriculture into the valleys of the Ohio and Mississippi, conditions did favor these parasites and no control measures were taken, or indeed known to most growers.

As the establishment of agriculture in the midwestern states preceded that of the adjacent Prairie Provinces, the build-up of cereal diseases in the former area was bound to have a significance for Western Canada when grain growing became established there. Most fungus diseases, including rusts and smuts, are propagated by wind-borne spores which, in the absence of any natural barriers in the prairie region, are readily transmitted northward to new agricultural areas. Before examining the scanty data on the development of cereal diseases in the early days of grain growing in Western Canada, it is, therefore, worth while to examine the cereal disease situation that was developing in adjoining areas of the United States.

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Despite the scarcity of accurate information on the development of cereal diseases in the midwestern states before the turn of the century it is evident that two diseases were of considerable importance. These are bunt of wheat and stem rust.

About 1890 it was estimated (Fischer and Holton, 1957, p. 89) that bunt sometimes destroyed as much as one quarter to one half of the wheat crop of the state of Kansas. The losses caused by this smut in Kansas and neighboring states were the chief stimulus to the attempts made by Kellerman and Swingle, in Kansas, to develop effective seed treatments for bunt control.

Just as the severity of bunt infection was responsible for the earliest research work on smuts in the Midwest, so was the build-up of rust infection the chief stimulus to the early investigations on the cereal rusts. In 1892, studies on the cereal rusts were undertaken by Hitchcock and Carleton (1893), presumably in consequence of the rust epidemic of 1891. Freeman (1905) placed the loss from wheat rusts in the United States in 1891 at $67 million. That wheat rusts had caused considerable losses in earlier years is suggested by the statement of the same author that losses from this source in the state of Minnesota in 1888 exceeded "the total loss by ravages of all insects including even the dreaded grasshopper."

In 1899 Carleton reported a survey designed to determine the importance of the cereal rusts in the United States in the last decade of the century. He concluded that the stem rusts of wheat and oats were the most destructive. Infection by these rusts was most severe in the area comprising Ohio, Indiana, Illinois, eastern and central Iowa, southern Wisconsin and southern Minnesota. In this area an estimate of damage to wheat for the years 1892 and 1894 ranged from 20 per cent in Ohio to 46 per cent in Iowa. In the latter state, wheat had been so frequently and heavily damaged by stem rust that, in some areas, wheat growing had been abandoned. Oats suffered as much from stem rust as wheat, in fact more so in the states of Ohio, Michigan and Illinois. In the last-mentioned state, 1890 and 1891 were particularly bad rust years. Leaf rust of wheat and crown rust of oats were more important than the stem rusts in the Atlantic and southern-coast states. In the midwestern states the leaf rusts were thought to be of much less economic importance than the stem rusts.

Of all the early rust epidemics, that of 1904 has received the most publicity. Carleton (1905) stated that the year 1904 was the third in a series of wet years in which rust infection mounted. He considered this the most severe rust epidemic thus far in the hard spring wheat region. The most severely affected states were North Dakota, South Dakota and Minnesota but much damage was also caused in Wisconsin, Iowa, Nebraska and Kansas. Both wheat and oats were damaged but wheat the most severely. Loss in wheat yield, attributed principally to stem rust, was estimated at from 25 to 40 million bushels for the two Dakotas and Minnesota; in some areas losses were estimated at 50 to 60 per cent of the crop.

CEREAL SMUTS IN WESTERN CANADA IN THE EARLY YEARS

Until 1879, when the first railway reached Manitoba, grain was grown in that province in a small way, chiefly for subsistence and for distribution to Hudson's Bay Company posts. After that date, wheat was exported in gradually increasing quantities. In 1880 about 1 million bushels of wheat was grown in Manitoba (Strange, 1954). By 1890 wheat production in this province had risen to nearly 15 million bushels while in the adjoining territory, later to become the province of Saskatchewan, about 1.6 million bushels was produced.

The establishment by the government of Canada of experimental farms at Brandon, Manitoba, and at Indian Head in the Northwest Territories in 1888 was a landmark in the agriculture of Western Canada. Two capable men were appointed superintendents of the farms: S. A. Bedford at Brandon and Angus Mackay at Indian Head. These experimental farms provided the settlers with essential guidance in agricultural practices, and their annual reports provide us with accurate information on the problems that beset the early grain growers of Western Canada.

The earlier reports of these two experimental farms show that bunt of wheat was the most important of the early plant disease problems. Mackay (1889)* stated that "smut [bunt], this year, was very prevalent all over the Territories." In the same report, he recorded that "blue vitriol [copper sulphate] dissolved in water and mixed with the seed has been the only remedy so far tried on the Experimental Farm [Indian Head]. One pound dissolved in one pail of water and thoroughly mixed with ten bushels of grain gives good results, though not perfectly efficacious." Bedford in the report of the Brandon Experimental Farm for 1891 made the following statement: "Both farmers and grain-buyers report that smut [bunt] is largely on the increase throughout the province [Manitoba], and that the direct loss to the farmer this year [1891] will reach thousands of dollars, besides the indirect loss arising from injury to the reputation of our wheats on the English markets." He referred to three different kinds of seed-treatment experiments carried out on the Experimental Farm in 1890: bluestone (copper sulphate), a salt-brine treatment, and Jensen's hot-water treatment; and he recorded that all three treatments greatly reduced the number of smutty heads and the number of bunt balls in the grain.

In the same year Mackay (1891) reported: "The attention of every settler is called to the result obtained from treating smutty seed with bluestone before sowing. I am told by a grain buyer that every third bushel he buys is damaged by smut, and that to such an extent that while he pays 40 to 50 cents for frozen grain, this smutty wheat realizes the grower only 30 to 35 cents. When it is considered that at a cost of a few cents a bushel seed can be successfully treated for this serious evil, it is reasonable to expect that no farmer will sow wheat next spring without being treated with bluestone."

Again, in the same year, James Fletcher, then Entomologist and Botanist, Department of Agriculture, Ottawa, stated: "The great damage by Smut to the immense wheat crop of the Dominion during the year 1891 has caused much inquiry from farmers. The Department of Agriculture for Manitoba has just issued a timely bulletin upon the subject. In a letter from Mr. A. Mackay, Superintendent of the Experimental Farm at Indian Head, he says: 'I think too much cannot be known regarding Smut, and anything you could put in our papers cannot but be of value to the farmers. I think every bushel of seed will this spring [1892] be treated for Smut, and it is important that the best way should be known how to treat it effectually.' " Fletcher went on to say, "In compliance with the above suggestion, I immediately wrote the following letter to the *Farmer's Advocate,* which has a large circulation in the North-West Territories and Manitoba." He then quoted his letter to the Editor, *Farmer's Advocate,* written March 19, 1892, in which he gave details of the use of the copper sulphate treatment for smut control and mentioned the hot-water treatment for the control of loose smut. The use of copper sulphate for smut control had been recommended already by Fletcher in a bulletin on smuts affecting wheat (Fletcher, 1888).

*All references to reports by Angus Mackay, S. A. Bedford and James Fletcher are to reports of the experimental farms. A citation refers to the year covered by the report, not to the year of publication.

It is apparent that these efforts to control bunt in wheat had some beneficial effect because Bedford (1893) referred to the rapidly increasing use of bluestone in the province and the almost total absence of bunt in 1893, which he considered evidence "that the fungus is being rapidly brought under control." It is, however, clear from a study of later Experimental Farms Reports that Angus Mackay's optimistic expectation, that every bushel of wheat sown would be treated with bluestone, was not to be realized. Bedford (1897) stated that "although experiments for the prevention of smut in wheat have been conducted here for a number of years, it is still one of the principal subjects dealt with by correspondents."* And in 1905 he commented that "in many parts of the province the injury from smut in wheat has been greater this year than usual, and much loss has resulted." Whereas only 3 per cent of the 1904 wheat crop was rejected for this cause by inspectors at Winnipeg 6 per cent was rejected in 1905. He gave it as his opinion that farmers were not taking enough care in treating grain with bluestone. Consequently experiments on the use of bluestone for control of smut were continued at Brandon and Indian Head for a number of years and information on methods of treatment was periodically given out to farmers. These efforts bore fruit; bunt never again became the problem it had been in earlier years. Though it is not expressly stated in the annual reports, it seems clear that the bluestone treatments were used more or less effectively in the older agricultural districts. In the first decade of this century complaints about the prevalence of bunt found in these reports usually referred to newly settled districts in which farmers had not yet learned the necessity for seed treatment or acquired the knowledge of how to apply it effectively.

The early studies on bunt were not entirely confined to seed treatments. Mackay (1908) reported "a test to determine whether smut dust sown on the land would cause smut in the grain." Two bushels of smut spores were sown by hand on five plots, each 8 feet square, the dust being well worked into the soil before the grain was sown. "The results obtained go to show that smut dust, when in any considerable quantity in the soil, produces smut in the grain, no matter how treated."

As wheat was the crop of major importance it is natural that the first efforts should be directed at the control of the most destructive smut of this crop. Less attention was given by experimenters and farmers to the smuts of oats and barley and there are, indeed, indications that the losses from smut infection of these crops were not excessive in the earliest days of western agriculture.

The first reference to severe losses resulting from smut infection in oats and barley appears to be a statement of Bedford (1894): "This fall many farmers report heavy losses from loose smut in coarse grains. Until the past season (1894), the losses from this kind of smut have been small in this province." He reported on experiments on the use of bluestone for the control of smut in barley and complained that soaking in bluestone solution severely injured the germination of the seed, and that sprinkling only destroyed about half of the smut. A year later Bedford (1895) reported: "At no time in the history of the province has there been so much smut among oats as prevailed this year; some varieties were so badly affected that the yield was reduced by one-half and the threshing made very disagreeable on account of the dust." Bedford (1896) referred again to the losses sustained in 1895: "It is estimated by good authorities that from 10 to 25 per cent of the oat and barley crop of

*How much saving could be effected by bluestone treatments is shown by the fact that in one experiment untreated grain produced 30 times as many smutted heads as treated grain, which yielded 6 to 7½ additional bushels per acre (Bedford, 1893). In similar experiments at Indian Head the increased yields from treated grain ranged from 7 to 10 bushels per acre (Mackay, 1893).

1895 was destroyed by loose smut, some fields examined by myself were found to have 75 per cent of the heads smutted." A very smutty sample of oats was treated with a bluestone solution with the result that the number of smutty heads was reduced by one-half and the yield increased by 25 bushels per acre (Bedford, 1895). On the basis of this experiment directions for treatment were issued to farmers.

Although the reports contain few details on losses caused to coarse grains by smut, it is evident that the control of these smuts was of continuing concern to the experimental farms. In the annual tests of seed treatments, bluestone was found less beneficial for the coarse grains than for wheat. Several other chemicals were tested, including potassium sulphide (Bedford, 1896), Bordeaux mixture and formalin (Bedford, 1898). Formalin was found effective in this test, and in subsequent years, for the control of oat smuts, and it became a practice at the experimental farms to treat all oat seed with this chemical before sowing. Its effectiveness for barley was less consistent; Bedford (1901) reported bluestone to be more effective for control of smut in barley.

CEREAL RUSTS IN WESTERN CANADA IN THE EARLY YEARS

It is probable that cereal rusts were not a hazard in the earliest years of grain growing in Western Canada. The first known record of cereal rusts dates from 1891, when Bedford reported that some wheat varieties suffered from rust on valley clay-loam soil at Brandon although on upland plots they were free from rust. Some of these varieties were badly rusted and much rust occurred also on oats grown on heavy soils. Mackay (1892) stated that, in 1892 at Indian Head, "rust struck nearly all the [oat] sorts before they were fully matured causing the grain to be somewhat shrunken." Many wheat varieties were also affected by rust. Of 26 wheat varieties sown on April 19, seven were listed as badly rusted and five as rusted. As less rust occurred at Brandon it is likely that 1892 was not a year of generally severe rust infection. The years 1893, 1894 and 1895 were years of light rust infection but in 1896 infection was severe at Brandon and considerable at Indian Head. Bedford (1896) stated that owing to a wet, late spring, wheat could not be sown until May 8. Abundant moisture encouraged soft growth "which showed signs of rust on the leaf by the end of May, and before the plants were a foot high. The warm moist weather of the middle of June appeared to encourage the rust, until it spread from leaf to stalk and from stalk to head, many of the fields turning a rusty yellow colour, seldom or never seen here before; its effects were soon seen in weakening of the straw, delayed ripening, and partially filled head and a shrunken berry." Of 40 wheat varieties, 22 were badly rusted and none was free from rust. Lodged grain was most affected by rust and damage was least on sandy and gravelly land. In oats "all the rank, coarse-strawed, late varieties suffered badly, both in yield and weight."

Rust infection appears to have been generally light in 1897, 1898 and 1899, though in the last two years it is recorded that late oats were damaged by rust at Brandon. In 1900 there was a moderate amount of rust on wheat and oats at Brandon and rust was recorded on barley. In the following year rust infection was severe at Brandon. Only one wheat variety (a durum wheat), of 72 varieties grown, was free from rust and 45 varieties were badly rusted. Whereas the highest yield was 45 bushels per acre, the yield of some of the badly rusted varieties was reduced to about 17 bushels and the weight per bushel to 55 lb. Of 65 oat varieties, 42 were badly rusted and only one was free from rust. In barley, "the yield of nearly all varieties was greatly lessened by rust, which attacked the plants very early this year." (Bedford, 1901). Rust infection in 1901 was much lighter at Indian Head where only 17 of 71 wheat varieties were rusted and no rust was reported on barley.

In his report for 1902 Bedford stated: "As usual the varieties least subject to rust were the most productive. It is evident that this disease is one of the chief factors in reducing the yield of wheat, especially during seasons of abundant rainfall, such as we have had these last two years." In the Northwest Territories damage was evidently less, as Mackay in his report for the same year stated that "rust, which has hitherto been almost unheard of in the territories, did a small amount of damage this year."

Rust damage occurred again, at Brandon, in 1903 when "both the yield and sample [of wheat] were greatly injured" (Bedford, 1903). In the same year wheat varieties rusted slightly to considerably at Indian Head.

The culmination of these years of rust damage was reached in 1904. Although this was perhaps the year of severest rust infection, up to that time, there appears to have been no generally severe epidemic. Bedford (1904) stated: "Although there has been some loss from rust and frost, the injury has been quite local in its character . . . the badly injured fields were sometimes scattered among others comparatively free from rust . . . excessive growth of straw from any cause appears to encourage the disease . . . all velvet-headed kinds such as Hayne's Blue Stem were severely injured, while the Macaroni wheats were comparatively uninjured." The extent of the area most affected is indicated by Fletcher (1904) who stated: "In Manitoba the injury by the Black Stem Rust caused great anxiety to farmers. Some crops were actually cut green before they were ripe to save further damage. The districts most affected were between Brandon and Winnipeg and in the south and west of the province." He added that this was a more severe outbreak of rust than any previously experienced. That rust infection diminished in a westerly direction is indicated by Mackay (1904) who stated that "rust, which did injury in parts of Manitoba, did not reach the dangerous stage in the Territories before the grain was ready to cut."

One of the new lines of investigation undertaken by Bedford at Brandon in the spring of 1904 was a study of "the effect of early harvesting in lessening the injury to wheat by rust." Wheat sown May 18 was cut at four stages: in the milk stage (on Aug. 30), in the dough stage (on Sept. 6), when nearly hard (on Sept. 13), and when quite hard (on Sept. 22). The differences in yield were slight; harvesting in the dough stage gave the best results. Bedford concluded that "this experiment should be repeated before definite opinions are reached." This appears to be the earliest attempt at experimental investigation of rust in Western Canada.

Damage by rust, comparable to that inflicted in the years 1902 to 1904, was not again experienced until 1916, although, according to Craigie (1957), rust was fairly prevalent in 1905 and did considerable damage in 1911 in western Manitoba and eastern Saskatchewan.

Despite the severity of local infection by rust in the years prior to 1916 it is doubtful that rust was a serious factor in reducing wheat yields in Western Canada except perhaps in 1904. In fact, most of the years in which rust infection is mentioned were years of abundant crop growth and high or moderately high yields. Either the infection did not reach the proportions of a general epidemic or the epidemic came too late to affect the general yield appreciably.

In 1916, the situation was entirely different. Seed germination and early growth of the crop were generally good. Crop prospects were satisfactory until the appearance of rust late in July. Infection appears to have spread with rather remarkable uniformity over Manitoba, Saskatchewan and parts of Alberta. In the words of Seager Wheeler (1919): "Rust played serious havoc in the wheat-fields of Saskatchewan, Manitoba, and, to a lesser degree, in Alberta. A considerable acreage was left uncut as absolutely worthless and it had to be fired in the spring of 1917, previous to seeding. Many thousands of acres were also

harvested that yielded grain of a very low quality... In many sections the grain was of such poor quality as to be unfit for seeding purposes. The estimated percentage of loss in the field for Canada is 43 per cent of the crop for 1916, and the loss in money is estimated as $102,250,000. Personally, I would consider the loss even greater. In Minnesota and the Dakotas the loss in the field is estimated at 72 per cent of the crop." Buller (1919) placed the loss for Canada at 100 million bushels and for the United States at 140 million.

The rust epidemic of 1916 had a significance beyond that of its destructiveness. The events of subsequent years showed that it provided a powerful stimulus for action against rust.

PLANS FOR DEALING WITH PLANT DISEASES

One of the chief landmarks in the history of agricultural science in Canada was the founding of the experimental farm system in 1888. William Saunders (1910) mentioned the depressed condition of agriculture in Canada before 1884. He attributed this condition largely to the ignorance of the farmers, who had received little advice on agricultural methods. In 1884, "the House of Commons appointed a Select Committee to inquire as to the best means to adopt to encourage and develop the agricultural interests of Canada... The Parliamentary Committee recommended the establishment of Experimental Farms, where tests should be carried on in all branches of agriculture and of horticulture, and that the results of this work should be published from time to time and disseminated freely among the farmers of the Dominion... During the session of Parliament for 1886, an Act was introduced... authorizing the Dominion Government to establish a Central Experimental Farm and four Branch Farms. The Central Farm was located near Ottawa, Ontario; the Branch Farm for the Maritime Province at Nappan, Nova Scotia; that for Manitoba at Brandon; the Farm for the North West Territories at Indian Head; and that for British Columbia at Agassiz."

The function of the experimental farms was twofold: first, to pass on to the farmer such useful agricultural knowledge as was available and, secondly, to provide new, useful knowledge through experimentation. These services of the experimental farms were soon of inestimable value to the Canadian farmer. An example has been given above in the reduction of the importance of wheat bunt in Manitoba and the Northwest Territories through the increasing use of bluestone, which was so strongly recommended by the experimental farms at Brandon and Indian Head. It is probable that in the first decade of the existence of the experimental farms they benefited the farmer most by providing him with knowledge already available though unknown to him. Research of a simple type such as the testing of crop varieties for local adaptation and the devising of practicable methods of using fungicides and insecticides was, however, not neglected. The production of new wheat varieties by means of crossing was initiated by William Saunders as early as 1888 and preliminary investigation of the chemical composition and physical characters of wheat varieties was undertaken by F. T. Shutt, the chemist of the experimental farms, about the same time as an effort to evaluate the quality of Ladoga, Red Fife and other varieties (Shutt, 1889). Experimental milling and baking tests were later introduced by Dr. C. E. Saunders.

To the Division of Entomology and Botany fell the duty of investigating the troubles caused by insect pests and plant diseases. This Division was under the direction of James Fletcher until his death in 1908. He was an entomologist and carried out numerous investigations on life histories and control of injurious insects and also provided advice on countermeasures against plant diseases. The reorganization of this Division in 1909, which involved the creation of a Division of Botany under the direction of H. T. Güssow, was a significant event

for the study of plant diseases in this country. Hans T. Güssow, through his training in applied botany and plant pathology at the universities of Breslau, Leipzig and Berlin, and his subsequent work on these subjects in England from 1901 to 1909, was eminently qualified to organize this type of work in Canada. He showed an immediate awareness of the importance of the diseases of agricultural plants in Canada and a realization of the necessity for initiating and organizing plant pathology services in the various regions of the country. For several reasons, progress was slow at first. Not the least of these was the virtual absence of trained plant pathologists and the inadequacy of facilities for their training. At the time, most students in universities and agricultural colleges failed to realize that plant pathology was a fruitful field of study. Güssow (1915) stated: "Students at agricultural colleges and universities are advised to devote their special attention to plant pathological science, the future of which, it is reasonable to state, is most promising in the Dominion. At the present moment difficulties are experienced in securing the services of young Canadians who possess such special knowledge."

Even at this early date some training facilities in mycology and plant pathology existed in Canada. J. H. Faull, well trained in mycology, was appointed Lecturer at the University of Toronto in 1902 and Associate Professor in 1907. A. H. R. Buller, already an enthusiastic mycologist, became Professor of Botany at the University of Manitoba in 1904. J. E. Howitt joined the staff of the Ontario Agricultural College in 1907 and was reinforced by the appointment of R. E. Stone in 1912. W. P. Fraser became Lecturer in Biology at Macdonald College, McGill University, in January 1912. These men were capable of training students in mycology and plant pathology if the opportunities were promising enough to attract them. Opportunities were not obvious until some time after the establishment of the Division of Botany in 1909. Another obstacle was the war of 1914-18 which almost depopulated Canadian universities. It was not until 1919 that the realization of opportunity, coinciding with the availability of students, made possible the training of any significant number of specialists in these fields.

Before this development was possible the great rust epidemic of 1916 had made many thinking agriculturists and botanists realize that some action must be taken, if possible, to prevent the recurrence of losses such as were suffered by wheat farmers in that year.

The attention of the Department of Agriculture was given to this problem although it was obvious that no immediately useful countermeasures against rust could be taken. In November 1916, H. T. Güssow, the Dominion Botanist, sent to a large number of farmers in the three Prairie Provinces a questionnaire designed to reveal information on the damage caused by the rust epidemic of that year and the various factors concerned in the spread of rust infection. The 560 replies were analyzed by W. P. Fraser (Fraser, 1918), who was appointed, on a part-time basis, Officer in Charge of Grain Disease Investigations in February 1917 on the recommendation of H. T. Güssow. The replies revealed that rust infection was most severe in southern Manitoba and south-eastern Saskatchewan and was less severe in the northern parts of these provinces, and that it caused little damage in Alberta. Yield reduction in wheat was placed at 10 bushels per acre in Manitoba and 8 bushels in Saskatchewan; the total yield reduction was estimated at nearly 100 million bushels which, according to Güssow (1924), represented a loss in excess of $150 million. The damage was found to be greatest in the best wheat lands and particularly in crops grown on summer fallow.

Attention was now directed to a study of the rust organism. In the spring of 1917, field laboratories for the study of grain rust and other diseases were established at Brandon, Manitoba and Indian Head, Saskatchewan (Grisdale,

1918), and Professor W. P. Fraser spent the summers of 1917 and 1918 in a study of the rust situation in Western Canada. The establishment of these field laboratories, however, was not a direct result of the rust epidemic of 1916. The financial provision for their establishment was made in the estimates for the fiscal year 1916-17 and, therefore, before the occurrence of the epidemic. In February 1919, Professor Fraser was appointed Officer in Charge of the newly established laboratory of plant pathology at Saskatoon.

At these laboratories studies were undertaken on the species of rust attacking grains and grasses, the role of native and cultivated grasses in the hibernation and spread of rusts, the course of development of epidemics, and the possible role of barberries in the spread of rust in Western Canada. Studies of cultures of rust in the greenhouse were undertaken at the Manitoba Agricultural College in the summer of 1918 by Margaret Newton, a student of Professor Fraser, "to determine the relationship of the stem rust in the native and wild grasses to that of the wheat rust" (Grisdale, 1920). Studies on the overwintering of stem rust were pursued at Brandon and attention was given to the location of bushes of the common barberry.

Outside the Department of Agriculture there were individuals who were also giving thought to the question of what could be done about reducing the losses caused by rust infection. One of these was A. H. Reginald Buller, Professor of Botany of the University of Manitoba. In January 1917, Professor Buller visited the Department of Plant Pathology of the University of Minnesota where Dr. E. C. Stakman and others were doing fundamental research on stem rust of wheat. From this visit he returned with the ideas that formed the basis of his "Memorandum on the Rust Disease of Wheat". The memorandum, dated June 1, 1917, is worth quoting. Early in June a copy of it was sent to each of the following: J. H. Gridsale, Director of the Experimental Farm, Ottawa; W. C. Murray, President of the University of Saskatchewan; and J. A. MacLean, President of the University of Manitoba. This memorandum is as follows:

> MEMORANDUM ON THE RUST DISEASE OF WHEAT. By A. H. Reginald Buller, Professor of Botany at the University of Manitoba. June 1, 1917.
>
> *Amount of Damage in 1916.* In Canada—depreciation of crop about 100,000,000 bushels (estimated from data obtained at the Winnipeg Grain Exchange). In the United States of America—depreciation of crop about 140,000,000 bushels (statement in a letter to the writer by Mr. Carleton, cerealist for the U.S. Dept. of Agriculture).
>
> *Investigation in Canada.* Up to the Spring of 1917 no one in the Dominion was investigating the Rust Disease of Cereals with a view to its suppression. However, the Dominion Department of Agriculture has recently appointed Mr. Fraser of Macdonald College to take charge of investigation on Rust at the field stations of Brandon and Indian Head.
>
> *A Co-operative Plan of Investigation suggested by the writer.* The Rust problem is a peculiarly difficult one requiring for its attempted solution the combined work of several able and well-trained scientific men. It involves a study of: (1) Rust strains as they occur on cereals and wild grasses; (2) the epidemiology of the disease, i.e., its mode of spreading and the manner in which it persists from year to year; and (3) a study of disease-resistance together with an effort to breed varieties of wheat which shall not only be rust-resisting but shall also be desirable for their yield as well as for their milling and baking qualities. For the investigation of the Rust Disease suitable laboratory and green-house facilities are essential. Ground must also be provided upon which to grow cereals and upon which to establish a rust-nursery where an artificial epidemic of Rust can be produced each year.
>
> The Rust Disease is of growing importance in Canada. In 1904 it reduced the wealth of Western Canada by not less than $20,000,000 while in 1916 the monetary loss due to Rust must have been in excess of $100,000,000. Rust is not only of national but also of international importance and there can be no doubt whatever that the depreciation of the wheat crop in North America in 1916 by about 240,000,000 bushels on account of Rust has been a factor in the great war unfavourable to the Allies and one of the chief causes of the world shortage in food-stuffs.

Since the destruction of wheat by Rust is not merely of local but also national importance, the Dominion Government ought to make itself responsible for investigation upon the Rust disease. Provision should be made to carry on research in Rust for a period of not less than ten years and funds should be provided which would in course of time come to a total of probably not less than $100,000.

For the purpose of economizing equipment and in order to obtain the most satisfactory results in the shortest time the writer strongly recommends that there should be co-operation between the Department of Agriculture at Ottawa and the Agricultural College at Winnipeg.

The first requisite is a man of proved ability to take charge of Rust investigation for the Dominion of Canada. I believe that the best man for such work, if he could be obtained, would be Mr. Stakman, assistant professor of Plant Pathology at the Agricultural College of the University of Minnesota. Already for several years he has been working at the Rust problem for the United States Government and has established his reputation as a first-class investigator. With the permission of the President of the University of Manitoba I made a visit to the United States last January (1917) in order to enquire how Canada might best help in the solution of the Rust problem. I spent five days at the University of Minnesota and then had every opportunity to become acquainted with Mr. Stakman and to judge of his ability and knowledge. I am convinced of his suitability to organize research on Rust for the Dominion of Canada, provided he could be induced to do so.

Mr. Stakman should be appointed Professor of Plant Pathology at the Agricultural College, Winnipeg, and should be asked to organize a Department of Plant Pathology in that institution. He should devote his energies in the main to the investigation of plant diseases, but he might also give a course of lectures on Plant Pathology to the senior students. He should deal with diseases of plants which occur in Manitoba, i.e., those of Flax, Potato, Alfalfa, etc., so that part of his work would be of immediate practical importance. His full salary should be $3,000. Of this perhaps $2,000 should be paid by the Agricultural College.

The Department of Agriculture at Ottawa should engage Mr. Stakman to take charge of Rust investigation for the Dominion and for that purpose it should pay him $1,000 annually and in addition provide him with all the assistance required to carry on the work. One of the workers under his direction might be Mr. Fraser now in charge of Rust investigations at field-stations in Brandon and Indian Head. Mr. Stakman would publish bulletins under the auspices of the Department of Agriculture at Ottawa embodying (1) the results of research and (2) advice to farmers. Mr. Stakman should be given free hand to choose his own assistants and to develop research on Rust along the lines he should think most suitable. Such freedom in my judgment would be essential to success. The Agricultural College at Winnipeg would provide laboratory accommodation and greenhouse facilities and also the requisite plot of ground for growing cereals and for a Rust nursery.

The writer believes that Winnipeg is the most suitable place for serious investigation on the Rust disease for the following reasons. Winnipeg is a large city, easily accessible by train. It contains a University and an Agricultural College so that the necessary contact of the men engaged on Rust research with pure science and with agriculture would be well provided for. Winnipeg is the commercial centre of the grain industry and contains a great Grain Exchange. Farmers often hold conventions at Winnipeg. The city is likely to provide the requisite library facilities. Already the writer has accumulated a valuable collection of mycological books and periodicals which would be available for consultation. Finally Winnipeg is situated in that part of the great wheat-growing area of the West where Rust in recent years has done most damage. The field stations at Brandon and Indian Head could be made use of for various purposes subsidiary to the research work centralized at Winnipeg; but I do not think that a man of the calibre of Mr. Stakman could be induced to make his headquarters at either of these places.

There are other serious diseases of wheat in addition to Rust, namely, (1) Smut, (2) Wheat Scab and (3) Root-rots. The last two have only been recently recognized but they do a great deal of damage in certain years. Mr. Stakman, in addition to his work on Rust, might be asked to investigate these new diseases also with the help of his assistants.

The writer is convinced that plant diseases constitute a factor of first-class importance in connection with agriculture in Western Canada. It therefore seems to him that the time has come for the immediate establishment

of a strong central investigation station somewhere on the prairies. The plan outlined appears to him to be the most promising one yet suggested and he trusts that it will be carried through, and thus promote the best interests of the Dominion.

Whether or not this memorandum was directly responsible for the rust conference held at Winnipeg, August 16-18, 1917, it was undoubtedly one of the incentives. Concerning this conference Neatby (unpublished) commented as follows:

> It is more than likely that Professor Buller's memorandum was partly, if not largely, responsible for this conference. The minutes are on file and are entitled "Summary of Proceedings at the Preliminary Rust Conference held at Winnipeg, Man., August 16-18, 1917." The following persons were listed as 'delegate present':
>
> J. H. Grisdale, Dr. W. C. Murray, Dr. J. A. MacLean, Prof. J. B. Reynolds, Dr. A. H. R. Buller, Prof. V. W. Jackson, Prof. T. J. Harrison, Prof. John Bracken, Prof. W. P. Thompson, Prof. G. H. Cutler, Dr. F. J. Lewis, Prof. W. P. Fraser, P. R. Cowan, Mr. W. H. Gibson, Mr. W. C. McKillican, Mr. S. A. Bjarnason, Dr. C. E. Saunders.
>
> From the Minutes it appears that Mr. J. H. Evans, Deputy Minister of Agriculture for Manitoba, and Mr. J. G. Carl Fraser were also present... At this meeting the administrative, scientific, and agricultural problems were discussed at some length and a number of resolutions were passed. The resolutions were related to legislation required in connection with the eradication of the common barberry, to the provision of greenhouse and laboratory space, to co-operation with agricultural colleges, particularly Manitoba and Saskatchewan, and to what was called preventive work and field crop investigation.
>
> To us perhaps the most significant and interesting feature of the meeting is the thoroughly scientific yet almost prophetic understanding of the problem by W. P. Thompson, W. P. Fraser, and Prof. A. H. Reginald Buller. On the purely scientific side our debt to these three men is stupendous. On the administrative side the contributions of Dr. J. H. Grisdale and Dr. W. C. Murray were perhaps no less impressive.

The plans envisioned in Professor Buller's memorandum and at the Rust Conference of 1917, which later came to be known as the First Cereal Rust Conference, could not immediately be implemented to any great extent. Canada was in the throes of the War of 1914-18 and considerations of finance as well as unavailability of trained scientists prevented development of these plans for the duration of and for some time after the war. One type of fundamentally important investigation was, however, undertaken even before the end of the war.

Late in 1917, Margaret Newton and W. P. Fraser began to study the parasitic behavior of stem rust by obtaining stem rust cultures from various cereals and grasses and growing these rust cultures on a variety of grain and grass hosts. This work confirmed the recently made discovery of E. C. Stakman of the University of Minnesota, at that time unknown to these two Canadian investigators, that wheat stem rust was not all pathogenically alike but consisted of many pathogenically distinct strains which he called 'biologic forms' and which later came to be known as 'physiologic races'.* Later, Newton pursued these investigations for a year in Fraser's laboratory at Saskatoon and

*In the fall of 1917, Professor Fraser brought to Macdonald College several specimens of rusted wheat. These he gave to Margaret Newton with the request that she make single-spore cultures from them. The testing with these cultures of a selection of Marquis wheat supplied by Dr. C. E. Saunders demonstrated that the seedlings infected with one of the rust collections were resistant whereas those infected with other collections were susceptible. In January, 1918, Professor Fraser was satisfied that they had two pathogenically distinct strains of wheat stem rust. The communication of these results to Dean E. M. Freeman of the University of Minnesota revealed that Dr. E. C. Stakman had already made a similar discovery. (Personal communication from Dr. Margaret Newton.)

for a year and a half in Dr. Stakman's laboratory. The annual surveys to determine the distribution of physiologic races were initiated in 1919 and have continued up to the present time as an indispensable aid to the production of rust-resistant varieties.

Immediately after the end of the war an increasing interest was taken by Canadian university students in plant pathology as a field of study. Two of these students, D. L. Bailey and I. L. Conners were attracted by rust investigation. The former worked at the plant Pathology Laboratory at Saskatoon, and in summer at the Field Laboratory at Indian Head, under the general direction of W. P. Fraser, in 1919 and 1920; the latter worked at the Field Laboratory in Brandon, Manitoba, in 1920 and at Winnipeg in 1921. Among the experiments carried on at Indian Head in 1919 were tests designed to gain information on the best time of cutting rusted grain. The experimental results indicated, as did also those obtained in a similar test at Winnipeg, that a greater yield was obtained by leaving the grain to mature than by cutting earlier. The summer of 1919 was suitable for this experiment as stem rust infection was severe in Manitoba and eastern Saskatchewan. In the spring of the same year it was found that the summer spores of stem rust may survive the winter on grasses until early spring, but no direct evidence was obtained that these surviving spores caused infection on spring-planted grain. The same year saw the first effort at the location and eradication of barberry bushes in Manitoba, of which several were found. In 1920, W. P. Fraser established, at a number of localities in Western Canada, the so-called uniform rust nurseries which were plots in which the resistance of cereal varieties to rust could be evaluated and which served also as convenient places for the collection of rust for physiologic-race studies. These lines of investigation were continued in 1920 and succeeding years as far as was possible with the limited staff available.

Heavy losses from stem rust infection in 1923 and moderate losses in 1919 and 1921 emphasized again the need of more active investigations on rust. Interest in the question of what action could be taken was not limited to the Department of Agriculture. At least as early as the rust conference of 1917, the National Research Council was conscious of the need for research on rust and willing to promote such research. Newton (1932) referred to a discussion in the 1918-19 report of the Research Council of a grant to W. P. Thompson to assist in the production of a rust-resistant variety. He stated also that when Dr. H. M. Tory became President of the National Research Council in 1923 "he immediately interested himself in the promotion of rust research". He quoted from an address given by Dr. Tory to the Canadian Club, Ottawa, on December 13, 1923: "In 1916 we lost 100,000,000 bushels of wheat by rust and this year, in southern Manitoba and Saskatchewan, we lost 50,000,000 bushels. These are losses not to be reckoned in tens of thousands of dollars but in tens of millions. What are we doing about it? At the present moment we have one man giving part of his time to the fundamental study of rust. Surely the time has come when a group of men of the highest training should be put to work upon such a problem. Why should we consider the cost of such an undertaking when we think of the magnitude of the problem to be solved and the saving to be made."

Early in January, 1924, Dr. Tory pursued the subject further "at a meeting of the Committee on Research of the Privy Council, attended by Honourable Charles Stewart, Honourable W. R. Motherwell and Honourable T. A. Lowe, all of whom cordially agreed with the suggestions Dr. Tory

put forward. Two days later the National Research Council, at its meeting of January 18, 1924, decided on the appointment of a Committee on Rust Research, and allocated an initial sum of $5,000.00 to assist in getting the work of the Committee under way." (Newton, 1932).

However, if any large-scale action was to be taken, it would naturally come under the auspices of the Honorable W. R. Motherwell, Minister of Agriculture, and himself a Saskatchewan farmer fully conscious of the need for action. An important step preparatory to action was an address by H. T. Güssow, on June 18, 1924, before the Select Standing Committee (of the House of Commons) on Agriculture and Colonization. In this report he discussed the rust problem in its various aspects, gave a statement of the inadequacy of current provisions for research, and put forward recommendations for research that should be undertaken. His general approach to the problem was defined by the statement: "The rust problem, it seems to me, should be approached from three well-defined points of attack—Plant Pathological, in its ordinarily accepted sense, Plant Breeding and Biochemical. There seems little doubt that the best interests of the work, where some of these lines [of] investigation parallel each other or even overlap, would be most effectively served by the close contact of workers which centralization of effort would necessarily involve. On the other hand, if such centralization demanded the divorcing of all our research problems from university contact and influence, some of the most fundamental, most essential and most significant phases of our research would suffer materially. Such is not the intention. Everyone should wholeheartedly aid." He suggested an appropriation of $100,000 to take care of the necessary land and buildings and other expenditures for the first year. (The Committee recommended to the House of Commons an appropriation of $50,000, which sum was later voted by the House.) As for the details of implementing these plans he stated that "the question where such co-operative scheme in which all interests should be represented, Federal, Provincial, College and University, should be inaugurated, may be left to the discussion of the subject on the occasion of a conference recently proposed by our Department to be held shortly in Winnipeg."

The decision as to when to hold this conference was made a week later, on June 25, when Dr. H. M. Tory and Dr. J. H. Grisdale met in the latter's office and decided to hold the conference on September 9 and 10. They made a list of the persons to be present and named a permanent committee "to have charge of the rust research work it is proposed to carry on with renewed vigour and more extensively in Western Canada than ever before" (Neatby, unpublished). The committee so named was made up of the following: H. M. Tory, W. P. Thompson, A. H. R. Buller and Robert Newton, to act on behalf of the National Research Council; J. H. Grisdale, E. S. Archibald, H. T. Güssow, W. P. Fraser and D. L. Bailey, to represent the federal department of agriculture. At the time of the conference the names of W. C. Murray, W. T. G. Wiener and L. H. Newman were added.

All of the above except Professor Buller attended the meeting.

The record of those in attendance shows that care had been taken to secure the presence of those best qualified to give advice on the future of rust research. The Honourable W. R. Motherwell, Minister of Agriculture, was present and his Department was represented, apart from those already mentioned, by I. L. Conners and P. M. Simmonds who were actively engaged in cereal disease investigations and by W. C. McKillican and W. R. Leslie from the Experimental Farms of Brandon and Morden. The University of Manitoba was represented by President J. A. McLean and the Manitoba Agricultural College by V. W. Jackson and G. R. Bisby who had been appointed Professor of Plant Pathology in 1920. Others present were J. B. Harrington from the

University of Saskatchewan, S. P. Eagleson and H. Cronyn from the National Research Council, and, by special invitation, four distinguished specialists from the United States. These were: H. L. Bolley, the noted plant pathologist of the North Dakota Experiment Station, Fargo, N.D.; J. G. Dickson, plant pathologist, from the University of Wisconsin; H. K. Hayes, Professor of Plant Breeding, University of Minnesota and acknowledged leader in breeding rust resistant wheat; E. C. Stakman, Professor of Plant Pathology at the same university and discoverer of physiologic specialization in wheat stem rust.

Neatby (unpublished) commented on this meeting as follows:

> After the Chairman's remarks the 'present status of the cereal rust situation' was reviewed by Mr. W. P. Fraser and Dr. E. C. Stakman. Investigations under way and review of results then followed and this subject was dealt with by D. L. Bailey, W. P. Fraser, G. R. Bisby, W. T. G. Wiener, W. P. Thompson, and R. Newton—the above for Canada. For the United States the work was reviewed by E. C. Stakman, H. K. Hayes, J. G. Dickson, and H. L. Bolley.
>
> Following the review of work in progress Dr. H. M. Tory and the Honourable W. R. Motherwell both delivered addresses before the meeting.
>
> Then followed a discussion of future research work on the rust problem and this included addresses by E. C. Stakman, W. P. Thompson, R. Newton, H. K. Hayes, J. G. Dickson, H. L. Bolley, W. T. G. Wiener, J. B. Harrington and G. R. Bisby.
>
> The last section of the proceedings deals with the reports of the Committee on Co-operation. 'The committee recommend that the following phases of the cereal rust problem be investigated co-operatively by investigators in Canada and the United States.' The proposal involved studies under four different headings as follows:
>
> (1) Epidemiology Studies, (2) Biologic Specialization, (3) Physiological and Ecological Studies, and (4) Breeding for Rust Resistance.
>
> At this meeting it was decided to hold a second national conference in the United States. Dr. Hayes and Dr. Stakman issued a very cordial invitation. However, so far as I can gather, this meeting was never held because another meeting was held in Winnipeg on January 26, 1925. This was not a full conference but a meeting of the permanent committee on rust investigations for the Dominion of Canada. According to the minutes the meeting was attended by Messrs. Grisdale, Buller, Güssow, Archibald, Murray, Fraser, Newton, Thompson, Wiener, and Bailey. This meeting was devoted to consideration of individual projects, of the places at which the work should be done, staff requirements, finance, etc.

Though not recorded by the Secretary, the meeting was also attended by Dr. C. H. Goulden.

The stage was now set for action. The first step was to decide upon the location of the new laboratory, a decision which had to be made by officials of the Department of Agriculture. According to Güssow (personal communication) two locations, the Agricultural College at Winnipeg, and the Experimental Station at Morden, were given consideration. The Winnipeg site, favored by Mr. Güssow, finally received the approval of the Minister, the Honorable W. R. Motherwell. In consequence, two greenhouses were erected in readiness for use in the summer of 1925 on land provided on its grounds by the Manitoba Agricultural College. Adjacent to the greenhouses, a building was constructed in the winter of 1925-26 and was ready for occupation late in the winter. The new building was given the name of the Dominion Rust Research Laboratory.

Staff to carry out the projected work was acquired during the summer of 1925 and, pending the erection of the new building, was provided working quarters in the Botany Building of the Agricultural College.

The plant pathology work, including that on rusts, was under the general direction of D. L. Bailey who had been located at the Agricultural College, was in charge of the Field Laboratory of Plant Pathology since April, 1923,

and had been joined by F. J. Greaney in 1924. In the summer of 1925 his staff was augmented by J. H. Craigie to undertake studies on the life history of stem rust, and by Margaret Newton to study the physiologic specialization of wheat stem rust. Two further appointments were made in the fall of that year: T. Johnson to collaborate in the work on physiologic specialization and W. L. Gordon to carry out research on oat-stem rust. In the same year I. L. Conners, who had been located at the Field Laboratory of Plant Pathology at Brandon, Manitoba was transferred to the institution at Winnipeg to continue his studies on the smuts of cereals.

The work on plant breeding was placed under the direction of C. H. Goulden who had just finished his gradute studies at the University of Minnesota. He arrived in the spring of 1925, and during the summer was joined by J. N. Welsh who assisted Dr. Goulden in the wheat-breeding work and later took charge, with conspicuous success, of the program of breeding rust-resistant oat varieties. A further valuable accession to Dr. Goulden's staff was K. W. Neatby who came from the University of Saskatchewan in the spring of 1926 to take direct charge of the wheat-breeding work. Thus, by the spring of 1926, the work of the new laboratory was organized and already in progress.

EARLY STUDIES ON STEM RUST, 1917-1924

The research work now to be undertaken on the stem-rust organism, *Puccinia graminis* Pers., had practical control measures as its chief objectives. But to decide what control measures were practicable it was obviously necessary to gain as thorough an understanding of stem rust as possible. It was necessary to ascertain what was known about the rust and what remained to be found out. It seems advisable, here, to outline briefly the state of knowledge concerning the stem rust organism at the time of the founding of the Dominion Rust Research Laboratory and to indicate the lines of research that seemed necessary to supplement what was known.

Since the work of the German scientist de Bary, just after the middle of the last century, it had been known that stem rust was one of the heteroecious rusts, that is, a part of its life cycle was spent on grain or grasses and a part on certain species of Berberis, of which the most important was the common barberry, *Berberis vulgaris* L. The spores of the red, summer stage (the urediospores) were formed continually through the summer on grain and grasses. As grain and grasses matured, late in summer, the red spores were no longer produced but in their place were found the thick-walled, black, winter spores (teliospores) from which the name black stem rust was derived. These black spores survived the winter, remaining in a dormant condition until spring, when they germinated through the production, by each spore, of a short germ tube which gave rise to four colorless, thin-walled spores known as basidiospores or sporidia. These sporidia were forcibly discharged into the atmosphere. Oddly enough, the sporidia did not infect cereals or grasses, but were capable of infecting many species of barberry. The first sign of infection on the barberry was the production on the upper side of a leaf of small eruptions on which appeared droplets of a yellow, sweet-flavored exudate. These eruptions were known as pycnia. Considerable earlier research work had failed to elucidate their function. The yellow, pycnial exudate contained innumerable very small spores which did not appear to have the ability to cause infection or even to germinate. Several days after the appearance of the pycnia on the upper leaf surface, yellow, tubular structures began to grow from corresponding positions on the lower surface of the leaf. These tubular structures, known as aecia, presently opened to reveal a mass of yellow spores (the aeciospores) beautifully arranged in long chains extending lengthwise in the aecia. Just before

the founding of the laboratory at Winnipeg it was discovered (Dodge, 1924) that these spores were forcibly ejected, singly or in small groups, into the air, each aecium acting as a gun.

The aeciospores, though produced on the barberry, were not capable of infecting barberry but readily infected cereals and grasses, with the result that spores of the red, summer stage were formed a few days after infection. The life cycle of the rust was thus completed.

The gap in the knowledge of the life cycle concerned the function of the pycnial stage. Were the pycnia 'residual' organs that had functioned at some earlier time but were now functionless? Or, had they some, as yet, not understood sexual function?

There was a corresponding lack of complete understanding concerning the nuclear phenomena of the rust. It was known that the red, summer spores were binucleate. The nuclei fused to produce one nucleus in the ripening black spore. This nucleus was subject to the process of 'reduction division' (meiosis) in the germinating black spore, with the result that each of the resulting four sporidia was uninucleate and haploid.*

It was known that the pycnial stage of the rust was haploid, and that the aeciospores were binucleate like the summer spores, each of these two nuclei presumably being haploid. It was not known exactly how the binucleate condition arose in the so-called aecial primordium at the base of the aecia.

It was considered necessary to fill these gaps in our knowledge, although it was not foreseen exactly how the filling of these gaps would profit the practical research work under way. It was to this problem that J. H. Craigie applied himself on his appointment in 1925.

Although the precise rewards of a more thorough knowledge of the life cycle were not foreseen it was surmised that such increase of knowledge would have a significance for the work already undertaken by Margaret Newton on the physiologic specialization of the rust.

The first glimmering of an understanding of the problem of specialization dates back to 1894 when Jakob Eriksson, a Swedish plant pathologist, showed that all stem rust was not pathogenically alike. He found that stem rust collected on oats attacked oats readily but not wheat, barley, or rye. That collected on wheat attacked wheat and barley but attacked rye with difficulty and oats scarcely at all. Stem rust from grasses frequently attacked the grass host on which it was found and closely related grasses, but not other grasses or cereals. It became evident to Eriksson that stem rust was divisible into strains specially adapted to the grass or cereal hosts on which they were found. He obtained evidence for the existence of six, or possibly more, such strains, which he called specialized forms of the rust (*formae speciales*).

From 1916 onwards, E. C. Stakman and his collaborators showed that wheat-stem rust was not a single pathogenic entity but could be subdivided, by the use of appropriate 'differential host varieties' into a number of pathogenically distinct strains, at first named biologic forms and later, physiologic races. These were given successive numbers, as they were found and described. By 1918, at least 15 such physiologic races had been found in wheat stem rust. Marquis, the wheat variety commonly grown at that time, was resistant to six of these 15 races but susceptible to the remaining 9; Kanred, a winter wheat grown at that time, was immune from 4, resistant to 4 and susceptible to 7

Haploid and *diploid* are contrasting terms having reference to chromosome content. The body cells of higher plants and animals are *diploid*, having a given number of pairs of chromosomes. The sexual cells, as pollen cells and ovules in plants, sperms and eggs in animals, are haploid, having only *one of each pair* of chromosomes and, therefore, only half the chromosome number of the diploid cells.

of these first 15 races. The physiologic race surveys carried out by W. P. Fraser and Margaret Newton from 1919 to 1924 had shown that at least 17 of these races were present in Canada during this period (Newton, 1938).

Evidence was already beginning to accumulate, in the studies of Stakman and his associates, that a greater variety of races occurred in rust collections derived from aecia than in those taken from the summer stage on wheat. Was this greater variety of races in the rust from barberry the result of hybridization betwen races? Although there was no understanding of how a sexual process functioned in the rust, there was general agreement that a sexual process of some sort must exist in the stage of the rust on barberry.

Apart from its possible function in contributing to the multiplicity of rust races, the barberry had a well-known function in the spread of rust. The barberry was introduced to North America from Europe as a cultivated shrub in the seventeenth century, became widespread as a cultivated and as a naturalized plant in the eastern United States, and was eventually introduced in the Mississippi Valley as it was settled in the nineteenth century. Its relation to the spread of stem rust had been realized by farmers in certain regions, as in northern France where farmers had secured the passage of a law (about 1660) requiring the destruction of barberry in wheat-growing areas, and in Connecticut, Massachusetts and Rhode Island where legislation against it was enacted in the eighteenth century (Fulling, 1943).

In the United States, the rust epidemic of 1916 was a spur to action against the barberry in the Mississippi Valley states. At a meeting of the American Association for the Advancement of Science held at Madison, Wisconsin, July 9-11, 1917, which (according to Neatby, unpublished) was attended by W. P. Fraser, the following resolution was passed at a meeting of cereal pathologists:

> Be it resolved that we the cereal pathologists of the American Phytopathological Society in summer session assembled at Madison, Wisconsin, respectfully ask the President of the United States to appoint a commission to consider the relation of the barberry to outbreaks of black stem rust of wheat, barley, other cereals and grasses, with a view to deciding upon the desirability of eradication of all cereal rust bearing strains of the barberry in the United States in order that this source of rust epidemics may be removed.
>
> Be it further resolved that the secretary be instructed to send a copy of this resolution to the President of the United States.
>
> *Signed,* C. W. Hungerford,
> *Secretary.*

Whether or not the commission requested was ever appointed it is likely that this resolution was one of the factors responsible for the initiation of the campaign to eradicate the barberry from the Mississippi Valley and North Central States for which an appropriation of $150,000 was allocated in 1918. This campaign, which has continued up to the present time had, by 1956, resulted in the destruction of more than 500 million barberry plants in 19 of the principal wheat-growing states.

In Canada, as in the United States, the first step towards barberry eradication was to provide a legal basis for the destruction of barberry bushes. This was done, according to Bailey (1928), by an amendment of the Destructive Insect and Pest Act in 1916 which "prohibited distribution of barberries from nurseries and gave the necessary authority to remove without compensation those which had already been introduced."

In the Prairie Provinces the destruction of barberries was also authorized under the provincial acts relating to noxious weeds.

As stated above, the first efforts to locate and destroy barberries in Western Canada were made in 1919. In the following years the location and

eradication of barberry was carried out co-operatively by plant pathologists of the Division of Botany and certain members of the staff of the western agricultural colleges. A summary of this early work is given by Jackson *et al.* (1925). Under V. W. Jackson's direction "the Botany Department of the [Manitoba] Agricultural College undertook to make a survey of the nurseries of the West, and to locate and make an estimate of the number that had been sold. It was found that most of the barberries were in the city parks of Winnipeg, over 3,000 in all, which Professor Buller urged be removed, and which the Parks Board promptly did in 1917." The time-consuming task of locating barberries in the small towns and villages and on farms was performed under the direction of W. P. Fraser for Saskatchewan, and of D. L. Bailey and, later, J. H. Craigie for Manitoba, extending intermittently, over the years 1919 to 1932. In country districts, few barberries were found except for occasional large hedges as at Gimli and Snowflake, Manitoba, and a few bushes in small towns and on farms. In a resurvey in Manitoba in 1957 (Basset, 1958) very few barberries were found and the opinion was expressed that the low incidence of this shrub is a consequence of the eradication carried out in earlier years.

Many of the earlier surveys for barberry included also surveys of the distribution of the European buckthorn, *Rhamnus cathartica* L., the aecial host of crown rust of oats, *Puccinia coronata* Corda. This shrub was more widely distributed than barberry and its eradication was less successful. In 1923, a survey in Saskatchewan showed that "large numbers of buckthorn have been planted in the cities and some of the larger towns, but that few are present in the smaller towns" (Fraser, 1925). In Manitoba, a similar survey in 1923 and 1924 included 173 towns and villages of which 20 were found to have buckthorn plantings (Bailey, 1925a). A resurvey in 1957 (Basset, 1958) led to the conclusion that "European buckthorn presents a serious problem in three areas of Manitoba, namely Winnipeg, north of Brandon and near Macdonald." Arrangements made in 1958 with the Parks Board of the City of Winnipeg led to eradication of European buckthorn in the city parks. Similar arrangements were made with the Manitoba Department of Agriculture for the destruction of buckthorn in smaller towns and rural areas. Although these efforts will not eliminate European buckthorn in Manitoba they will greatly reduce the concentration of the shrub.

As briefly mentioned above, the epidemiology of stem rust was one of the first subjects to receive the attention of W. P. Fraser when he came to Western Canada after the epidemic of 1916. Canadian studies on this subject, which have been thoroughly reviewed by Craigie (1945), deal with most of the factors affecting the spread of stem rust. Between 1918 and 1924, much attention was given to the important question of whether or not stem rust could survive the Canadian winter on grain and grasses and through such survival reinfect the young crop in the spring. These studies showed that the summer spores would frequently survive until spring, especially in protected places as under the sheaths of grasses such as wild barley, *Hordeum jubatum* L., but the work provided little, if any, evidence that such surviving spores were responsible for the renewed infection of cereals or grasses. The first infections, each year, were evidently traceable to windborne spores.

The determination of the time of arrival of windborne spores was studied as early as 1918 by placing vaseline-covered glass slides in the open air. The number of spores adhering to a given area of the slide provided a rough measure of the relative numbers of spores arriving at different times and made possible, if the slides could be examined promptly, a prediction of the time and intensity of rust outbreak. This phase of epidemiology was to receive increased attention after the establishment of the new laboratory in 1925.

The research undertaken in the period from 1917 to 1924 reflects the highest credit on the Dominion Botanist, H. T. Güssow, and on Professor W. P. Fraser and his few associates. They had begun work on urgent problems such as the location and destruction of barberry and buckthorn, the significance of these plants in the spread of rust, the extent to which the red stage of stem rust could overwinter, the appropriate time of the cutting of rusted grain, and the movement of rust spores during the spring and summer months. The establishment, in 1920, of rust nurseries at various points in the Prairie Provinces provided opportunities for observing annually the rust reaction of a group of selected varieties some of which were good habitats for collecting the various physiologic races. However, investigations bearing directly on the two major means of rust control—the breeding of resistant varieties and the control of rust by application of fungicides—were beyond the resources of this small group of workers. These researches had to await the foundation of the Dominion Rust Research Laboratory.

EARLY WORK ON CEREAL BREEDING

During the nineteenth century numerous varieties of wheat and other cereals were produced in all the important cereal growing countries, chiefly by selection. Before the end of the century, however, hybridization as a means of varietal production was used with notable success by a number of men, of whom William Farrer in Australia is perhaps the best known. According to Clark (1936) the production in the United States of commercial wheat varieties by this means began about 1890. The rediscovery of Mendel's principles of inheritance at the end of the nineteenth century was a stimulus to plant breeding. The realization that many plant characters were simply inherited and could be transmitted to new varieties with little or no change stimulated plant breeding with specific objects in view. Sir Rowland Biffen, in the first decade of this century, was the first to show that disease resistance was heritable according to Mendelian laws. He found that resistance of wheat to stripe rust, *Puccinia glumarum* (Schmidt) Erikss. & Henn., was recessive to susceptibility and was inherited in later generations as a simple, Mendelian recessive. The fact that rust resistance could be separated from other plant characters and recombined, in a new variety, with other desirable characters was a discovery of great significance for breeding for rust resistance.

The breeding of rust-resistant bread wheats was obviously made more complex by Stakman's discovery (about 1916) that wheat stem rust was not a unit pathogenically but consisted of many parasitically differing physiologic races. One of the first questions was whether these physiologic races were pathogenically constant. If they changed pathogenically from time to time, breeding of resistant varieties might be impossible because of adaptation of races to the resistant varieties. Fortunately, Stakman and his associates were able to show that the races could be kept in culture over long periods without any apparent change either by adaptation or by mutation. Races, therefore, showed considerable stability, which gave promise that new resistant varieties would retain their resistance against them for long periods.

Another difficulty facing the plant breeder lay in the multiplicity of physiologic races, of which 37 had been discovered by 1922 (Stakman and Levine, 1922). Although many useful bread wheat varieties were resistant to several races, no variety appeared to be resistant to all the races. There were obviously two possible approaches to the production of rust-resistant varieties of the bread-wheat type. The first was to increase the range of resistance by crosses between bread-wheat varieties. A variety resistant to a group of races could be crossed with another variety resistant to a different group of races

and there was a good prospect that some of the hybrids might be resistant to both race groups. The most resistant hybrids might be crossed with other varieties to broaden still further the spectrum of resistance. The advantage of a breeding program of this type was that the bread wheats—all belonging to the species *Triticum vulgare* (Vill.) Host—were so closely related that the breeder had little intersterility to contend with and would have little difficulty in producing wheats of adequate quality. The fact, already demonstrated by H. K. Hayes and his collaborators as early as 1923, that resistance to individual physiologic races, and even resistance to groups of races, was inherited in accordance with Mendelian principles (Aamodt, 1923), gave promise that considerable progress might be made by such a program. The difficulty remained, however, of finding adequate resistance in bread wheats to all the known races as well as the new races discovered year by year.

It was this difficulty that turned the attention of plant breeders to the second approach to breeding rust-resistant bread wheats, namely, the production of such wheats through crossing bread wheats with the more highly resistant durum wheats (*Triticum durum* Desf.) and emmer wheats (*Triticum dicoccum* Schubl.). There were obvious obstacles in the way of this approach. The bread wheats had 21 pairs of chromosomes; the durum and emmer wheats had 14 pairs. Because of the difference in chromosome numbers and a considerable degree of chromosome incompatability such crosses were difficult to make and, even when successful, they displayed much sterility in the hybrid populations. Moreover, the early crosses made by Hayes and others in the United States and by W. P. Thompson in Canada showed that in the hybrid progeny there was a distinct correlation between rust resistance and durum or emmer characters; that is, most of the rust-resistant progeny resembled durum or emmer wheats rather than bread wheats. Nevertheless, there was a promise of progress in the fact that a few rust-resistant plants of bread-wheat type occurred in the progeny of some crosses.

One of the first of the resistant bread-wheat types derived from interspecies crosses was the variety Marquillo derived from a cross made in 1915 between the bread wheat Marquis and the rust-resistant durum wheat Iumillo (Hayes and others, 1936). Iumillo, which had been observed by Carleton, in 1904, to be highly resistant to stem rust in the epidemic of that year, has contributed valuable resistance to many varieties of bread wheat. In the third generation of the cross of Marquis and Iumillo a few resistant plants of bread-wheat type were found in 1918. Although these, which included the plant giving rise to Marquillo, did not produce lines of commercial quality, they were of value for future crossing. One of the sister lines of Marquillo, designated N. S. N. II-15-51, was crossed with a derivative of the cross Kanred × Marquis to give rise to the famous variety Thatcher which combined the Kanred immunity from many physiologic races with the broader resistance of Iumillo.

Another successful interspecies cross was the cross between Marquis and Yaroslav Emmer made by E. S. McFadden at Brookings, South Dakota, in 1915 (McFadden, 1930). The two bread-wheat types developed from this cross (Hope and H 44), though deficient in agronomic and milling qualities, were highly resistant, especially in the adult-plant stage, to a large number of physiologic races. This emmer-derived resistance was to be transmitted in later years to many commercial wheat varieties.

When the Dominion Rust Research Laboratory was established, in 1925, the first important steps towards the breeding of rust-resistant bread wheats had been taken. Stakman's studies on specialization had thrown much light on the nature of the enemy, the stem-rust organism. A rudimentary knowledge had been gained on the manner of inheritance of stem-rust resistance. Resistance factors had been brought into bread wheats from the more highly

resistant durum and emmer wheats. But the problem of combining these resistance factors with the necessary agronomic characters and milling and baking qualities remained to be solved.

RESEARCH ON RUST, 1925-1937

LIFE HISTORY, HYBRIDIZATION AND SPECIALIZATION

As already stated, an investigation was undertaken in 1925 by J. H. Craigie on the function of the pycnial stage of the stem-rust organism. Several experimental methods were tried including attempts to establish infections on barberry by each of the four sporidia produced by the germinating winter spores, which, if successful, would have provided direct proof that the rust was either homothallic (capable of producing aeciospores from infection with a single sporidium) or heterothallic (requiring the union of elements from two such infections). If the rust proved to be heterothallic a sexual process would obviously be involved. Although this method of obtaining infection from individual sporidia proved too difficult to be practicable, other methods were devised to demonstrate the function of the pycnial infections. In 1927, Craigie showed that when sunflower leaves were sparsely infected by sporidia discharged from germinating winter spores (teliospores) of sunflower rust (*Puccinia helianthi* Schw.) the resulting infections rarely gave rise to aeciospores unless the yellow exudate which contained the pycniospores was transferred from one infection to another. In the same year he made a similar demonstration for stem rust on its alternate host, the barberry. His experiments showed very clearly that both rusts were heterothallic.

Through this work the function of the pycnial stage of the rusts became clear (Craigie, 1931). The pycnia were not vestigial organs without significance in the life cycle of the rusts, as some had thought. The pycnia, and the pycniospores, were of two kinds which Craigie designated (+) and (—). In pycnia derived from single sporidia, no aeciospores would be produced unless pycniospores were introduced from a pycnium of the opposite kind, or unless the rust mycelia of the two opposite kinds came into contact. Each pycnium was provided with threadlike, receptive rust hyphae, designated 'flexuous hyphae'. These flexuous hyphae could not be fertilized by the pycniospores of their own pycnium but were fertilized by the pycniospores of a pycnium of an opposite kind. In a (—) pycnium a pycniospore from a (+) pycnium could transmit its nucleus to a flexuous hypha. This nucleus would then work its way to the aecial primordium, a weft of haploid rust mycelium which had developed below the pycnium, and there it would become associated with a haploid nucleus of the opposite (—) sign. This aeciospore mother cell, now containing two haploid nuclei of opposite kind, would then give rise to one or more chains of aeciospores. The binucleate (dikaryotic) condition, thus established in the aeciospores persisted in the mycelia and spores of the red, summer stage, the actual fusion of the two haploid nuclei not occurring until in the maturing or mature winter spore. In the germination of the winter spore, reduction to the haploid condition took place, with a halving of the chromosome number. The presence of four sporidia on the germ tube of the winter spore was due to a second, vegetative, division, which did not further change the chromosome number.

The significance of Craigie's discovery for variation in the rusts was at once apparent. Here was a mechanism whereby haploid nuclei of one race could come into association with haploid nuclei of another race. The same mechanism provided for the redistribution of the genetic material of a single

race. The ‘crossing’ of two races could be accomplished by transferring pycniospores from a (+) pycnium of one race to a (—) pycnium of another, or vice versa. The ‘selfing’ of a race could be accomplished by intermixing the exudates of pycnia of the same race.

A study was at once undertaken by Margaret Newton and her collaborators T. Johnson and A. M. Brown of the nature of the pathogenic variation that could be induced in wheat stem rust races by selfing and crossing. The results showed that few races were homozygous. The majority, when selfed, produced two or more races. Similarly, the crossing of two races generally produced one or more races quite different pathogenically from the two parent races (Newton and others, 1930).

In their early work, the discovery of two color mutants—a mutant of race 9 producing yellow summer spores and a mutant of race 36 producing grayish-brown spores—made possible the establishment of the fact that some characters of the rust were inherited in accordance with Mendelian laws. The F_1 (first generation) hybrid between these mutants was of the normal, red spore color. The selfing of this hybrid gave rise to rust strains that fell into four distinct color groups: red, yellow, grayish-brown and white. The distribution in these groups suggested a 9:3:3:1 ratio, which could be accounted for by the presence of two complementary pairs of genes. It was evident that the yellow mutant, lacking spore-wall pigment, had lost a factor governing the formation of that pigment. The grayish-brown mutant, lacking the carotinoid pigment of the center of the spore, had lost the factor governing the formation of that pigment. The F_1 heterozygote contained both pigments and, therefore, produced red spores but, because of its heterozygosity, it could, on selfing, produce red spores (when both factors were present), yellow or grayish-brown spores (when one or the other was present), and white spores (when neither factor was present).

These same crosses revealed another interesting phenomenon. Both mutants were considered virulent to Marquis wheat, that is, Marquis was susceptible to both. But the yellow mutant of race 9 produced a somewhat smaller rust infection surrounded by a chlorotic halo. It differed noticeably in that respect from the other mutant and also from red cultures of race 9. It was therefore properly to be regarded as a variant (biotype) of race 9. Crosses between the two mutants were made by bringing pycniospores of the yellow race 9 to haploid pycnial pustules of the grayish-brown race 36 and, reciprocally, by bringing pycniospores of the grayish-brown race 36 to haploid pycnial pustules of the yellow race 9. In the first case the ‘hybrid’ aeciospores were formed from a haploid infection of race 36; in the second case they were formed from a haploid infection of race 9.

In both cases the hybrid race was race 17 of red color but with the difference that when the hybrid arose from the race-9 side of the cross it displayed, on Marquis, the smaller rust pustule and chlorotic halo characteristic of the yellow mutant of race 9. The race 17 derived from the reciprocal cross produced larger pustules without the halo, as did the grayish-brown parent rust. Since the nuclear state of the reciprocal hybrids was presumed to be identical it was assumed that the difference must be due to a difference in the cytoplasmic constitution of the hybrids. It is conceivable that the nucleus of a pycniospore of the grayish-brown race 36, brought to a haploid pycnial pustule of race 9, would lose most of its accompanying cytoplasm on the long journey down the flexuous hypha to the aecial primordium near the base of the leaf. If so, the constitution of the resulting aeciospore would be: one nucleus of race 36, one nucleus of race 9, cytoplasm of race 9. In the aeciospores developing from the reciprocal cross, the nuclear constitution would be the same but the cytoplasm would be that of race 36.

This hypothesis, supported by studies in the F_2 and F_3 generations of these hybrids, is of interest principally because evidence of the effect of the cytoplasm on inheritance is somewhat scarce. Although similar results were obtained later, in certain crosses between races of oat stem rust, there is little reason to suppose that cytoplasmic inheritance is of great significance in the rusts.

Further work by Newton and Johnson on these and other crosses provided considerable information on the inheritance of rust characters, including evidence that pathogenic characteristics are inherited, generally, according to Mendelian principles (Johnson and Newton, 1940). In a study of the F_1, F_2 and F_3 generations of the above-mentioned crosses certain facts were established. Some infection characteristics were dominant to others. The O type of infection (inability to produce rust) shown by race 9 on the variety Kanred was dominant to the 4 type infection (large rust pustules) shown by race 36. In the F_2 generation, the O type infection occurred almost three times as frequently as the 4 type, suggesting simple (monogenic) Mendelian inheritance. The 1 type of infection (very small rust pustules) characteristic of race 36 on the variety Vernal was dominant to the large, 4-type pustules produced by race 9 on that variety. In the F_2 generation the small pustule-type occurred about 18 times as frequently as the large type, suggesting that two pairs of genetic factors were involved in such a way that the large pustules were produced only by those rust cultures in which both genetic factors were present in the recessive state. A third characteristic, the 4 type of infection on the variety Mindum, was dominant to the 1 type and reappeared three times as frequently in the F_2 generation, and was, therefore, presumably governed by a single pair of genetic factors.

The significant features of this work were the dominance in the F_1 generation of one character over another and the reappearance of the suppressed characters without any appreciable blending in the next generation. The genetic factors determining these characters maintained their identities but were recombined in various ways in the next generation, with the result that several physiologic races appeared. The race containing all the dominant factors (race 17) naturally occurred most frequently in the F_2 generation. The race containing only the recessive factors (race 52) occurred least frequently.

Inbreeding, especially in this cross and other crosses between races differing in color, brought to light a number of abnormal characteristics that had not been observed in stem rust as seen in nature (Johnson and Newton, 1938). On the barberry, some rust clones lost, partially or entirely, the ability to produce aecia. Some of these clones occasionally produced urediospores and teliospores in place of aeciospores in the infections formed on barberry leaves. As the urediospores infected wheat and not barberry there was no evidence that these abnormalities implied the formation of a correlated rust species capable of producing all its spore forms on barberry. These facts may, however, be regarded as evidence of a remarkable plasticity or capacity for variation in the rust which would suggest that the species is less fixed in its parasitic habits than had been expected. Abnormalities were also encountered in the uredial stage on wheat. Some of the rust cultures from inbred lines, though capable of causing infection, were unable to produce enough spores to enable the uredial pustules to break out through the surface of the wheat plant. In general, it may be said that all abnormalities observed were disadvantageous to the rust. In nature such abnormal strains would not be found because the only strains to survive would be those well fitted for propagation.

Because most wheat varieties were resistant to certain races and susceptible to others a study of the specialization of the rust was considered of great importance. After the founding of the Rust Research Laboratory two

kinds of studies on specialization were carried out with both wheat stem rust and oat stem rust. The first was a study of the constancy or stability of the various races. The second was a study of their distribution year by year in the various parts of Canada: the so-called survey of physiologic races.

A study of the stability of these races was necessary to ensure to the worker the knowledge that he was working with an entity of which he could measure the pathogenicity within a given range of environmental conditions. Since the races all looked much alike his only measuring stick was their pathogenicity. How reliable were their pathogenic characteristics? Did they change from time to time? Did they vary greatly under different conditions of temperature and light intensity? The answers, as given by Johnson for wheat stem rust, Gordon for oat stem rust and Peturson for crown rust of oats, were that most of the interactions between host plant and race, especially the resistant reactions and the susceptible reactions, could be reliably measured under a wide range of temperature and light. Certain races, on certain host plants, however, produced indeterminate reactions under average greenhouse conditions. At low temperatures these indeterminate reactions were generally expressed as resistant reactions, at high temperatures as susceptible reactions. In general, the result of this work confirmed that most rust races were readily identifiable entities. Physiologic-race surveys could, therefore, be confidently carried out under reasonably controlled greenhouse conditions, but the instability of certain reactions had to be taken into account. Hence it would be advisable to group together as one unit certain races differentiated from one another only by the less reliable infection types. Thus the wheat stem rust races 3, 18 and 36 were considered as a unit and the oat stem rust races 1, 2 and 5 were generally grouped as one race.

The annual surveys for the distribution of wheat stem rust races from 1919 to 1937 showed clearly that the physiologic-race population underwent changes from time to time. At the opening of this period, race 17 was the predominant race followed rather closely by races 21 and 36. After 1923 race 17 was less frequently found whereas race 21 maintained its place and race 36 increased yearly in abundance to a position of high predominance which it held until 1931 after which its abundance diminished sharply. Race 49, first found in 1926, was moderately important in 1929 and 1930 but had almost disappeared by 1937. Race 56, first found in the United States in 1928 and in Canada in 1931, became the most abundant race in 1934 and played a major part in the rust epidemic of 1935. The reasons for these fluctuations in race population are not known except for the increase of race 56 which appears to be related to the wide distribution of the wheat variety Ceres which was moderately resistant to the prevalent races but was sufficiently susceptible to race 56 to permit its rapid increase. The many races of stem rust, other than those mentioned above, that occurred during these years were of minor significance.

Physiologic races were identified on plants in the seedling stage by means of the infection types produced on the leaves by the various races. For most wheat varieties, the infection types on the seedling leaves bore a fairly close relation to the infection types produced by the same races on the adult plants. The races were, therefore, of obvious practical significance. Their practical significance was, however, greatly reduced by the discovery of 'mature-plant resistance'. This was a type of resistance most strikingly manifested by the varieties Hope and H 44, both derived from crosses between Marquis and Yaroslav Emmer. Although, in the seedling stage, these varieties were resistant to some races and susceptible to others yet, in the mature-plant stage, they appeared to ignore the physiologic races altogether, manifesting a high degree of resistance to all of the races known in North America in the twenties and early thirties. If this type of resistance could be transferred

by means of crosses to economically useful varieties it seemed that the time might come when physiologic races would have no economic significance. Nevertheless, there was no certainty that races did not exist, or might not come into being, that could attack these varieties, and consequently the race surveys were continued even after varieties with mature-plant resistance were distributed among farmers.

Studies on the physiologic races of oat stem rust were undertaken by D. L. Bailey in 1921 (Bailey, 1925b) and were continued by W. L. Gordon from 1925 to 1932 after which they were conducted by Margaret Newton and T. Johnson. From 1921 to 1924 the three closely related races 1, 2 and 5 appeared to constitute the whole rust population and remained by far the predominant races during the period 1925 to 1937. During this period specialization in this rust may not have had much practical significance as nearly all oat varieties grown in Canada were susceptible to all known races. Specialization, however, had a significance in relation to the program for breeding rust-resistant oat varieties which was undertaken in 1925 at the Dominion Rust Research Laboratory. At that time no variety had resistance to all the six races then known to exist. But since the type of resistance of the variety Hajira was adequate against races 1, 2, and 5, which were the only races known to be present in the country, it was decided to develop agronomically useful varieties with this kind of resistance. The occurrence of any races that could overcome this type of resistance would be a matter of concern. Although such races were soon found (races 4 and 6 in 1925 and race 8 in 1929) they were extremely rare and showed no sign of increased distribution for many years. Despite their appearance the race situation seemed to be relatively stable until after 1940.

Since the wheat-breeding program at Winnipeg entailed the incorporation into the new varieties of leaf-rust resistance as well as stem-rust resistance, it was considered advisable to study specialization in leaf rust of wheat, *Puccinia recondita* Rob. ex Desm. (= *Puccinia triticina* Erikss.). This work, which was commenced in 1931, showed that a great variety of races of this rust occurred annually in Canada; no less than 16 races were identified from 57 rust collections in the first year. It showed also that the races present in the Prairie Provinces were somewhat different from those in Eastern Canada and in British Columbia, a fact perhaps attributable to the difference in the wheat varieties grown in the three regions and to natural barriers between them. As the varieties grown in all three regions were susceptible the practical significance of specialization was not very apparent.

Studies on the specialization of crown rust of oats (*Puccinia coronata* Corda f. sp. *avenae* Erikss.) undertaken by B. Peturson in 1929 showed that more than a dozen races occurred in Canada during the period 1929-1936. The more prevalent of these races occurred in both Eastern and Western Canada but two of these (races 1 and 4) were more common in the west than in the east.

Similar studies, though on a smaller scale, were made with two other rusts of less economic importance, leaf rust of barley (*Puccinia hordei* Otth) studied by A. M. Brown and stripe rust (*Puccinia glumarum*), studied by Margaret Newton and T. Johnson. Both rusts were found to be specialized into races though these were fewer than in the other rusts. Both rusts occurred annually in the Prairie Provinces, leaf rust of barley in the eastern and stripe rust in the western parts; but as neither rust was of much economic importance the studies made were largely exploratory.

In all the work on physiologic specialization the Uniform Rust Nurseries played an important part as sources of rust collections for race studies and as a guide to the amount of rust infection and the reaction of various wheat

and oat varieties in different parts of the country. These rust nurseries, established by W. P. Fraser in 1920 in the Prairie Provinces were extended to a number of localities in British Columbia and Eastern Canada in 1926 by Margaret Newton. As it was impossible to visit all these nurseries at the appropriate time, it became the practice to have sheaves of each variety sent from the more distant nurseries to Winnipeg for observation at the time of maximum rust infection. The planting, general care, harvesting, and shipping of this material became the function of the various experimental stations and agricultural colleges at which the nursery plots were located and, consequently, this work could not have been carried out without their generous co-operation.

STUDIES ON THE EPIDEMIOLOGY OF RUST

One important phase of rust research is epidemiology: the studies of the initial sources of infection each year, the mode of dissemination of the spores, the manner of infection and the spread of rust outbreaks, and the effect of the environment on their development. This is a complex field of study in which all of the spore forms must be considered—in the case of stem rust, those on barberry as well as those on grain and grasses.

As already stated, some work in this field was undertaken by W. P. Fraser as early as 1918. In that year the first attempts were made to determine the time and amount of windborne distribution of summer spores by means of spore traps in which the spores were caught on the surface of vaselined glass slides. Fraser and his associates also gave attention to the role of barberry in initiating infection on grain and grasses and they investigated annually the problem of the overwintering of urediospores on cereals and grasses.

After the establishment of the Dominion Rust Research Laboratory in 1925 studies on epidemiology, which had previously been carried on principally at Saskatoon, were expanded on a co-operative basis. At Winnipeg, J. H. Craigie took charge of these investigations with the assistance, at different times of F. J. Greaney, W. Popp and B. Peturson. At the Saskatoon laboratory, which was directed by Dr. P. M. Simmonds from 1925 onwards, the epidemiology studies were performed for several years by G. A. Scott. After the establishment, in 1928, of the Dominion Laboratory of Plant Pathology at Edmonton, Alberta, under the direction of Dr. G. B. Sanford, he and his associates took part in this work.

The only phase of epidemiology that received no appreciable attention during the years following 1925 was the role of barberry as a source of infection. That plant had been almost completely eliminated from the Prairie Provinces by the work of barberry eradication carried out between 1918 and 1924 and had ceased to be a significant factor in the initiation of local rust infection.

The studies on overwintering of the summer spores on grain and grasess were continued and they confirmed the earlier work of Fraser and his associates, which had shown that a few spores occasionally retained germinability until April or early May but were not instrumental, as far as could be determined, in re-establishing the uredial stage on the new crop.

Since barberry and overwintering were obviously not significant sources of infection in Western Canada, it was evident that infection in early summer must come predominantly, if not entirely, from windborne spores brought from other areas. Two methods were employed in the study of windborne spores: (1) the use of stationary spore traps; (2) the use of spore traps exposed on aeroplane flights.

Vaseline-coated glass slides were exposed as early as 1918 in fixed positions on posts or on the roofs of buildings. As spores adhered readily to the vaselined surface it was possible to make counts, under the microscope, of the number

of spores trapped on a unit aera and so to obtain information on the relative spore content of the air on different days. In 1925 P. M. Simmonds devised a weather-vane type of slide-holder in which a vaselined microscope slide was protected from rain and so oriented as always to face the wind. This device became the standard spore trap for stationary slide exposures.

In 1926, the studies on spore movement were greatly expanded. Spore traps were located at four places in Manitoba, five in Saskatchewan and five in Alberta. The task of examining the slides exposed simultaneously at these 14 points between May and August was no minor chore.

Craigie (1945) has admirably summarized the results of the epidemiological investigations. The initial inoculum each year, was found to consist largely, if not entirely, of windbore spores originating in more southerly areas. These spores produced infections that increased the rust locally and this local inoculum was augmented periodically by further windborne spores from the south.

Aeroplane exposures, by means of spore traps specially designed for the purpose, were made from 1926 to 1929 at Cormorant Lake, 300 miles north of Winnipeg and separated from cultivated land by 150 miles of lake and forest. These exposures showed that stem rust spores were present there on most days in July and August at levels of 3,000 to 5,000 feet. Exposures at Portage la Prairie in 1930 and at Winnipeg in 1931 showed that spores were present at all elevations up to 14,000 feet (the highest investigated) between the middle of June and the middle of August. In 1930, a year of severe rust infection, the concentration of spores was markedly greater at an altitude of 1,000 feet than at 5,000 feet. In 1931, a year of light rust infection, there was a somewhat uniform distribution of spores up to the 5,000 foot level. In both years the spore concentration at the highest level, 14,000 feet, was great enough to indicate that spores must have reached far higher levels.

The studies on the movement of air-borne rust spores made it evident that there was a close relation between the abundance of air-borne spores and the amount of rust infection, both being greatest in the so-called rust area of Manitoba and eastern Saskatchewan. From there, the concentration of air-borne inoculum diminished, as did also the amount of infection, in a northwesterly and a westerly direction. That wind-borne spores may cause infection at great distance is indicated, however, by the fact that rust was found, by Margaret Newton, on volunteer wheat as far north as Churchill, Manitoba (600 miles north of Winnipeg), and at Hay River, N.W.T. (500 miles north of Edmonton), where it occurred on wild barley.

Although the epidemiological studies showed that the distribution of rust inoculum was closely related to the development of stem-rust epidemics, they showed also that other factors were of great importance. A measurement of the quantity of air-borne inoculum alone would not permit the prediction of the amount of rust infection. There was also an association of high rainfall with heavy rust infection and an indication that the conditions of precipitation and temperature in the 'rust area' were more congenial to rust development than in the drier and somewhat cooler areas farther west.

CONTROL OF RUST BY SULPHUR DUSTING

In planning the work of the new Dominion Rust Research Laboratory the major emphasis was placed on the control of rust by means of breeding rust-resistant varieties. But it was realized that at least 10 years would elapse before these varieties would be ready for distribution and, moreover, there was no absolute certainty of the success of this project. The need to explore the alternative method of control of rust by means of chemicals was therefore apparent.

Of the fungicidal chemicals known in 1925, sulphur appeared to be the most promising for investigation. Its value for the control of certain plant diseases had been known for almost a century. In 1924, C. V. Kightlinger, at Cornell University, obtained experimental results that indicated the possibility of controlling cereal rusts by dusting the growing plants with sulphur. In 1925, D. L. Bailey and F. J. Greaney began a study designed to explore the effectiveness of sulphur as a fungicide for the control of cereal rusts. This study was carried out jointly until Dr. Bailey left to take up his new post at the University of Toronto, in 1928, and was thereafter continued by F. J. Greaney.

These investigations, adequately recorded by Greaney (1934a, 1934b), may be regarded as definitive in the sense that, when they were concluded, there was little need of further study on the effectiveness of sulphur as a cereal-rust fungicide.

Many aspects of this problem were explored. In laboratory tests, the relative toxicities to rust spores of copper and sulphur dusts were compared and it was determined that whereas the two kinds of dust were about equally toxic, the sulphur dusts were less harmful to cereal plants. In a comparison of the toxic effectiveness of the various available types of sulphur dust the most finely divided, colloidal dusts proved most effective. The various factors that might influence the effectiveness of sulphur dusting were studied; they included the effect of temperature, the effect of the presence of free moisture on the plant, and the effect of the lapse of time between spore application and the application of sulphur, which would determine how soon after inoculation sulphur had to be applied in order to prevent the development of rust.

These laboratory and greenhouse experiments provided information essential to intelligent manipulation of sulphur dust in field experiments. It was now established that the effectiveness of the fungicide diminished in proportion to the time elapsing between the application of the spores and the application of the sulphur. If this period was three hours or less the development of rust was inhibited; if it was 12 hours or more, sulphur was ineffective in preventing rust development. Once the fungus had penetrated into the plant tissues it was beyond the influence of the chemical. Sulphur was a protective fungicide, not a curative one.

The main emphasis in this work was, of course, on the field experiments. In these, sulphur was applied both by ground dusting machines and by aeroplanes. It was applied by hand-operated dusters to replicated series of small plots in which the effect of different rates of dusting and different intervals between dustings could be accurately gauged. It was applied, in farmers' fields, by horse-drawn or tractor-drawn dusters because it was only through such large-scale experiments that the economic practicability of sulphur dusting could be determined. It was applied to farmers' fields by aeroplane because this method provided a rapid means of large-scale application without the disadvantage, inherent in ground-based application, of a certain amount of trampling damage to the standing grain.

The results of these experiments may be summarized briefly.

The small-plot experiments, which provided the most accurate data, showed that dusting at frequent intervals could almost entirely prevent rust infection and thereby produce a grain yield comparable to that of a rust-free year. In the severe rust year 1925, yield ranged from 17.7 bushels per acre in the nondusted control plots to 55.1 bushels per acre in plots dusted at intervals of two to three days. In 1927, another year of severe rust infection, the corresponding yields were 12.2 and 39.2 bushels. These experiments showed that, given a sufficiently large number of sulphur applications, it was possible to obtain perfect rust control. However, the number of applications required

for such ideal control, which might involve as many as 24 applications, was prohibitive for farm practice. Eight applications, at 7-day intervals, yielded a 17 bushel increase in yield in 1925 and an 11 bushel increase in 1927. In the latter year, practical farm tests based on eight weekly dustings at 7-day intervals indicated a profit of about 15 dollars per acre. Although such a schedule was practicable it was nevertheless, from the farmer's point of view, a formidable undertaking.

In 1927, 1928, and 1930, applications of sulphur dust were made to farmers' fields by aeroplane through the co-operation of the Civil Air Operations Branch of the Canadian Department of Militia and Defence. The applications were performed with great skill by Flight Lt. T. M. (Jock) Shields who occasionally (and especially when Dr. D. L. Bailey was present) exercised his super-abundant sense of humor by barely missing tree-tops, haystacks and telephone lines. These trials were highly satisfactory in two respects. They developed the technique of aeroplane dusting, and they showed that aeroplane applications, properly performed, resulted in notable yield increases; in 1927 two separate series of three dustings, one week apart, increased the yield by 13 and 20 bushels respectively. At the grain prices prevailing in these years the cost of application by aeroplane was, however, too great for profitable use.

An important by-product of the replicated field-plot experiments was Greaney's demonstration that there was a direct relationship between the amount of rust present on the plant and its grain yield, each 10 per cent increment of rust leading to a loss of about 8 per cent. This demonstration was valuable not only for the estimation of losses caused by rust infection but also because of the applicability of the methods employed to the estimation of losses from other foliage diseases.

The sulphur-dusting experiments from 1925 to 1932, performed chiefly under the direction of F. J. Greaney, developed the technique of sulphur application and showed that in years of severe rust infection this was a practicable and economically rewarding means of rust control. That it was never widely adopted in the rust area was probably due chiefly to two factors: the cost of suitable machinery and the impending release of rust-resistant cereal varieties which would render chemical control of rust unnecessary.

BREEDING FOR RUST RESISTANCE, 1925-1937

WHEAT BREEDING

It should not be overlooked in any record of Canadian wheat breeding that the first attempts to breed rust-resistant varieties and to study the cytological situations in crosses beween different species of wheat were those of W. P. Thompson at the University of Saskatchewan. As reported by Newton (1932) he had begun wheat breeding "in 1915, at first chiefly in relation to earliness but extended to include rust resistance when he observed during the epidemic of 1916 that two varieties in his plots, an emmer and a durum, showed resistance." In his crosses of emmer and durum wheats with common wheats, he was among the first to study the chromosome incompatibilities that led to sterility in the first and subsequent generations of species crosses (Thompson, 1925). He found that fewer common wheat types appeared in crosses with emmers than with durums and that in both types of crosses the rust-resistant progeny resembled the emmer and durum parents more than the common wheat parents. Although these difficulties and the realization, about 1918, that stem-rust races existed that could attack the emmer and durum resistance sources brought his practical breeding work to a close, his experiments, nevertheless, left a legacy of genetical and cytological information that was valuable to his successors.

In the wheat breeding begun by Dr. C. H. Goulden and his associates at the Dominion Rust Research Laboratory in 1925 the variety H 44-24, derived from E. S. McFadden's cross between Marquis and Yaroslav Emmer, was the principal source of rust resistance, whereas Marquis and Reward were selected as the most promising sources of quality and good agronomic characters.

At Saskatoon, Saskatchewan, a breeding program with the same objectives was begun at approximately the same time under the direction of Dr. J. B. Harrington, another Canadian who had studied with Dr. H. K. Hayes at the University of Minnesota. In his program, the chief source of rust resistance was a hybrid line deriving from the cross H 44-24 × Double Cross. As Double Cross was (Marquis × Iumillo) × (Marquis × Kanred), Dr. Harrington's hybrid line contained genes for rust resistance originating from the durum wheat Iumillo as well as from the emmer-derived H 44-24. The quality parent in this breeding program was the variety Marquis.

In the breeding programs at Winnipeg and Saskatoon the resistance sources were of the 'mature-plant' type. Since the inheritance of mature-plant resistance had been little studied, it was essential to gain an understanding of how it was inherited if the breeding work was to progress intelligently.

As has already been stated, varieties with mature-plant resistance, such as H 44-24, appeared to ignore the physiologic races, being resistant to all those known at that time in North America. Would it be possible to transfer this kind of resistance intact to new varieties of high quality and good agronomic traits? Was mature-plant resistance inherited on a simple Mendelian basis, or was its inheritance of a complexity that would make the progress of breeding difficult? Was this type of resistance genetically linked with any undesirable agronomic or quality characters? At Winnipeg, Dr. Goulden and his associates planned and performed experiments designed to answer these questions.

At this time there was little exact knowledge of the inheritance of rust resistance although Aamodt (1923) had shown that in the cross Marquis × Kanred the Kanred immunity to eight races of stem rust was governed by a single gene, a fact that facilitated the breeding for resistance to these races. If mature-plant resistance were thus simply inherited the breeding problem would be considerably simplified.

The answer to this question came almost simultaneously from the studies of the Winnipeg group and those of American investigators. Goulden, Neatby and Welsh (1927, 1928) showed that mature-plant resistance to stem rust, in the cross H 44-24 × Marquis, was a dominant characteristic inherited in simple Mendelian fashion, and inherited quite independently of the seedling reaction to the various races. In the United States, Clark and Ausemus (1928) showed that when Hope was crossed with Marquis or Reliance its mature-plant resistance was a dominant character governed, apparently, by two pairs of Mendelian factors. The important conclusion to be derived from these studies was that mature-plant resistance could be "manipulated in wheat breeding as readily as any other simply inherited character provided that local conditions are suited to the development of heavy epidemics of stem rust" (Neatby, 1942).

The breeding of rust-resistant wheat varieties, now resting on a secure scientific basis, was energetically carried on at Winnipeg from 1926 onwards under the immediate supervision of Dr. K. W. Neatby. On Neatby's acceptance, in 1935, of a post at the University of Alberta, the work was continued by Dr. R. F. Peterson. The chief empasis was on crosses of H 44-24 with Marquis and Reward but Double Cross, made available by Dr. H. K. Hayes of the University of Minnesota, was also used in crosses with Ceres and Marquis; and the durum variety Pentad was used in crosses with Marquis. It was impossible to foretell which of these crosses would be the most successful. The rust-resistant variety

of the future might derive its quality from Marquis, Reward or Ceres and its rust resistance from emmer wheat through H 44-24 or from durum wheat through Double Cross or Pentad.

Dr. C. H. Goulden, in addition to exercising general supervision over the breeding work, turned his attention increasingly to two other problems: the development of statistical methods for the accurate evaluation of the agronomic and quality characteristics of the hybrids; and the development of machinery for seeding, harvesting, threshing and other handling operations relating to the rapid expansion of the breeding project. His statistical studies resulted in great improvements in plot design and in a great increase in the accuracy of the interpretation of agronomic and quality data by the application of the statistical methods of R. A. Fisher to this type of experimental work (Goulden, 1937), and incidentally they led to the publication of his widely used textbook on statistics for agricultural workers. Dr. Goulden's mechanical experimentation, through co-operation with H. J. Kemp of the Swift Current experimental farm, led to an increasing mechanization of field-plot work, which effected a notable saving of time and labor.

The foregoing may give the erroneous impression that the work of developing rust-resistant varieties was confined to the research organizations at Winnipeg and Saskatoon. This was by no means true. Although the selecting of parental material, the crossing, the selecting of rust-resistant lines, and much testing of their argonomic qualities were done at these institutions there were other facets of this work that could not readily be accomplished there. Two of these deserve special mention. First, the testing of the new lines for their adaptability to the different soil and climatic areas of Western Canada; and, second, the determination of the milling and baking qualities of the lines.

Although important wheat varieties such as Red Fife and Marquis have a wide adaptability that ensures high performance under diverse soil and climatic conditions, this is by no means a characteristic of all wheat varieties. To enable new hybrid lines with this characteristic to be selected, the practice was developed of growing the most promising hybrid lines for three years at 23 locations in the Prairie Provinces before a decision was reached as to their suitability for general cultivation. These tests, known as Co-operative Tests of Wheat Varieties, could be performed only through the co-operation of the universities, experimental stations and individuals on whose properties they were located.

The testing of the milling and baking qualities of the new hybrid lines was another facet of the breeding project that was indispensable to its success and that could not be accomplished without outside assistance. From the beginning of wheat growing in Western Canada wheat has been grown primarily for export to foreign markets. The United Kingdom has been traditionally the most important. This market came to associate high milling and baking quality with the characteristics of Red Fife wheat, a quality perpetuated in its descendant Marquis. To satisfy the demands of British millers, it became essential to maintain this type of quality in any new variety that might succeed Marquis on the farms of Western Canada. Delimiting the quality characteristics permissible in the new hybrid lines became the task of the Grain Research Laboratory of the Department of Trade and Commerce, Winnipeg, and the milling and baking laboratory of the Cereal Crops Division, Ottawa. No hybrid line that failed to gain the approval of these organizations had even a remote chance of licensing and distribution.

The development of appropriate milling, baking, and chemical tests for the determination of quality engaged the attention, almost from the beginning of the wheat-breeding project, not only of the two laboratories mentioned above but also of groups of biochemists at the universities of Manitoba, Saskatchewan,

and Alberta. As stated by Newton (1951) this quality research project had its origin in a conference called by Dr. H. M. Troy at the University of Alberta on January 15, 1926. At this conference a program was outlined by means of which the Grain Research Laboratory and the three western universities were to take part, co-operatively, in research designed to develop adequate methods of quality testing for wheat. From this date onwards, significant research on this project was performed at the three universities, at Alberta by Dr. Robert Newton and J. G. Malloch, at Saskatchewan by Dr. R. K. Larmour, and at Manitoba by Dr. W. F. Geddes. Similar studies were carried on at the Cereal Crops Division, Ottawa, under the direction of A. G. O. Whiteside.

With the transfer of Dr. Geddes to the directorship of the Grain Research Laboratory in 1933 that institution became a leading center of all grain research work including that of quality testing, a status which has been maintained by Dr. J. A. Anderson who succeeded him in 1938.

Through this research, adequate methods of quality testing were developed even while the new rust-resistant varieties were in the course of production. These methods involved the determination of the content of protein, ash, and yellow pigment; the evaluation of the physical properties of the dough and of baking quality, not only judged by standardized baking tests but also by subsidiary tests to determine how the flour of each variety reacted to long and short periods of mixing. As these tests were annually applied to all of the 25 varieties grown in the Co-operative Test plots at 23 different stations, the amount of work involved was very considerable.

From the beginning, the dispersion of research among institutions far removed from one another made it obvious that some organization would have to be set up to co-ordinate the work. The Committee on Rust Research, appointed by the National Research Council, as previously stated, in 1924, was a ready-made vehicle for this co-ordination. The first meeting, following the establishment of the Rust Research Laboratory, to consider the current status and future planning of rust research was held at Winnipeg, on April 13, 1926. This is recorded as the Third Meeting of the Associate Committee on Cereal Grain Rust (the 1917 and 1924 meetings being considered as the First and Second meetings). It was held under the chairmanship of Dr. H. M. Tory, President of the National Research Council, and was attended by A. H. R. Buller, W. P. Thompson and W. T. G. Wiener on behalf of the Council, and by D. L. Bailey, C. H. Goulden, H. T. Güssow and L. H. Newman on behalf of the Department of Agriculture. Others present were W. C. McKillican, J. B. Harrington, Margaret Newton, H. F. Roberts, G. B. Sanford, T. J. Harrison, J. H. Craigie, A. T. Elders, W. L. Gordon, W. F. Hanna, T. Johnson, K. W. Neatby, J. N. Welsh and I. L. Conners who acted as Secretary.

This was the first of the meetings held annually until the outbreak of the Second World War. The expanding scope of the work and the natural division of interest according to the fields of research activity made a division into separate committees expedient. Indeed, one such subdivision had already taken place through the formation in 1926 of the Associate Committee on Grain Research which, thereafter, dealt with the quality aspects of rust research. The realization that important diseases such as smuts and root rots could not be ignored in the production of rust-resistant varieties and, moreover, required investigation for other reasons, led to the formation of the Associate Committee of Field Crop Diseases which held its first meeting April 12-13, 1928. Plant breeding activities were taken care of by a subcommittee, but eventually an Associate Committee of Plant Breeding was organized in 1946. With the establishment of these Associate Committees of the National Research Council the organization for handling rust research was substantially achieved although minor modifications were to take place in future years. It became the practice of these committees to meet simultaneously in February of each

year. At these meetings, progress made during the preceeding year was reviewed, and plans were laid for future work. The meetings ended with a plenary session of all committees at which matters of general policy were discussed and decisions reached on recommendations for the licensing of new varieties.

WHEAT BREEDING FOR RESISTANCE TO DISEASES OTHER THAN RUSTS

The work of producing rust-resistant wheat varieties was not without its difficulties and disappointments. It was realized in planning the work that the objective could not be simply the production of varieties resistant to rust. There were other diseases of importance to be considered. Loose smut and bunt were second in importance only to the rusts. Common root rot, caused principally by the fungi *Helminthosporium sativum* P. K. & B. and species of Fusarium, could not be ignored and take-all, a root rot caused by the fungus *Ophiobolus graminis* Sacc., appeared to be an important disease in certain areas. To produce a wheat variety resistant to the rusts but susceptible to one or another of these diseases might have the consequence of increasing the importance of the disease to which the new variety was not resistant. It was therefore necessary to incorporate in new varieties resistance to as many diseases as was possible. To attain this objective it was necessary to examine all parental material to be used in crosses for reaction to various diseases and to subject hybrid populations to screening tests for the elimination of the more susceptible hybrids. Since 1924, evidence had begun to accumulate that the smuts as well as the rusts, were composed of many physiologic races. In that year Faris, in the United States, had shown this to be the case for covered smut of barley and Reed for the oat smuts. In 1927, Rodenhiser and Stakman had shown a similar specialization into races in the bunt of wheat, *Tilletia caries* (DC.) Tul. and *T. foetida* (Wallr.) Liro. In 1930, W. F. Hanna and W. Popp, working at the Dominion Rust Research Laboratory, showed that the oat smuts *Ustilago avenae* (Pers.) Jens. and *Ustilago levis* (Kell. & Sw.) Magn. (= *U. Kolleri* Wille) were heterothallic and could, through this primitive form of sexuality, produce hybrids between the two species (Hanna and Popp, 1930). The same research workers showed, in 1932, that two physiologic races of loose smut of wheat, *Ustilago tritici* (Pers.) Rostr., occurred in Manitoba. It was, therefore, evident that, for plant-breeding purposes, the smuts had to be treated as the rusts; surveys had to be made, physiologic races identified and used in the testing of hybrids for smut resistance. This testing was more laborious for the smuts than for the rusts. For the covered smuts, resistance had to be judged by the reaction of adult plants grown from seed inoculated with smut at the time of germination; for the loose smut of wheat, inoculation was made at the time of flowering, usually in the field, and resistance was judged by smut development in the mature plants grown from the florally infected seed, a process requiring a year or, at best about six months if the plants could be tested in the greenhouse.

The testing for resistance to root rots presented equally formidable difficulties. Studies by F. J. Greaney and J. E. Machacek, at Winnipeg, and P. M. Simmonds and his collaborators, at Saskatoon, showed that the pathogenicity of the root-rotting fungi was markedly influenced by the physical and chemical composition of the soil and by its moisture content. The resistance of a wheat plant in one type of soil was no exact criterion of its resistance in another type. By testing hybrids and new varieties in 'root-rot nurseries' at various points with different types of soil and examining the roots and crowns of the plants for disease symptoms it was found possible to distinguish the more resistant hybrids from those that were more susceptible. Tests of this type were performed annually and reported to the plant breeders at their annual meetings.

Other desiderata in the new varieties were resistance to bacterial black chaff caused by *Xanthomonas translucens* (J. J. & R.) Dowson var. *undulosa* (S. J. & R.) Hagborg and freedom from melanism, the dark discoloration that disfigured the stems and heads of many of the lines descended from crosses with Hope and H 44. Studies on bacterial black chaff were undertaken by W. A. F. Hagborg in 1932 and some of his attention, as well as that of T. Johnson, was given to a study of the causes of melanism. By means of this work methods were devised for determining the resistance of hybrid lines to black chaff and their freedom from melanism.

In this breeding program the objective was to combine in one variety all, or as many as possible, of the following characteristics: resistance to stem rust, leaf rust, bunt, loose smut, root rots, and black chaff; relative freedom from melanism; high yield and other good agronomic qualities; and a milling and baking quality at least equal to that of Marquis. This was a formidable task and it is not surprising that disappointments were occasionally encountered. Fortuntely, the various characteristics were independently inherited. If the essential desirable characters such as high yield and good quality had been associated in inheritance with undesirable characters such as susceptibility to rust or smut, the task would have been impossible. Nevertheless, the statistical probability of a single line in a necessarily limited population containing a combination of *all* the most desirable characters was low and, consequently, it happened repeatedly that the most promising hybrid line of a given year would possess all the necessary requirements except high yield, or good quality, or smut resistance. Some of these disappointments were bitterly felt by the research workers as, for example, the rejection of the agronomically outstanding line R.L. 704, in 1934, because it did not quite equal Marquis in quality. The severe rust epidemic of 1935 re-emphasized the urgency of the need for a rust-resistant variety, an urgency only partly alleviated by the release, in 1936, of the American variety Thatcher which, despite its stem-rust resistance, was highly susceptible to leaf rust. The release in 1937, of the variety Renown, produced by the Dominion Rust Research Laboratory, and the variety Apex, produced at the University of Saskatchewan by Dr. J. B. Harrington, was therefore equally welcomed by the research workers who had labored unremittingly to that end and by the farmers of the rust area who had impatiently awaited relief from the plague of rust. Renown, resistant to stem rust and leaf rust and the smuts was particularly suited to the eastern part of the rust area where leaf rust was usually severe. Apex, resistant to stem rust and moderately resistant to the smuts but lacking resistance to leaf rust, was more suitable for the western part of the rust area where leaf rust was less prevalent.

The distribution to farmers of Thatcher and the two Canadian varieties, in a sense, marks the end of an era. The production of rust-resistant wheat varieties had been accomplished. The public, generally, felt that the work was finished and that there was no more to be done; but the research worker, who had gained some insight into the variability of the disease-producing enemies of wheat, wondered, and hoped for the best.

OAT BREEDING

In 1925, oat stem rust was second in importance to wheat stem rust in Western Canada as a plant-disease problem. Breeding of varieties resistant to oat stem rust was begun at the Dominion Rust Research Laboratory simultaneously with the wheat-breeding program and was, in 1927, officially made the responsibility of J. N. Welsh. As stated earlier, studies on the physiologic specialization of this rust had shown that before 1925 oat stem rust in Canada

was composed (as far as could be determined) entirely of races 1, 2, and 5. Several oat varieties were known to be resistant to these races. Richland, which had been grown to a moderate extent by farmers in the United States, was resistant. Hajira and certain other varieties had a similar type of resistance. White Tartar and several related varieties had a different type of resistance, which was adequate against the known races. None of these varieties, however, had sufficiently good yielding ability or agronomic qualities to induce the farmers of Western Canada to grow them. In the spring of 1925, the problem of producing economically valuable, rust-resistant varieties appeared to be simply a matter of combining, by crosses, the resistance of one of these varieties with the yielding and agronomic qualities of a variety such as Banner. The variety Hajira was chosen as a source of rust resistance and the variety Banner as a source of agronomic quality. Later years were to show that there was an element of luck in the choice of Hajira as a source of rust resistance.

The physiologic-race surveys of 1925 introduced a complicating element. Races 3, 4, and 6 were found in the Prairie Provinces, although only in small quantities (Gordon and Welsh, 1932). The presence of race 6 was of particular concern because at that time no source of resistance to this race was known. Of these races, race 3 was not dangerous because Hajira provided resistance against it. Race 4, which could attack Hajira, was provided for by introducing into the breeding program the variety Jostrain, which was resistant to it. No resistance could, at that time, be provided against race 6.

The discovery of race 8 in Western Canada in 1929 was of some concern because Hajira lacked resistance to this race; but resistance to it was already provided for by the inclusion in the breeding program of White Tartar and other varieties with similar resistance.

One advantage possessed by the wheat breeders was not available to those breeding for resistance to oat stem rust. There was, in oats, no mature-plant resistance comparable to that provided in wheat by Hope and H 44. In oats, the reaction of the adult plants corresponded closely to that of the seedlings of the same variety. The races, as identified by means of seedlings, were consequently of primary importance, and resistance to them had to be incorporated in new varieties by an additive process, new races often requiring new sources of resistance. This process was somewhat simplified by the fact that as more races were discovered it was found that they fell into groups with respect to their interaction with the sources of resistance. The Hajira type of resistance was adequate against races 1, 2, and 5 and against races 3, 7, and 12. The White Tartar resistance provided against race group 1, 2, 5 and race group 8, 10, 11. The resistance of Jostrain was effective against races 3, 4, and 11, and, to a lesser extent, against races 5, 10, 12, and 13. The additive process of building into one variety these various resistance sources was time-consuming and, even if successful, would not provide resistance against one of the races, race 6.

The threat posed by the new races appeared to subside as the physiologic-race surveys from 1930 to 1937 indicated their gradual disappearance. The production of the first rust-resistant oat variety of economic importance, Vanguard, in 1937, therefore provided the farmer with an effectively resistant variety although its resistance was effective only against races 1, 2, 3, 5, 7, and 12. At the time of its distribution, other races were of no significance in Western Canada.

Although Vanguard provided the farmer of the rust area with temporarily effective stem-rust resistance it did not solve all the grower's difficulties arising from oat diseases. Though resistant to stem rust and moderately resistant to the oat smuts it was susceptible to crown rust. Compared with stem rust, this rust was of secondary importance.

EARLY STUDIES ON HOST-PARASITE RELATIONS, 1926-1937

At the third meeting of the Associate Committee on Cereal Grain Rust, in April 1926, W. F. Hanna gave a report on research on host-rust relations already initiated at Dr. Robert Newton's laboratory at the University of Alberta and he outlined an ambitious research program. Four fields of activity were suggested: studies on the physiology of the host; studies on the physical and chemical properties of host-cell contents; studies on rust-inhibiting substances; and studies on the physiology of the rust.

Two points about this program are worth noting. First, the proposed investigations were soundly based on a thorough examination of the literature on host-parasite relations. Second, all the phases of research included in the original outline were explored by Dr. Newton and his collaborators during the period 1926-1936. The series of papers published during these years represent a carefully conducted study of host-rust relations by the use of biochemical methods available at that time.

Among these studies may be mentioned those of W. F. Hanna on the enzymatic activities (catalase, diastase and oxidase) in a group of wheat varieties differing in rust reaction. Varietal rates of respiration, and content of chlorophyll, xanthophyll and carotin were also investigated. Although differences between varieties were established for some of these factors it was not possible to prove that these differences were closely related to rust reaction. Other analyses by Dr. J. A. Anderson involving many plant constituents led to similarly inconclusive results.

In these chemical studies, a particular interest attaches to the investigation of phenolic compounds. Some of the earliest studies revealed that leaves of the highly rust-resistant variety Khapli were unusually rich in phenols. As these substances, even in dilute concentrations, had an inhibitory effect on spore germination, they were deemed worthy of investigation. Studies by J. A. Anderson showed that the phenolic compounds of Khapli wheat leaves were chiefly yellow coloring matters of the flavone class. His studies revealed the chemical structure of two new compounds of this class which he named tricin and tricetin. Although it was not possible to establish the exact contribution of these compounds to the rust resistance of Khapli the studies contributed greatly to the knowledge of the phenolic compounds in wheat.

Although the studies of Newton and his group did not, and could scarcely be expected to, make clear the physiological or chemical basis of rust resistance, they did provide a number of vantage points for further research and they narrowed the field of investigation by eliminating certain factors from consideration.

RESEARCH ON DISEASES OTHER THAN RUSTS, 1925-1937

The development of methods of testing new varieties for resistance to diseases other than rusts has already been discussed. These methods could not be developed or effectively used without a considerable knowledge of the nature of the micro-organisms causing these diseases. It was necessary to know how they invaded their hosts, how and under what conditions they thrived and multiplied, how they survived from year to year and, not least, what were their potentialities of variation in disease-producing capacity. Much of this information was not available although studies on the most important diseases, the smuts and the root rots, had been initiated by the Division of Botany and Plant Pathology several years before 1925. The necessity of incorporating smut resistance and root-rot resistance in the new rust-resistant varieties gave an added impetus to research on these diseases, and the annual meetings of the Associate Committees from 1926 onwards gave the necessary opportunities

for discussion and planning of the work. The Plant Disease Survey conducted annually by the staff of the Division of Botany and Plant Pathology provided information on the economic importance of the various diseases and, therefore, gave guidance as to the relative empasis that should be placed on their investigation.

Two other factors that favored the adequate investigation of plant diseases in the Prairie Provinces were the interest that was being taken in plant-disease research by the three universities, and the provision of funds by the National Research Council in the form of grants-in-aid for postgraduate research. At the University of Manitoba, Prof. A. H. R. Buller had long been a powerful influence in favor of this type of research, and G. R. Bisby had devoted himself to plant pathology at the Manitoba Agricultural College since 1920. A further impetus to research was the appointment of A. W. Henry as plant pathologist at the University of Alberta, in 1927, and T. C. Vanterpool in the same capacity at the University of Saskatchewan, in 1928. From this time onward, the universities played an increasingly important part in plant-disease research in Western Canada.

The realization that diverse cereal disease symptoms observed in the field must trace their causes to improper root development directed the attention of plant pathologists to nutritional conditions and to pathogenic micro-organisms that might be associated with deficient root development. By 1921, root-rot studies were already begun under the direction of W. P. Fraser at the Dominion Laboratory of Plant Pathology at Saskatoon. In that year he reported that root rot of wheat, apparently resulting from infection by the fungus *Helminthosporium sativum,* was common in some districts in Saskatchewan. Following this, increasing attention to root rots of cereals was given by several investigators including P. M. Simmonds, R. C. Russell and T. C. Vanterpool at Saskatoon, A. W. Henry and G. B. Sanford at Edmonton and D. L. Bailey and F. J. Greaney at Winnipeg (Simmonds, 1939). Before 1930 it had become clear that wheat was subject to at least three different kinds of root rot: common root rot, caused principally by species of Helminthosporium and Fusarium; take-all, caused by *Ophiobolus graminis;* and browning root rot, caused by certain species of Pythium and related fungi. The progress of these investigations will be briefly related.

With reference to common root rot, P. M. Simmonds had shown as early as 1922 that species of Fusarium were important causes of root rot of oats and could also affect the roots of wheat and barley; and in the following year D. L. Bailey and F. J. Greaney demonstrated that species of Helminthosporium were common inhabitants of the roots of wheat plants. Studies by several investigators soon made it apparent that the disease expression of these fungi was greatly influenced by various factors in the soil environment. The growth processes of various other soil micro-organisms influenced the growth and pathogenicity of the root-rotting fungi, as exemplified by A. W. Henry's demonstration, in 1931, that other soil micro-organisms inhibited the sporulation of *H. sativum.* It had become apparent by 1933, through the work of Greaney and Machacek and others, that the general condition of health of the plant was an important factor in its reaction to root rot. Plants grown from injured seed were more severely affected than those grown from sound seed. Adverse growing conditions, such as drought, predisposed the plants to infection and, in a measure, explained why common root rot was most severe in years of drought and in areas of low rainfall.

Two important lines of investigation were the refinement of the techniques of isolation of the fungi from diseased roots, to which P. M. Simmonds made important contributions, and the devising of improved methods of inoculation of plants in the greenhouse and in field plots, which was studied extensively

by Greaney and Machacek in the early thirties. Both these types of investigation were essential for two purposes: the testing of the pathogenic capabilities of different strains of the fungi, and the testing of cereal varieties for their reaction to these strains. Research of this type showed that *H. sativum* and species of Fusarium were composed of many different cultural types but lacked the sharply defined pathogenic specialization characteristic of the rusts and smuts. Tests with the host plants showed, similarly, that varieties differed in reaction to root rot though these differences were less sharply defined than in their reactions to rusts and smuts. For these reasons, and because of the difficulties involved in varietal testing for root-rot reaction, the breeding of resistant varieties, though not totally ineffective, was less effective against root rots than against the rusts. Other control methods, however, were explored. Greaney and Bailey, in 1927, and Simmonds and Scott, in 1928, had found that certain fungicidal dusts, used as seed treatments, reduced root-rot injury. Further work confirmed these results. As some of these fungicides were effective in smut control, their protective effect against root rots became an additional reason for strong recommendation for a more general use of seed treatments by farmers.

All studies with the pathogens of common root rot (species of Helminthosporium and Fusarium) had shown a great cultural and morphological variation in these organisms. As the identification and classification of pathogenic fungi was a first essential to their further study, investigations of this type were undertaken in 1932 by J. E. Machacek for species of Helminthosporium and by W. L. Gordon for species of Fusarium. The identification of Fusarium species, particularly, presented difficulties that were gradually overcome by Dr. Gordon, to the extent that he became one of the world's foremost authorities on the classification of these fungi.

It is possible that H. T. Güssow's discovery of a perithecium of Ophiobolus on wheat grown at Scott, Saskatchewan, in 1916, (Simmonds, 1939) represents the first finding of the take-all fungus in North America. Be that as it may, the demonstration, by W. P. Fraser in 1923, that the fungus was present on wheat roots in Saskatchewan was disconcerting, as it was known to cause an important root rot of wheat in Australia, New Zealand and Europe. Surveys, commenced by R. C. Russell in 1924, showed that it was widely prevalent in the parkland area of Saskatchewan. It was discovered in Manitoba in 1925 and was later found by G. B. Sanford to be widespread in the semiwooded zones of black soil in Alberta. The alarm occasioned by the discovery of take-all was considerably diminished by Russell's demonstration in 1927 that the disease could be largely controlled by crop rotations in which two years were allowed to elapse between sowing of wheat. His further studies, in which the host range of the fungus was investigated, showed that wheat varieties and wheat relatives, including many grasses, were generally susceptible, but that oats, corn, and non-grass species were resistant. The susceptibility of grasses was obviously one of the reasons for the frequent occurrence of the disease in wheat sown on 'breaking' of grassland.

As in the studies with the pathogens causing common root rot, it was found that some micro-organisms were antibiotic to Ophiobolus. In 1931, G. B. Sanford and W. C. Broadfoot showed that some fungi, actinomyces, and bacteria suppressed growth of the fungus while others had a stimulatory effect. The suppressive action of these organisms evidently tended to eliminate the fungus during periods of summerfallow.

Browning root rot, a condition most commonly seen in the early growth stages of wheat on summerfallow, was observed in the early twenties in southern Saskatchewan by W. P. Fraser and D. L. Bailey. Simmonds, in 1926, found Pythium-like bodies in the roots of wheat plants suffering from this

disease. T. C. Vanterpool made a thorough study of this disease in which he proved that it is caused by species of Pythium and related fungi. His physiological and chemical studies showed that the patches of soil in which the disease appeared were lower in available phosphorus and higher in nitrate nitrogen than soil on which the disease was not found. His studies showed also that the disease could be controlled to a large extent by the application of phosphates.

By the mid-thirties the studies on root rots had made it clear that the root-rotting fungi were greatly influenced in their activities by their biological and chemical environment. It had become apparent that the area of the root system of a plant, the rhizosphere, was an unstable biological world made up of closely interacting components comprising many living organisms each of which was a chemical factory influenced by such soil factors as water content, hydrogen-ion concentration, concentration of various chemicals, and physical properties of the soil. The need for research in this complex field of study was so apparent that, at the 1936 meeting of the Associate Committee on Field Crop Diseases, H. T. Güssow "moved that the secretary direct the attention of the President of the National Research Council and the Deputy Minister of Agriculture to the urgent representations made by the Committee that there is a definite need for assistance in respect to soil research as related to root-rot of grain." It was thereupon agreed to set up a Subcommittee on Soil Microbiology under the chairmanship of A. G. Lochhead. The other members of this committee were G. R. Bisby, J. H. Ellis, J. S. Mitchell and J. D. Newton. In the years that followed, the research directed by this subcommittee was to become one of the scientifically rewarding activities of the Associate Committee on Field Crop Diseases.

Research work on the smut fungi in Western Canada may be said to have originated with W. P. Fraser's studies, begun in 1918, on the biology and control of the smut of western rye grass, *Ustilago bullata* Berk. Experiments on the control of cereal smuts by seed treatment were undertaken by Fraser at Saskatoon in 1922 and were continued by I. L. Conners at the Field Laboratory of Plant Pathology at Brandon, Manitoba, in 1923 and 1924, and, subsequently, until 1929, at the Dominion Rust Research Laboratory, Winnipeg. The principal objective of the seed-treatment experiments was to discover a satisfactory substitute in dust form for the liquid, formalin treatment. Copper carbonate, in the form of dust, was first tested by Fraser in 1922 and gave sufficiently satisfactory results in this and succeeding years to warrant recommendation for farm use. The corrosive nature of copper carbonate, however, was a defect militating against its widespread acceptance by farmers, and so the search for more satisfactory seed-treatment chemicals continued. The first organic mercury compounds (Semesan and Chlorophol), in liquid form, were tested by Fraser in 1923 and the testing of this type of chemical in dust form was begun by Conners in 1926. With the first testing of Ceresan in Western Canada by Conners in 1929, it became apparent that the organic mercury dusts had reached a quality that might justify their recommendation to farmers. Later studies confirmed this conclusion, and in the thirties this type of fungicide largely replaced the earlier seed-treatment chemicals.

Other types of investigation included the testing of cereal varieties for smut resistance, begun by Conners at Brandon in 1924, and studies on the identities and biology of the cereal smuts in Western Canada. In 1924, he showed that *Tilletia caries,* which had been thought to be confined to the Pacific Coast area, occurred in the Prairie Provinces as commonly as *T. foetida.*

The lines of investigation followed by Conners were continued from 1930 onwards by W. F. Hanna and W. Popp with increased emphasis on varietal testing necessitated by the breeding of smut-resistant cereal varieties and an

expansion of studies on the biology of the smuts. As already mentioned in the preceding section on plant breeding, a study was made of the specialization of loose smut of wheat (*U. tritici*) in which four physiologic races had been found by 1937. The discovery made by Hanna and Popp, in 1930, that the loose smut of oats (*U. avenae*) could hybridize with the covered smut (*U. levis*) was followed by studies on the pathogenicity of the smut hybrids through several generations and by genetical studies on the spore morphology and the symptomatic characteristics of the hybrids.

One other scientific study related to the development of disease-resistant wheat varieties was W. A. F. Hagborg's investigation of the causes of black chaff, the glume discoloration frequently seen on the heads of wheat hybrids derived from crosses involving Hope and H 44. The plant breeders had been led to suspect that the various manifestations of melanism on glumes, necks and internodes were not all due to the same cause. Hagborg's studies, undertaken in 1930, showed that this suspicion was well grounded (Hagborg, 1942). The glume discoloration was shown to be frequently caused by invasion of the bacterium *Xanthomonas translucens* var. *undulosa,* a species first described in the United States in 1919. Intensive study of this organism and closely related bacteria led him to the conclusion that *X. translucens* was subdivisible into several physiologically and pathogenically distinct varieties of which var. *undulosa* was pathogenic to wheat, var. *hordei* to barley, var. *secalis* to rye, var. *hordei-avenae* to barley with a more limited ability to attack oats, and var. *cerealis* to wheat with some ability to attack barley, oats, and rye.

Other studies, by Hagborg and Johnson, showed that melanistic symptoms could also result from the invasion of certain fungi, including rusts. Many lines that had derived rust resistance from Hope or H 44 responded to rust infection by producing brown areas (brown necrosis). Different lines had different capacities of developing the brown pigment in response to fungal invasion, and some lines could even develop it in response to certain environmental conditions. These studies facilitated the development of methods of determining which lines were relatively free from these undesirable characteristics.

THE YEARS OF IMMUNITY: 1938-1949

THE WHEAT RUSTS

It is perhaps permissible to speak of the period from 1938 to 1949 as the years of immunity from rust. This immunity however, was not absolute. It is true that stem rust did not do very much damage to the rust-resistant varieties Thatcher, Renown and Apex, or to the newer varieties Regent and Redman produced in 1939 and 1946, respectively, by the Rust Research Laboratory. But Thatcher and Apex were susceptible to leaf rust and despite a considerable reduction of leaf-rust inoculum through the growing of resistant varieties it cannot be doubted that these two varieties suffered a moderate reduction in yield in years favorable to rust infection. Moreover, leaf-rust infection on the other varieties increased gradually from 1943 onward and reached a point, about 1945, at which damage could no longer be considered negligible. Craigie (1944) has estimated that during the six-year period 1938-1943 the growing of rust-resistant varieties increased the average annual wheat production of the rust area of Western Canada by about 41 million bushels. To this may be added a considerable increase in oat production resulting from the widespread cultivation of the varieties Vanguard and Ajax (the latter released in 1942), which were not affected by stem rust until 1943.

It was natural that the first production of rust-resistant varieties should be followed by a reconsideration of the program of rust research. Since the

objective had been attained, was it necessary to continue the wheat-breeding work? Was there any need to continue the physiologic-race surveys, especially in view of the fact that the new varieties appeared to be resistant to all the races? Reasons of economy lent a special urgency to these considerations after the outbreak of war in 1939 and, inevitably, these questions were discussed with the staff of the Rust Research Laboratory by responsible administrative officials. The research workers were forced to admit that they could not categorically answer these questions. The students of the specialization of the rusts pointed out that each year they found physiologic races previously unknown to them. Although the new races found since the release of the resistant varieties were no more pathogenic to them than the older races, it was, nevertheless, possible that at some future day a more dangerous race would be found. Stem rust had two known means of variation: hybridization and mutation. There were no a priori reasons for supposing that this rust, or leaf rust, could not produce races more pathogenic to the new varieties than the races already known. The plant breeders stated that for a few years, at least, they wished to effect improvements in the quality and yield of the new varieties, and they emphasized that so long as this breeding work continued they needed the assistance of the plant pathologists to ensure that no rust resistance was lost in the process of varietal improvement. These discussions led to the decision to continue the rust research and plant breeding work, although on a scale somewhat smaller than hitherto.

In the years following the distribution of rust-resistant wheat varieties their reaction to leaf rust and stem rust was carefully observed in farmers' fields and in experimental plots such as the 'rust nurseries', which were distributed through all the provinces of Canada. If rust pustules of unusual size were found, analyses were made to determine the race or races present. The rust surveys were carried out, as before, in an effort to discover new rust races and to determine whether the cultivation of the new varieties had effected any shift in the composition of the physiologic-race population.

The first intimation of a pathogenic change in the rusts came in 1943 when it was observed that Renown, Regent, and other derivatives of H 44 or Hope, were severely infected with leaf rust in field plots at Winnipeg. An analysis of the races did not indicate the presence of new races; the severity of infection was attributed to the influence of environmental conditions, a conclusion proved to be wrong by subsequent events.

In 1945, a widespread breakdown was observed in the leaf-rust resistance of Regent wheat and other varietes possessing a simlar type of rust resistance (Johnson and Newton, 1946). Studies of the pathogenicity of the leaf rust collected from these varieties showed that the races, as determined by means of the standard differential hosts, were, for the most part, the same races that had occurred in previous years. Nevertheless, the rust had changed pathogenically. There were now discernible two distinct pathogenic types in several of the common races: a type that, as in former years, was not pathogenic to the new varieties, and a type that was highly pathogenic to them. The new type could not be called a new race because races were identified according to the reaction of 'standard' differential hosts that did not include these new varietes. These rust strains were regarded as 'biotypes' or 'subraces' and they were distinguishable from the original racial type, though often with difficulty, by the reaction of seedling plants of certain varietes, such as Hope and Renown. The observation that the rust was adapting itself to new rust-resistant varieties by the formation of subraces of standard races was important. It had now become clear that the race analyst could not depend on standard differential hosts to tell him what he needed to know about pathogenic variation in the

rust, and that he must modify the differential hosts by the addition of supplementary varieties that would give him the information he needed. It clarified the situation, too, for the plant breeder who now realized that he must seek new sources of resistance to leaf rust.

With respect to stem rust, the performance of the new wheat varieties was satisfactory for the first decade after their distribution. The slight amount of stem rust that occasionally developed on them was economically insignificant and was not associated with the appearance of new races or subraces. Despite this satisfactory situation there was concern among plant breeders and plant pathologists, from 1940 onward, over some facts brought to light by the annual physiologic-race surveys made by the rust specialists at the University of Minnesota. In 1939, and in some years thereafter, certain isolates of race 15 were found to be more pathogenic than ordinary isolates of that race to some of the new American wheat varieties that had derived their resistance from Hope or H 44. This was a matter of concern to Canadian wheat breeders whose varieties contained that type of resistance. Varietal testing, in the United States, indicated that this subrace, now designated race 15B, possessed such a wide range of pathogenicity that it was capable of attacking all the rust-resistant American and Canadian wheat varieties. Although the alarm occasioned by the existence of this subrace was somewhat allayed by its extreme scarcity (it was not found in Canada until 1946), it seemed prudent to the plant breeders and pathologists at Winnipeg to provide for resistance to race 15B in their breeding program on the contingency that it might at some future time take hold in the wheat-growing areas of the Mississippi Valley. A major difficulty in carrying out this program was that the race, not having been found in Canada, was not available at Winnipeg. Unless a culture of it could be obtained for use in greenhouse studies it would not be possible to find sources of resistance to it or to select resistant hybrids. A culture of the race was therefore obtained from the University of Minnesota and a search for satisfactory sources of resistance to it was commenced in 1945. In that year, a high degree of resistance to race 15B was found in the varieties Red Egyptian, Kenya R. L. 1373, and McMurachy. A point of interest in relation to the last two varieties was that Peterson and Masson (1939) had shown that these two varieties possessed the same gene for stem-rust resistance. The fact that McMurachy was one of the varieties resistant to race 15B was important to the plant breeding program because this variety, known from previous testing to be resistant to many stem-rust races, had already been used in crosses designed to improve the stem-rust and leaf-rust resistance of existing varieties.

The origin of McMurachy deserves attention. A single, stem-rust-resistant plant was observed in a badly rusted field of Garnet wheat, in 1930, by Mr. Malcolm S. J. McMurachy of Strathclair, Manitoba. By 1935, he had six acres of this selection growing on his farm. In that year of severe rust infection this selection was free from stem rust although severely infected by leaf rust. In the same year the selection was brought to the attention of Dr. C. H. Goulden who arranged for tests of its rust resistance and its quality and agronomic characteristics. These tests, carried out over several years, showed that this selection, now designated by the name of the originator, possessed high resistance in the seedling and adult stage to the races of stem rust known to occur in North America at that time, a resistance, however, much less effective at high than at low or moderate temperatures. Unfortunately, the agronomic characteristics were unsatisfactory and the milling and baking qualities were poor. The conclusion reached was that McMurachy was, in itself, of no value as a cultivated variety but possessed a stem-rust resistance

that made it useful breeding material.* In consequence, it was crossed, in 1939, with the leaf-rust resistant variety Exchange (obtained from Dr. Ralph M. Caldwell, Purdue University, Lafayette, Indiana) and, fortunately, a hybrid line, R. L. 2265, possessed resistance to race 15B combined with the leaf-rust resistance of Exchange. Through the fortunate use of McMurachy in this cross the program of developing a variety resistant to race 15B was under way before the existence of that race was known to the Canadian research workers.

After the discovery, in 1945, that the McMurachy × Exchange hybrid line R. L. 2265 had high resistance to race 15B as well as to other stem-rust races, this line was crossed, and then back-crossed twice, with the new variety Redman with the purpose of producing a 15B resistant variety with the agronomic and quality characteristics of Redman (Peterson, 1958). This breeding program was to lead to the development of the variety Selkirk, but before that was accomplished a radical change had taken place in the physiologic-race population.

Another variety of the future was to have its origin in these crosses. To make use of the fine agronomic and milling qualities of Thatcher some of the most promising lines derived from the above-mentioned crosses with Redman were crossed with Thatcher, in 1948. Selections from these crosses were, later, to give rise to the variety Pembina.

THE OAT RUSTS

As stated earlier, the oat-breeding program for the development of varieties resistant to stem rust had led to the production, in 1937, of Vanguard, the first Canadian oat variety resistant to that rust. Vanguard was followed by Ajax and Exeter in 1941. These varieties, which rapidly gained popularity among farmers, were resistant to oat stem rust races 1, 2, 3, 5, 7, and 12, of which races 1, 2 and 5 were the only ones commonly present until 1943. In that year, three rather similar races, 8, 10, and 11, appeared in the Prairie Provinces in sufficient quantity to give plant breeders and pathologists concern about the rust reaction of the resistant varieties already distributed, which were susceptible to these races. The prevalence of these new races was one reason for modifying the oat-breeding program; but there was another valid reason. The varieties hitherto distributed were susceptible to crown rust, which often caused severe infection of oats in Manitoba and eastern Saskatchewan. Resistance to the known races of this rust was available in the variety Victoria, introduced to North America in 1927.

The problem of providing resistance to oat stem-rust races 4, 6, 8, 10 and 11 was unexpectedly resolved by the original choice of Hajira as a source of stem-rust resistance, despite the fact that this variety had been shown to be susceptible to all these races. About 1931, Welsh unexpectedly found resistance to race 6 in certain hybrid lines derived from the cross Hajira × Jostrain. (Welsh, 1937). This discovery was important because neither Hajira nor Jostrain nor any other oat variety thus far tested was known to be resistant to this race. Another point of importance was that the lines resistant to race 6 were also resistant to all other known oat stem-rust races. Later studies (Welsh and Johnson, 1951) showed that some samples of Hajira contained about 10 per cent of plants resistant to all the races. Unknowingly, the Hajira × Jostrain cross studied by Welsh had been derived from a Hajira plant containing this resistance.

* In 1954, a monetary award was made to Mr. McMurachy by the Government of Canada in recognition of the contribution of his rust-resistant selection to the breeding of rust-resistant wheat varieties.

The breeding program designed to combine stem-rust resistance to the known races with crown-rust resistance to all known races began in 1939 with the cross Victory × (Victoria × (Hajira × Banner)) in which agronomic qualities were to be supplied by Victory and Banner. From this program arose the variety Garry, distributed to farmers in 1947. It had the desired qualities of rust resistance and yield but presently displayed a defect which had not been anticipated in the course of its production. It was susceptible to a root rot caused by the fungus *Helminthosporium victoriae* Meehan & Murphy. This fungus was unknown as a root-rotting organism until 1944 when it was found to cause a root rot on oat varieties derived from crosses with the crown rust resistant variety Victoria. It was soon discovered that Victoria and most of its derivatives were highly susceptible to this disease (Victoria blight) whereas other oat varieties were unaffected by it. The production of Garry was, however, not wasted effort because further investigations by Welsh and collaborating pathologists showed that Garry contained lines that were resistant to Victoria blight and were resistant to all the stem-rust races and about half the known crown-rust races. The fact that these lines had considerable crown-rust resistance came as a pleasant surprise because American investigators had maintained that there was a complete linkage between resistance to crown rust and susceptibility to Victoria blight. If this had been true, all Garry lines possessing crown-rust resistance would have been susceptible to root rot. The new Victoria-blight-resistant Garry, released in 1953, was higher yielding than the original variety and was so widely adaptable that it soon thereafter became a popular variety in Canada and the United States. Released in the same year was the variety Rodney, which had a similar disease reaction and was well adapted to the rust area where it became the most widely grown oat variety.

PLANT BREEDING

The period 1938-1949, although a period of economy in administration and of distraction owing to the Second World War, saw steady progress in the fields of plant breeding and plant pathology as well as in the more recently undertaken work on soil microbiology.

In plant breeding, there was a gradually increasing emphasis placed on the backcrossing method of breeding because this method was particularly well adapted to the rapid production of new varieties with predictable characteristics. By this method, for which R. F. Peterson was the chief Canadian spokesman, it was possible, by repeated backcrossing to a given variety, to add to that variety certain desirable characteristics without introducing any other appreciable changes. This method was used in the production of the variety Selkirk, which is, essentially, the recurrent parent, Redman, with added rust resistance from the varieties McMurachy and Exchange.

Another development, which had its beginnings in this period, was the introduction into wheat of rust-resistance factors from related species. From the cross Chinese ^{2} × *Agropyron elongatum* (Host) Beauv. a perennial wheat was developed which had high rust resistance derived from the grass parent. This perennial wheat was not, in itself, of agronomic value but it did contain rust-resistance genes that might be valuable if transferable to bread wheat. Although the transfer of this resistance to other varieties by means of crossing was difficult, because of the perennial wheat containing 56 instead of the usual 42 chromosomes, it nevertheless proved possible eventually to translocate, by means of irradiation methods, a fragment of a chromosome bearing genes for rust resistance to the wheat variety Redman. This type of plant breeding was to assume greater significance in later years.

In plant pathology, perhaps the most significant problem of the period 1938-1949 was the question of how the cereal rusts would respond to the widespread growing of resistant varieties. Mention has already been made of the appearance of subrace 15B of wheat stem rust, of new races of oat stem rust, and of subraces of wheat leaf rust. A similar occurrence took place in crown rust of oats in which new races and subraces appeared and increased rapidly. The attention of plant pathologists was naturally attracted to the various mechanisms that might be instrumental in the production of new races. The origin of races through hybridization and mutation had come to be better understood through work done at the Rust Research Laboratory. The relationship between rust and host had been given some clarification by the studies on flax rust by H. H. Flor of Fargo, North Dakota, who postulated a gene-for-gene relationship between rust and host—a gene for pathogenicity in the rust interacting with a gene for resistance in the host. In Canada and the United States, a beginning was made at exploring the possibility that there might be another mechanism of variation besides hybridization and mutation, that is, that heterokaryosis might be a mechanism of interchange of nuclear material between rust races.

CHANGES IN ORGANIZATION AND STAFF

Organizational and staff changes that took place in the Department of Agriculture are worth mentioning. Originally, the plant breeding and the plant pathology work had been administered by separate divisions of the Experimental Farms Branch. In 1937, the Division of Botany and Plant Pathology was placed in the newly organized Science Service, headed by Dr. J. M. Swaine. This change had little effect on the research work carried on at Winnipeg but, simultaneously, a change was made in the name of the Winnipeg laboratory. The name, Dominon Rust Research Laboratory was discontinued and replaced by the two names Dominion Laboratory of Cereal Breeding and Dominion Laboratory of Plant Pathology. The change came into effect in 1938.

About the end of the Second World War considerable changes took place in the personnel of the Department of Agriculture concerned with rust research. In 1946, Dr. J. M. Swaine retired as Director of Science Service and was succeeded by Dr. K. W. Neatby. Dr. Neatby's accession to this post, coming as it did after a long period of forced economy and at a time when it was possible to convince the Government of Canada of the great need of revitalizing agricultural research, was a significant event the consequences of which were soon apparent by the erecting and equipping of fine Science Service laboratories in many parts of the country. In 1946, Dr. H. T. Güssow, who had organized and developed the plant pathological services of the Department of Agriculture, retired to be succeeded as Chief of the Division of Botany and Plant Pathology by Dr. J. H. Craigie. Dr. W. F. Hanna, absent in the armed services for the duration of the war, returned to Winnipeg in 1945 and succeeded Dr. Craigie as Officer in Charge of the Plant Pathology Laboratory. Dr. Margaret Newton, after many years of distinguished research on physiologic specialization in the cereal rusts and related problems, retired for reasons of health in 1945. Dr. F. J. Greaney resigned his positon in 1946 to become Agricultural Director of the North-West Line Elevators Association. In 1948, Dr. C. H. Goulden succeeded Dr. L. H. Newman as Chief of the Cereal Division of the Department of Agriculture, Ottawa. His former position as Officer in Charge of the Cereal Breeding Laboratory, Winnipeg, was assumed by Dr. R. F. Peterson. The transfer of Dr. Craigie and Dr. Goulden to departmental headquarters in Ottawa ensured a continuation of able administrative direction but at the same time deprived rust research of their distinguished research services.

Accessions to the staff of the Plant Pathology Laboratory at Winnipeg included Dr. W. J. Cherewick, who was appointed in 1936 and took charge of the research work on cereal smuts in 1948, and Dr. W. E. Sackston, appointed in 1941. In 1949, Dr. A. B. Campbell joined the Cereal Breeding Laboratory to take charge, in 1950, of breeding disease-resistant varieties of common wheat.

CHALLENGE AND RESPONSE, 1950 TO THE PRESENT TIME

THE INCREASE OF RACE 15B AND COUNTERMEASURES AGAINST IT

About midsummer, 1950, it was observed in the North Central States that large infections of stem rust were appearing on wheat varieties that had hitherto been resistant to stem rust. These varieties included bread wheats with resistance derived from Iumillo or from Hope and H 44, and durum wheats such as Carleton and Stewart of which a large acreage was grown in Minnesota and North Dakota. Race analyses showed that the rust responsible for these infections was race 15B, which up to then had been rarely found.

The summer of 1950 was peculiarly suited to the spread of rust. In the Prairie Provinces and the adjoining United States the season was about four weeks late. The rust therefore had ample opportunity to develop far into the month of September. The result was a stem-rust epidemic, severe on the previously resistant durum varieties but generally only moderate on bread-wheat varieties. The lateness of this rust development presented an element of great danger, because the rust spores produced in the northern states and Canada in September could be, and undoubtely were, blown southward to the Gulf States, where they could cause infection of fall-sown wheat. The probability that race 15B had become established in the Mississippi Valley was therefore great.

It was immediately realized that all varieties of rust-resistant wheat grown, or worth growing, by farmers were susceptible to this race. The concern felt by plant breeders and plant pathologists was so great that a meeting was called at St. Paul, Minnesota, November 17-18, 1950, to discuss this new situation. It was attended by the leading American wheat breeders and rust investigators and by representatives from Mexico and Canada. The latter was represented by Dr. W. F. Hanna, Dr. T. Johnson and Dr. R. F. Peterson.

Among the various decisions reached at this conference (later to be known as the First International Wheat Rust Conference) the most important was that practical rust research should be organized on an international basis. This decision had, indeed, been anticipated by Dr. H. A. Rodenhiser, of the United States Department of Agriculture, who had already arranged for the planting, in the fall of 1950, of a collection of 740 strains of wheat, 80 strains of oats, and six strains of barley at six locations in South America, two in Mexico and one in Texas. These strains, comprising the most rust-resistant varieties then known, were to be observed for resistance to rusts and other diseases and were also to be tested for their resistance to race 15B in the greenhouses at Beltsville, Maryland. In subsequent years, these International Spring Wheat Rust Nurseries were extended to other locations; in 1957, they were grown at 43 locations in 22 countries on six continents. Although this project could only be carried out with the co-operation of the countries and the experimental stations in which the nurseries were grown, nevertheless, the heavy burden of making all arrangements—including the sending of seed, taking or arranging for observations, assembling the data and publishing and distributing reports—fell on the United States Department of Agriculture. Officials of that department, particularly Dr. H. A. Rodenhiser, Dr. B. B. Bayles and Dr. W. Q. Loegering, also

played the major part in the arrangements for the Second and Third International Wheat Rust Conferences held, respectively, at Winnipeg, January 5-7, 1953, and Mexico City, March 18-24, 1956. These three rust conferences and the international rust nurseries did much to place rust research on an international basis. European rust investigators who attended the conferences or read the reports soon saw the applicability of international co-operation to their own rust problems. Consequently a somewhat similar organization was set up in relation to European and North African rust studies. The first meeting of this group of research men, the "Premier Colloque Européen sur la Rouille Noire des Céréales", was held at Versailles, France, in October, 1958.

The advent of race 15B had a stimulative effect not only on practical measures for rust control but also on thinking and experimentation on the origination of new races and subraces. If hybridization were the main source of new pathogenic types of stem rust, it would be expected that the destruction since 1918 of more than 500 million barberry plants in wheat-growing areas of the United States would have greatly reduced the development of new races. Notwithstanding, new races and subraces were found frequently. Did these arise by mutation or was there some hitherto unknown mechanism at work?

The American investigators Rodenhiser and Hurd-Karrer (1947) raised the question of the possible role of heterokaryosis in the origination of new races. As the nuclei in a rust mycelium were associated in pairs it seemed possible that when the mycelia of two races came into contact, as they occasionally did, there might be an interchange of nuclei—a nucleus of one race becoming associated with a nucleus of another race. Such a reassociation of nuclei would probably produce new races or subraces but the variety of races thus obtainable would not be as great as in true hybridization because, by nuclear exchange, two races would be expected to yield only two new combinations.

One of the first studies in this field, by Brown and Johnson who used races of leaf rust of wheat, failed to demonstrate the appearance of new races. Later studies in the United States and Australia, however, have made it clear that heterokaryosis must be reckoned with as one of the mechanisms of origin of new pathogenic types in rust. The great variety of races and subraces produced in some of these experiments appears to prove that heterokaryosis must be supplemented by some sort of 'somatic hybridization'.

In Canada, the first response to the outbreak of race 15B was to give all possible consideration to a rapid development of a 15B-resistant wheat variety. The breeding program, with this objective, was in its later stages. The most promising lines from the cross (McMurachy × Exchange) × Redman[3] were already in the co-operative tests. The first urgent decision was that of determining which, if any, of the lines under study would make an agronomically and commercially satisfactory variety. By the fall of 1952 it was clear that the line known as C. T. 181 had good promise from the standpoints of disease resistance, yield, and milling and baking quality. It had more stem-rust resistance than either McMurachy or Redman, it had considerable leaf-rust resistance, and it had resistance to bunt and loose smut. A decision was made to purify this line and to increase seed supply of it as rapidly as possible.

To ensure a rapid increase of seed, arrangements were made with the United States Department of Agriculture and other agencies to grow a crop of C.T. 186 (a selection of C. T. 181) in California and Arizona. To provide for a maximum yield, irrigated land was selected and to minimize the risk of damage from weather or other agencies the crop was grown at two locations, one in California, the other in Arizona. Enough seed was available to sow 150 acres in the fall of 1952. From this acreage about 5,000 bushels were harvested in the spring of 1953. This seed, sown in Western Canada in the spring of the same year, produced a crop yielding 186,000 bushels. This increase of seed

supply, carried out efficiently under the direction of Mr. A. B. Masson of the Cereal Breeding Laboratory, Winnipeg, had produced enough grain to sow approximately 170,000 acres in the spring of 1954. In the meantime, the variety was licensed, under the name of Selkirk, and accepted for registered status in 1953 (Peterson, 1956).

In the interval between the outbreak of race 15B, in 1950, and the production of Selkirk the Prairie Provinces had been faced with a rust situation of gradually increasing gravity. Infection by race 15B increased, year by year, from 1950 to 1952, but damage was not severe except to durum wheat which was an important crop only in a few localities. In 1953, a year of late sowing and of weather conditions favorable to rust, losses resulting from rust infection were greater than in any year since 1935, and were estimated by Peturson (1958) as amounting to about 40 million bushels in the rust area of Manitoba and eastern Saskatchewan.

In 1954, all circumstances were favorable to the development of rust: the wheat varieties grown were susceptible to race 15B and wholly or moderately susceptible to leaf rust (except for Selkirk, which occupied only about 170,000 acres); in consequence of a wet spring, sowing was late; a severe infection by stem rust and leaf rust occurred in May in the vast wheatlands of Kansas and adjoining states; strong and persistent south winds at the end of May carried great quantities of rust spores from this area and deposited them on the young wheat plants throughout Manitoba and Saskatchewan. As the wet weather that prevailed through June, July and August was highly favorable to further rust development, the ultimate outcome was a rust epidemic of hitherto unequalled proportions. Although it is impossible to determine the relative damage caused by stem rust and leaf rust it is possible to estimate with reasonable accuracy the total reduction in yield. Peturson (1958) placed this at 150 million bushels.

The presence of Selkirk wheat in numerous locations in Manitoba and Saskatchewan facilitated the calculation of the losses. In Manitoba, Selkirk, resistant to stem rust and leaf rust, yielded 35 bushels per acre. Lee, resistant to leaf rust but not to race 15B of stem rust, yielded 21 bushels. Thatcher, resistant to neither rust, yielded 14 bushels. These figures indicate that about one third of the loss was caused by leaf rust and two thirds by race 15B. Yields of Selkirk and Thatcher in Saskatchewan were 31 and 13 bushels respectively. As all these yields were derived from grain grown on summerfallow, they are not representative of average yields, which were much lower. They are quoted merely to show the relative yields of resistant and susceptible varieties under the best growing conditions, and because they provide a yardstick for the measurement of rust losses.

The acreage of Selkirk grown in 1954 was too small to reduce total yield losses appreciably. Its good performance, however, created a demand for seed, which resulted in the sowing of about three million acres of this variety in 1955. As conditions were again favorable for rust infection in the summer of 1955, it cannot be doubted that the growing of Selkirk was an important factor in preventing serious yield losses in the wheat crop. By 1956, Selkirk had become the predominant wheat variety in Manitoba, eastern Saskatchewan, North Dakota, and northern Minnesota.

During these years of severe rust infection the stem rust occurring on the formerly rust-resistant wheat varieties was composed almost entirely of race 15B. Studies carried out at Winnipeg and at St. Paul, Minnesota, on numerous collections of this face showed that it was not, pathogenically, a single unit. By infecting many wheat varieties with different isolates of the race it was found that the isolates differed considerably in pathogenic capacity. In 1952, one isolate was found to be capable of causing large rust infections on both McMurachy and Selkirk. It was realized that if this biotype, designated 15B-3

Can., should increase, the rust resistance of Selkirk would be endangered. Tests with this biotype revealed that the variety Kenya 338 AC. 2 E. 2 was highly resistant to it as well as to other known biotypes of race 15B. Since it also contained good resistance against other North American stem-rust races it became at Winnipeg, under the name of Kenya Farmer, the basis of a new breeding program designed to combine its rust resistance with the agronomic and milling qualities of Thatcher and other varieties.

The response in Canada to the outbreak of race 15B was not confined to the devising of control measures such as the breeding of new, resistant varieties. Many of those concerned with rust research fully realized that during the depression and the years of war that followed it there had been too little emphasis placed on basic research. One reason for this neglect was economic, the difficulty of finding funds for research. Another reason for neglect was a by-product of the highly successful method of controlling rust by plant breeding. Since it was possible to produce disease-resistant varieties by well established methods of plant breeding, was there any good reason for embarking upon the difficult and expensive process of trying to discover why some varieties were resistant and other susceptible? Was there even any adequate reason for attempting to broaden the basis of rust resistance by the slow and uncertain process of building into wheat resistance genes from species such as Aegilops or other grass relatives of wheat? Because of the success of the plant-breeding programs there was often a negative response, not only from administrative officials but even from some of the research workers.

After the outbreak of race 15B there was a general consciousness, among research workers and many others, including individuals and companies engaged in the grain trade, of the need of reconsidering the whole question of the adequacy of rust research. The Associate Committee meeting of February 1951 provided a favorable opportunity of doing so. Discussion was led by Dr. T. Johnson and Dr. R. F. Peterson. Dr. Johnson pointed out three relatively neglected fields of research: (1) The nature of rust resistance, which could now be studied by means of physiological and biochemical methods not known in earlier years. (2) Cytogenetic research on wheat parents and hybrids, to which interesting new approaches had been opened by the work of Dr. E. R. Sears in the United States. (3) New protective or eradicative chemicals as a means of rust control. Dr. Peterson emphasized three research activities that should receive attention: (1) The collecting and testing for rust resistance of wheat and wheat relatives from various parts of the world. (2) Cytological studies of certain species of Aegilops and other wheat relatives known to have genes for rust resistance and the incorporation of these genes in wheat. (3) The provision of prediction tests of the quality of new varieties at an early stage of breeding.

Following a general discussion of the current status and probable future requirements of rust research a Special Committee on Rust Investigation was appointed, under the direction of Dr. W. F. Hanna. This committee reported to the Associate Committee, in February 1952, to the effect that the Canada Department of Agriculture had decided to support research on genetic and cytogenetic problems in connection with the breeding of rust-resistant wheat varieties at the universities of Saskatchewan and Alberta, and to support studies of physiological problems relating to rust resistance at the universities of Manitoba and Saskatchewan. The funds for this research were administered by an Extra-mural Research Committee set up by Science Service under the direction of Dr. H. A. Senn. Through this arrangement it became possible to utilize the best talent available in Western Canada in the fields of genetics, cytogenetics and plant physiology for the purpose of rust research. The initiative, thus taken by the Department of Agriculture, rendered unnecessary

any expenditures by the 'grain trade' in this field. The grain trade, however, supported rust research by means of funds made available by the North-West Line Elevators Association over a period of years to aid cytological studies on stem rust undertaken by Dr. J. H. Craigie after his retirement as Chief of the Division of Botany and Plant Pathology in 1952.

Although these measures did much to place the resources of modern science at the disposal of rust research, the Department of Agriculture went one step further by the appointment, in 1952, of a cytogeneticist, Dr. R. C. McGinnis, and a plant physiologist, Dr. F. R. Forsyth, to the staff of their laboratories in Winnipeg. As far as the Canadian government was concerned, the possible measures to meet the challenge posed by the appearance of race 15B had been taken by the summer of 1952.

NEW GENETICAL AND CYTOGENETICAL RESEARCH

The genetical and cytogenetical work now undertaken fell into three main lines of investigation. The first of these concerned the identification of genes for rust resistance in various wheat varieties and their separation and transfer, by crosses, to other varieties or hybrid lines in which they might be combined with other useful qualities. This type of research, pursued by Dr. D. R. Knott and Dr. R. G. Anderson, led to the identification of half a dozen hitherto undetermined genes (Knott, 1957). By transferring these genes one by one, by means of crosses, to the variety Marquis, it was possible to determine the nature and the range of resistance conferred by each gene. These genes differed greatly in their effectiveness. Gene Sr. 6, for example, provided resistance against a large number of stem-rust races at low and moderate temperatures but was ineffective at high temperatures. Gene Sr. 7, though effective against race 15B, was ineffective against many North American races including the very prevalent race 56. The knowledge concerning the nature of the resistance conferred by each gene was highly advantageous to the wheat breeders who, by placing known genes singly or in various combinations in their hybrids, could now forecast more effectively than before the scope of the rust resistance of their new varieties. The separation of the genes and their incorporation one by one in wheat varieties was, furthermore, very useful to the specialist concerned with the identification of stem-rust races. He could now begin to use varieties containing known genes for the identification of rust races and pass along to the plant breeder the information that such and such a gene was effective against a given group of races and that a combination of certain genes would probably give the breeder the desired range of resistance. This type of investigation was pursued intensively by Dr. G. J. Green, who joined the staff of the Plant Pathology Laboratory, Winnipeg, in 1949. This manipulation of rust-resistance genes naturally resulted in an increasingly intelligent planning of the wheat-breeding work.

The identification and isolation of a gene for rust resistance could be done, and generally was done, without knowing on which chromosome the gene was located. If it were possible to determine on which chromosome a gene was located and if, furthermore, this chromosome could be transferred to another variety, the plant breeder would find his position vastly improved. He could then modify a variety by placing in it a chromosome known to be responsible for a desirable characteristic in another variety; or, given sufficient knowledge of chromosomal effects, he might even synthesize an ideal variety. These ideas, purely visionary in earlier years, became practical possibilities through the nullisomic and monosomic lines of wheat developed by Dr. E. R. Sears of Columbia, Missouri (Sears, 1953). A nullisomic, in common wheat, is a line lacking one pair of chromosomes and, therefore, containing 20 instead of 21 pairs. A monosomic differs by lacking only a single chromosome and thus

possesses 20 pairs plus a single chromosome. Dr. Sears, over a period of years, built up in the variety Chinese 21 nullisomic lines each lacking a different pair of chromosomes, and 21 monosomic lines each lacking a single chromosome. It was found possible, by means of crosses, to replace the missing chromosomes of Chinese by the corresponding chromosomes of another variety. This discovery had far-reaching consequences. By crossing with, let us say, Thatcher, it became possible to develop 21 different lines of Chinese each containing 20 pairs of Chinese chromosomes and one pair of Thatcher chromosomes. As Chinese possesses no stem rust resistance, any resistance displayed by any of these lines would be due to the Thatcher chromosomes. If the line containing Thatcher chromosome X were resistant its resistance could be attributed to that chromosome. These lines, in which chromosomes of one variety are substituted for the missing ones of another variety, are known as 'substitution lines'. By methods that will not be described here, Sears' nullisomic and monosomic lines were used to develop similar lines in other varieties. Dr. J. Unrau and his collaborators at the University of Alberta developed such lines in the varieties Thatcher and Lemhi (Unrau and others, 1956), and A. B. Campbell and R. C. McGinnis in the varieties Redman and Prelude (Campbell and McGinnis, 1958). The creation of nullisomic or monosomic lines and of substitution lines is a protracted process which has not yet had time to bear its full fruit. It has already given the plant breeder a better understanding than he had before of the way in which genes on different chromosomes interact with each other, and it can be expected to yield the plant breeder a control over his breeding programs that he did not have in former years.

The third line of investigation, the transfer to wheat of genes for rust resistance from grasses and other wheat relatives, has been briefly mentioned in the preceding section. This field of study has presented great difficulties owing to the difficulty of obtaining viable hybrids and the chromosomal instability of the few successful hybrids. This work, pursued principally by Dr. R. C. McGinnis, has, however, given some information on the relationship of the various grass relatives to wheat and has, as noted previously, resulted in the transfer to the variety Redman of genes for rust resistance originally present in the grass *Agropyron elongatum*.

RESEARCH ON HOST-PARASITE RELATIONS

In the work on the physiology and biochemistry of host-parasite relationship the objectives could not be defined as specifically as in other work related to rust research. The broad, general objective, which may well have great practical significance, was to discover physiological and chemical processes associated with resistance and susceptibility to rust. Despite earlier work, there was no agreement among rust research investigators as to whether a given plant variety was resistant because the plant lacked the food substances required by the fungus or because it contained, or was capable of producing, antibodies or toxins that inhibited its growth. There was need of studying various phenomena such as assimilation, respiration, and the movement of various metabolites in relation to susceptible and resistant host tissues. The complexity of the problem becomes evident when it is realized that, owing to the physiologic specialization of the rust, a host tissue that is resistant to one rust race may be susceptible to another. In view of this complication it was uncertain whether investigations designed to illuminate the general phenomena of resistance and susceptibility would give the information necessary for an understanding of the physiology of host-parasite relations. The genetical work of Flor on flax rust and its host had, indeed, indicated that the visible rust reaction was the result of an interaction between a gene-conditioned physiologic process of the rust and a gene-conditioned process or condition in the host

(Flor, 1956). As the brilliant work of the American scientists Beadle and Tatum with the fungus Neurospora had shown that genes operated through the medium of specific enzymes, it was clear that the methods of the enzymologist would be important in a study of host-parasite relations. The employment of these methods, however, was much easier in the study of the fungus Neurospora, which could be grown on artificial media, than in the study of rust which would grow only on its natural hosts. It was chiefly this consideration that led Dr. G. A. Ledingham of the Prairie Regional Laboratory of the National Research Council to undertake a study of the enzymes produced by germinating rust spores and to attempt, thus far with only partial success, the cultivation of rust on artificial media.

At the University of Saskatchewan, Dr. Michael Shaw, Dr. D. J. Samborski and their collaborators studied the uptake and movement in rusted and non-rusted wheat leaves of radioactive carbon, phosphorus and calcium. They found a rapid accumulation of these elements at the rust infection centers, an accumulation paralleled by greatly increased aerobic respiration. They considered this accumulation indicative of a rapid movement of metabolites to the infection center. A consideration of how such a movement of metabolites might be initiated led to a study of the levels of indoleacetic acid which suggested that this substance might play a role, immediately after infection, in regulating the mobilization of metabolites required by the rust. The metabolic processes in resistant and susceptible tissues were not substantially different, but in the resistant tissues the respiratory rise was more rapid and was checked by the formation of the necrotic areas that soon develop in resistant infections. Intensive studies by this group of workers on the respiratory pattern in rusted and healthy leaves have indicated that rust infection not only raises the rate of respiration but also alters the respiratory pathway in the host tissues.

A research approach that has been followed by Dr. F. R. Forsyth of the Plant Pathology Laboratory at Winnipeg involves a study of the physiology of resistance and susceptibility in the same wheat variety. This was accomplished by breaking down resistance in various ways as, for instance, by applications of DDT, maleic hydrazide or other chemicals, heat treatment or detachment of leaves. These metabolic disturbances, which increased rust susceptibility, also increased the levels of soluble carbohydrates and amino acids. It was concluded that the increased levels of these materials were responsible for the increased susceptibility to rust.

The discovery by Doctors C. O. Person, D. J. Samborski and F. R. Forsyth, that the application of small amounts of benzimidazole to detached wheat leaves prevented the breakdown of resistance which normally occurs in such leaves and maintained them in good condition for long periods, made physiological studies of a different kind possible. Benzimidazole (which is closely related to some of the structural components of nucleic acid) apparently stabilizes the original rust reaction of the leaf by preventing the breakdown of proteins and other leaf components. The effect of other chemicals on this equilibrium can be readily studied. It is of particular interest that Dr. E. R. Waygood and his collaborators at the University of Manitoba were able to establish that benzimidazole forms in the wheat leaf a benzimidazole-riboside which becomes associated with the nucleic acid of the wheat leaves. The fact that this chemical may effect the vitally important nucleic acids and exercise some influence on rust infection may open up an interesting avenue of physiological research.

Another line of research not wholly unrelated to the study of host-parasite relationships was the search for fungicides better adapted to rust control than those previously known. Neither the Department of Agriculture nor the National Research Council had developed any large-scale research organization designed to produce fungicidal chemicals for rust control. Some of the companies engaged

in the production of agricultural chemicals were, however, interested in this subject because of the profits that might possibly be derived from any chemical that would control rust economically. The Plant Pathology Laboratory at Winnipeg adopted the policy of testing the effectiveness for rust control of any chemical which the research officers of that laboratory considered promising. As none of these research officers was assigned to this type of work the research in this field had to be limited to 'systemic fungicides', that is, fungicides that were absorbed into the host tissues and might, therefore, be expected to provide prolonged protection against rust infection.

In 1956, several organic nickel salts produced by the Rohm and Haas Company, Philadelphia, were given tests for rust control by Dr. F. R. Forsyth and Dr. B. Peturson. These had a specific effect on the rust, consisting in the destruction of rust infections already established and, besides, provided protection against new infection for a period of several days. Further studies, at Winnipeg and Philadelphia, showed that the nickel ion was the effective agent and that simple nickel salts would produce the same eradicative and protective effect. These studies were followed by experiments by Dr. Forsyth and Dr. E. R. Waygood, of the University of Manitoba, on the physiological effect on host and rust of the ions of other heavy metals. The latter established that apart from its specific effect on the rust the nickel ion tends to inhibit the breakdown of chlorophyll in detached leaves and to inhibit the synthesis of chlorophyll from protochlorophyll.

These studies, undertaken chiefly for practical purposes, showed that the study of systemic fungicides should not be entirely neglected as one possible approach to the understanding of host-parasite relations. These studies also indicated, though not yet conclusively, that nickel-containing fungicides may have some practical value for rust control.

STEM RUST OF OATS

Because of the economic value of the wheat crop the major research effort has been on rust research in relation to that crop. But a record of rust research in relation to oats cannot be neglected for two reasons: first, for the considerable economic value of the work and, secondly for the scientifically interesting results that emerged in connection with the breeding of rust-resistant oat varieties.

In 1950, simultaneously with the outbreak of wheat-stem-rust race 15B, there was a sudden increase in the prevalence of race 7 of oat-stem rust. The increase of this race was of considerable concern in the United States where many varieties possessed the White-Tartar type of resistance which was ineffective against it; but it was of little concern in Western Canada where varieties with resistance derived from Hajira were grown.

As stated in a preceding section, the oat varieties Garry, released in 1953, and Rodney, released in 1954, were, in the course of their production, resistant to the known races of oat-stem rust, including race 7. In 1952, however, when Rodney was being increased for distribution, large infections of stem rust were found on some of the plants in one increase field in Manitoba. Race analysis showed that this rust, as identified on the standard differential hosts, was identical with race 7, but it differed from ordinary specimens of that race by its ability to attack Rodney. It was therefore considered a subrace of race 7 and was designated race 7A (Welsh and Johnson, 1954). Unexpectedly, it was found that Garry was resistant to this new race. Up to that time, Rodney and Garry were thought to have identical stem-rust resistance. In this instance, as so often before, an increase in the complexity of the rust had brought to light a corresponding diversity in the host.

The presence of race 7A provided a favorable opportunity for determining the inheritance of rust resistance against this and other races in various crosses involving Hajira and other sources of resistance.

It was known, from earlier work, that Hajira contained a resistance gene effective against the race groups 1, 2, 5 and 3, 7, 12. This gene was also present in a number of other oat varieties including Richland, and was by some referred to as the Richland gene. This gene was now found to be effective against race 7A as well as race 7. It was designated gene A.

The discovery by J. N. Welsh, mentioned earlier, that Hajira contained a small proportion of plants resistant to all the races of oat-stem rust known before the finding of race 7A, revealed a type of resistance (often referred to as the Canadian resistance) which was effective against races 1 to 13 but was now found to be ineffective against race 7A. This resistance was originally considered by Mr. Welsh to be conditioned by two closely linked genes B and C but may possibly be conditioned by a single gene. The broader resistance of Garry, effective also against race 7A is explained by its possessing genes A and B (or BC).

Other resistance genes in oats, revealed by studies in Canada and the United States, are gene D possessed by White Tartar and many varieties with similar resistance, effective against race groups 1, 2, 5 and 8, 10, 11, and gene E possessed by Jostrain and varieties of similar reaction to rust, effective against races 1, 3, 4, and 11 and partially against races 5, 10, 12 and 13.

Until the recent occurrence (in 1957 and 1958) of subraces in races 6, 8 and 13, the above-mentioned genes were the only ones known to condition resistance to oat-stem rust. The occurrence of these subraces has revealed the existence in oats of yet other genes for rust resistance.

The encouraging feature of these studies is that up to the present the discovery of new races and subraces has always enabled the investigator to discover a hitherto unknown source of rust resistance. It would appear that the variation potential of the host plant is of approximately the same order as that of the rust.

RESEARCH ON THE SMUTS

Since it is a basic assumption that the control of the cereal smuts should go hand in hand with the control of the rusts, it is necessary to outline the major developments in the field of smut control. In this connection, three chief developments need to be mentioned: study of the variation of the cereal smuts through the phenomenon of specialization, the development of embryo examination as a method of prediction of the amount of loose smut in barley and wheat, and the improvement of methods of seed treatment for loose-smut control.

The absence of Dr. W. F. Hanna on active service in the Second World War, 1939-1945, brought the investigation of physiologic specialization to a temporary halt. These studies were resumed when the activities of Dr. W. J. Cherewick were transferred to this field in 1948. In this work (Cherewick, 1958), particular attention was given to the loose and covered smuts of oats, *U. avenae* and *U. levis* (= *U. kolleri* Wille), and the three barley smuts: the covered smut, *U. hordei* (Pers.) Lagerh., the false loose smut, *U. nigra* Tapke, and the loose smut, *U. nuda* (Jens.) Rostr.

The most striking feature of these studies was the pathogenic instability of most of the cultures studied. Only a few collections were genetically pure for pathogenicity. Repeated passages of variable cultures through selected hosts only occasionally yielded stable strains. The different smuts differed in variability, covered smut of oats being the least variable while covered smut of barley, loose smut of oats and false loose smut of barley were progressively more variable.

Some of the smuts were found capable of interspecific hybridization. The two oat smuts hybridized (as had been formerly shown by Hanna and Popp) with the production of hybrids of loose-smut appearance. The covered and the false loose smut of barley also hybridized. Artificial hybrids and natural hybrids found in the field tended to be more vigorous pathogenically than the parent smuts. Crosses between races of a given species, on the other hand, tended to be less virulent on some hosts than the parent races.

The studies showed that these cereal smuts are generally in a very heterozygous condition, which is not surprising since they annually pass through a sexual cycle at which time recombinations between clones may occur. The studies showed, too, that purification of a race by selection for one pathogenic character does not purify it for another, and, consequently, the purification of a race for many pathogenic traits is a very time-consuming process. The adaptability of some races to resistant hosts, observed in these studies, is perhaps explainable on the basis of extreme heterozygosity but may possibly be due to the mutability of certain smut lines.

Another type of smut investigation of considerable interest is the development of embryo examination as a means of predicting the amount of loose smut. P. M. Simmonds showed, in 1946, that the presence of loose-smut mycelium in the embryos of barley seeds could be detected by microscopic examination of detached embryos (Simmonds, 1946). If the percentage of infected embryos agreed closely with the percentage of smutted plants produced by the seed, it was clear that embryo examination would provide a substitute for the determination of smuttiness by field examination. In 1950, R. C. Russell showed that the agreement between the embryo tests and the growth tests was very close.

W. Popp, in 1951, demonstrated that seed of wheat with a high proportion of infected embryos "might produce a corresponding number of smutted plants, a lower number, or none at all, depending on the variety of wheat and the particular race of loose smut with which it was infected." Further work by Popp showed (Popp, 1959) that wheat "embryos are characterized by one of three types of reaction to races of the fungus: resistance of the entire embryo, susceptibility of all but the plumular bud, and susceptibility of all tissues including the plumular bud. Only infection of plumular bud tissue is correlated with infection in growing plants, giving a reasonably accurate prediction of percentage of smut infection in adult plants."

Embryo examination for the prediction of loose smut by the methods developed by Simmonds and Russell has been applied successfully to barley and is required for the estimation of the degree of loose-smut infection in 'elite' and 'registered' seed. The success of these methods is due to the fact that the barley varieties now grown are susceptible to loose smut and, therefore, any seed that shows smut in the embryo may give rise to a smutted plant. The situation is more complex in reference to wheat, in which various degrees of varietal resistance occur. For wheat only Popp's method, which demonstrates infection of the plumule, will provide an adequate guide to field infection.

A third type of smut investigation deserving of mention concerned the improvement of seed treatment for the control of loose smut in wheat and barley. The difficulty of application of the standard hot-water treatment has incited many efforts to find a different treatment that would control the smut without damaging the seed.

In 1951, L. E. Tyner reported on experiments designed to control loose smut by chemical and physical treatments. Of the chemicals tested, Spergon, in dilute aqueous solution, proved the most effective. This treatment, however, resulted in a certain amount of seed injury. In subsequent experiments it was found by both Tyner and R. C. Russell that a measure of control could be secured by soaking infected seed in water without the addition of any

chemical substance. The uptake of water by the seed evidently awakened the mycelium from its dormant state and at the same time created an anaerobic condition harmful to the fungus. The discovery that the loose-smut mycelium was less tolerant than the seed to the anaerobic conditions resulting from immersion in water led to a thorough investigation of anaerobic methods of control. Research in Canada and elsewhere established the fact that prolonged immersion of loose-smut-infected seed resulted in almost perfect control of the smut; but prolonged immersion had the disadvantage of waterlogging the seed.

Recent studies have shown that short immersions (about 2 hours), followed by draining and a holding period of 24 hours or more in airtight containers, will control loose smut without raising the water content of the seed excessively. In this type of treatment, the short immersion in water sensitizes the mycelium and establishes an anaerobic condition and the subsequent holding of the moist grain in airtight containers maintains the anaerobic condition long enough to destroy the fungus without undue rise of the moisture content of the grain. Treatments of this type promise to replace the hot-water method of treatment.

OTHER RUST RESEARCH

BREEDING RUST-RESISTANT BARLEY

The foregoing account of Canadian rust research may give the impression that this work was confined to the wheat and oat crops and their diseases. This is by no means true. The story would lack its proper perspective if no mention were made of the development of disease-resistant varieties of barley, linseed flax, and sunflowers.

The breeding for rust resistance in barley was less urgent than for that in wheat despite the susceptibility of the barley varieties grown to both stem rust and leaf rust. Owing to the short growing period of barley this crop usually escaped severe injury from rust infection. However, the yield losses sustained by barley in Manitoba in the rust epidemic of 1935 called attention to the need of developing rust-resistant varieties. Barley breeding had been in progress at the Brandon Experimental Farm since 1924. In 1937, Mr. W. H. Johnston, the barley breeder, turned his attention to the breeding of varieties resistant to stem rust. Only one satisfactory source of stem-rust resistance was known, the American variety Peatland selected in 1916 from seedstock imported from Switzerland. From the cross (Newal × Peatland) × Plush arose Vantage, the first stem-rust-resistant variety produced in Canada. Vantage, distributed to growers in 1947, had several desirable characters including smooth awns and stem-rust resistance but lacked resistance to leaf rust and loose and covered smut, and was susceptible to leaf-blotching diseases. It was followed by another stem-rust-resistant Peatland derivative, the variety Husky, produced in 1953, by Dr. J. B. Harrington of the University of Saskatchewan. In disease reaction and many other characteristics it was similar to Vantage.

The substantial demand by the brewing and malting industry for malting barley, and the premium paid for it, greatly increased the popularity of varieties with good malting quality. Montcalm, produced in Eastern Canada in 1945, gained great popularity in Western Canada because of its malting quality. Its high susceptibility to rusts and most other diseases led to disappointing yields in some years and showed a need for the production of a more disease-resistant malting variety. This need was, to some extent, met by the production of the variety Parkland by the Brandon Experimental Farm in 1956. It has resistance to stem rust but is moderately susceptible to the smuts and is susceptible to the leaf-blotching diseases.

The demand for malting barley, that is for varieties with specific chemical qualities, made the services of the barley chemist a prerequisite for a successful breeding program. The development of satisfactory malting tests for small samples of barley was undertaken as early as 1936 in work performed for the National Research Council by Dr. J. A. Anderson, and this type of research was continued by Dr. W. O. S. Meredith in the Grain Research Laboratory. The Barley Improvement Institute, founded in 1948, under the direction of Prof. T. J. Harrison, developed a quality prediction laboratory in which the malting quality of the numerous hybrid lines produced by the breeder could be tested in an early stage of the breeding program. This laboratory, partially supported by the Department of Agriculture from 1951 onwards, was wholly taken over by the Department in 1957 and was transferred to the Canada Department of Agriculture Research Station, Winnipeg, where it forms an essential part of the mechanism of producing malting varieties.

Studies on the stem-rust reaction of barley varieties and hybrids have shown that specialization of the rust towards barley is much less clearly marked than towards wheat or oats. Barley is attacked by both wheat stem rust and rye stem rust, but most infection is caused by the former. Compared with wheat, barley possesses few known sources of resistance to stem rust—in fact, the gene found in Peatland is the only important source of resistance. Fortunately this gene confers such a broad resistance against wheat stem rust races that for a time it appeared to be effective against all North American races. That this source of resistance was not effective against all wheat-stem rust became clear in 1952 when Peatland and its derivatives showed full susceptibility to certain naturally occurring strains of race 11. Unless other resistance sources can be found, Peatland-virulent rust strains will remain a threat to the resistant barley varieties now in cultivation. Another possible threat to this type of resistance was exposed by Johnson and Buchannon (1954) who found that Peatland derivatives are, at times, attacked by rye stem rust in Eastern Canada.

Another difficulty confronting barley breeders has been the provision of resistance to the barley smuts. All three of these smuts are specialized into a number of races. The barley varieties mentioned are susceptible to these smuts but the discovery of genes for smut resistance in the variety Jet has enabled barley breeders in recent years to incorporate in their new varieties a high resistance to loose smut and a moderate resistance to covered smut and false loose smut. In achieving this objective, studies on the specialization of the smuts have been made by Dr. W. J. Cherewick (Cherewick, 1958) and have been closely coordinated with breeding activities at the Brandon Experimental Farm, and at Winnipeg since barley breeding was undertaken at the Cereal Breeding Laboratory at Winnipeg in 1949. In the breeding programs, particularly those at Winnipeg, an added objective is the incorporation in new varieties of resistance to the leaf-spotting diseases (net blotch, spot blotch, and Septoria leaf blotch) whose economic importance increased in proportion to the increased use by farmers of the trash-cover method of cultivation.

The investigation of barley diseases has not been confined to those of major economic significance in Western Canada. The physiologic specialization of dwarf leaf rust of barley (*P. hordei*), a disease of more importance in Eastern than in Western Canada, was studied by Dr. W. J. Cherewick, and the specialization of wheat and barley mildew, also of importance chiefly in Eastern Canada, was investigated by Newton and Cherewick (1947).

SUNFLOWER BREEDING

Owing to shortage of vegetable oils during the Second World War, sunflowers came to be grown on a rapidly increasing acreage in southern Manitoba from 1943 onwards. By 1949, acreage, concentrated in a relatively small area,

had increased to 60,000 acres. Sunflower rust, which increased correspondingly, became the major disease problem that culminated in a devastating rust epidemic in 1951.

Sunflower rust, first studied intensively by Bailey (1923), produces all its spore forms (pycniospores, aeciospores, urediospores and teliospores) on the sunflower plant. As the teliospores (the winter spores) survive the winter to reinfect young sunflowers the following spring, the increase of the rust was a natural corollary of increased sunflower cultivation.

When the sunflower-rust problem come to the attention of the pathologists at the Plant Pathology Laboratory, Winnipeg, in 1948, it was evident that there was a close parallel between the sunflower-rust problem of that time and the wheat-rust situation as it existed before the breeding of rust-resistant varieties was undertaken. All sunflower varieties were susceptible to the rust. Until a source of resistance could be found the breeding of resistant varieties was not possible. Other means of control, such as sanitation and the use of fungicides, were tried but proved ineffective.

This stalemate was broken in 1949 by the discovery of a single resistant plant in the progeny of a natural cross of the variety Sunrise with Texas Wild Annual (Putt, 1957). This plant was selfed and its resistant derivatives were crossed with both parents of the hybrid sunflower Advance. From these crosses, grown in Manitoba in summer and in Chile, South America, in winter, the most rust-resistant and highest-yielding plants were selected. The selections were bulked and distributed to farmers under the name Beacon in 1954. In this manner arose the first rust-resistant variety of sunflower.

After the discovery of a source of resistance the problem of varietal production became a joint project in which the breeding was done by Dr. E. D. Putt at the Morden Experimental Station and the varietal testing for resistance, as well as other pathological work, was performed by Dr. W. E. Sackston.

Two other sources of resistance have brought to this breeding program a badly needed diversity of resistance. One of these sources was a plant discovered in 1951 in the F_3 progeny of the natural cross California Oil Seed × Texas Wild Annual; another was a plant found in 1952 in a plot grown from seed of open-pollinated plants of the variety Hopi. It seems possible that this resistance may also trace back to Texas Wild Annual; the possibility that this species may contain a reservoir of resistance genes is promising.

BREEDING LINSEED FLAX FOR RESISTANCE TO DISEASE

Although linseed flax and its various diseases have been studied in Canada, the chief beneficial developments arising from research have come from the United States. The first important disease of the flax crop, wilt caused by species of Fusarium, was studied by Dr. H. L. Bolley, at Fargo, North Dakota, in the early years of this century, and from his work came the first wilt-resistant varieties.

The foundation of breeding for rust resistance in linseed was laid by a Canadian, Dr. A. W. Henry, through work done in the United States between 1923 and 1930 (Henry, 1930). Later work in the United States, by Dr. W. M. Myers and Dr. H. H. Flor, led not only to the production of rust-resistant varieties but also to an adequate understanding of the genic composition of the resistant varieties in relation to their reaction to various rust races.

The first flax variety to afford a moderate protection against rust in the Prairie Provinces was Royal, developed by Dr. J. B. Harrington of the University of Saskatchewan by means of selection from the variety Crown.

Royal, produced in 1939, was for a decade or longer the most widely grown flax variety in Manitoba and eastern Saskatchewan. It had moderate resistance to wilt and a considerable mature-plant resistance to rust. This type of resistance was no longer effective after the radical change in the physiologic-race population that took place in 1948 and 1949, and the acreage of Royal had diminished sharply by 1956.

The American variety Dakota was brought to Canada in 1947 on account of its high resistance to rust and wilt. Like other varieties depending for their rust resistance on the Newland gene, it succumbed to the new rust races which began to spread in 1948 and its cultivation was soon discontinued. Other American varieties with a much more broadly based rust resistance were thereafter introduced: Sheyenne in 1947, Redwood in 1951, and Marine in 1952.

Canadian breeding for resistance to flax rust, *Melampsora lini* (Pers.) Lév., began in Ottawa in 1936 under the direction of Dr. W. G. McGregor. As flax rust occurs only occasionally in the Ottawa area it was necessary to arrange for a flax rust nursery at Winnipeg. A survey of the races of flax rust present in Canada was undertaken by Dr. B. Peturson and Dr. Margaret Newton at Winnipeg, in 1940. This annual survey served two useful purposes. It provided knowledge of the distribution of the various rust races; and it provided a source of specific races for varietal testing in the greenhouse in Ottawa and in both greenhouse and field at Winnipeg.

The first fruits of this breeding program at Ottawa were the varieties Rocket, produced in 1947 and Raja in 1954. Both were economically desirable and resistant to the known North American races.

In breeding for resistance to rust, two other diseases had to be taken into consideration: wilt and pasmo. To aid the elimination of wilt-susceptible progeny a 'wilt nursery' was established on a plot of ground, at Ottawa, where wilt was first seen in 1923. The development of resistant varieties was somewhat complicated by the discovery by Broadfoot (1926) that the wilt fungus (*Fusarium lini* Bolley) was made up of pathogenically distinct strains. This pathogenic specialization was undoubtedly reflected in the fiinding by Prof. T. C. Vanterpool, in 1943, that the wilt-susceptible variety Crown was less susceptible to wilt in wilt-infested soil at Ottawa than at Saskatoon whereas the moderately wilt-resistant selection (Royal) that Prof. Harrington had made from it was less resistant at Ottawa than at Saskatoon. The maintenance of wilt nurseries at these two locations has given plant breeders the opportunity of eliminating wilt-susceptible lines from their breeding populations

Pasmo, a disease caused by the fungus *Septoria linicola* (Speg.) Garass., increased in distribution and severity in Manitoba and eastern Saskatchewan, between 1940 and 1946, to the point where it could not be ignored in flax breeding programs. A breeding project was begun by Dr. W. G. McGregor at Ottawa in 1944 and, since the pasmo disease occurred only irregularly in that locality, a 'pasmo nursery' was established at Winnipeg by Dr. W. E. Sackston in the following year. A difficulty confronting this breeding program has been the absence of any significant resistance to pasmo in the numerous flax varieties tested. The fact that certain varieties have been found to be more tolerant of pasmo than others has, however, made possible some progress in developing varieties that are not excessively susceptible to the disease. Current knowledge of the pasmo fungus is largely due to the studies carried out by Dr. Sackston, which have shown that compared with rusts, smuts, and other obligate parasites, the pasmo organism is relatively unspecialized. All collections of the fungus are pathogenically similar, though perhaps not identical, and all have a wide range of pathogenicity.

RETROSPECT

In this account of Canadian rust research an attempt has been made to describe the circumstances that called forth this research effort and to outline the main significance, economic and scientific, of the investigations that were undertaken. Although the ramifications of this research have been so extensive that many worthwhile investigations have been left unmentioned, it is hoped that the main lines of study have been clearly and fairly stated. It is more difficult to do justice to the less tangible but equally important contributions made by many individuals who played important roles in initiating and guiding the research work. To obtain a balanced view of this research effort it seems necessary to attempt an evaluation of the contributions of certain individuals whose names have been mentioned but whose participation has been implied rather than specifically stated.

It seems likely that the first economically significant activities in Western Canada in relation to plant diseases were the efforts of S. A. Bedford and Angus Mackay to reduce bunt infestation of wheat in the last decade of the nineteenth century. The success of their efforts must be gathered by implication from reading their reports. The opinion has been given that these efforts were not in vain. Furthermore, the detailed annual observations of Bedford on the amount of rust infection on numerous cereal varieties at Brandon have given us our earliest records of varietal reaction to rusts and of the intensity of rust infection in different years.

The production of Marquis wheat by Sir Charles Saunders was, though not planned as such, a measure for the mitigation of rust losses. If the later-maturing Red Fife had been widely grown in 1916 the losses from rust would undoubtedly have been greater than they were. To Dr. Saunders must also go a large share of the credit for initiating the quality testing of Canadian wheat, which was later to become an indispensable component of rust research.

In a large measure, the story of rust research has been one of challenge and response. The immediate challenge that brought Canadian rust research into being was the great rust epidemic of 1916. But a challenge is only followed by response if men of vision are present in strategic positions from which they can exert their influence. It is fortunate that such men were then available where and when they were needed.

In the rust area itself, where they could see with their own eyes the havoc caused by the 1916 rust epidemic, were two men who by virtue of their scientific training were in a position to visualize some of the measures that might be taken in the hope of mitigating rust losses: Professor A. H. R. Buller, Professor of Botany at the University of Manitoba and Professor W. P. Thompson, Professor of Biology at the University of Saskatchewan. At the head of the recently established Division of Botany and Plant Pathology of the Department of Agriculture in Ottawa was H. T. Güssow, a well-trained plant pathologist already engaged in building up his division with the scanty materials then available. The response of these men was motivated not only from the economic but also from the scientific standpoint. They saw in the challenge an opportunity not only of doing what could be done on the basis of current scientific knowledge but also of extending the boundaries of knowledge by new studies in the fields of science related to the rusts and their hosts. Professor Thompson, who had already initiated a wheat breeding program at Saskatoon, was perhaps the first Canadian to see the economic possibilities of interspecies wheat breeding in relation to rust control and to realize the scientifically interesting problems inherent in this type of breeding.

Professor Buller, as is clearly shown in his memorandum of June 1, 1917, was fully cognizant of all aspects of the rust problem but was primarily interested in gaining a fuller understanding of the life cycle of the stem-rust organism.

To Dr. Güssow goes the credit for initiating the first Canadian investigation of stem rust by enlisting the services of Professor W. P. Fraser, on a part-time basis, in February, 1917. The choice of Prof. Fraser was a fortunate one. A quiet, reserved man, he was a fine naturalist with a keen interest in research and a balanced scientific judgment. His choice of associates in his work showed that he was a good judge of men, and he had the quality of inspiring in those who worked with him a deep personal attachment and a lasting respect for his scientific judgment. Until 1925, research on rusts and other cereal diseases in Western Canada was carried on almost entirely under his guidance.

In his planning for the development of rust research, Dr. Güssow was fortunate in receiving sympathetic consideration from high departmental officials, including J. H. Grisdale, Director of the Experimental Farms until 1919 and thereafter Deputy Minister of Agriculture, and E. S. Archibald who succeeded him as director in 1920. It was fortunate, too that the idea of rust research had a strong appeal to the Honorable W. R. Motherwell who became Minister of Agriculture in 1922. A farmer in eastern Saskatchewan with personal experience of the damaging effects of rust, he gave his whole-hearted support to the project of rust research and, once the Dominion Rust Research Laboratory was established, his personal interest in it was shown by his visits and inquiries concerning the progress of the work.

As has been stated earlier in this report, powerful support for the project came also from another source—the National Research Council of Canada. From the time that he assumed presidency of the Council, in 1923, Dr. H. M. Tory was a strong guiding influence. He acted as Chairman of the Associate Committee meetings until his retirement in 1935 and, as President of the Research Council, he was in a position to give rust research the full backing of that organization. The participation of the universities in the research work was largely possible because of financial grants from the Research Council. Those who took part in the deliberations of the earlier Associate Committee meetings will readily recall Dr. Tory sitting in the Chair flanked on one side by Dr. W. C. Murray, President of the University of Saskatchewan, and on the other by Dr. J. H. Grisdale, the Deputy Minister of Agriculture. The friendly rivalry for support of rust research resulting from the presence of the highest officials of the Research Council and the Department of Agriculture was highly beneficial to the research project in those early days when funds for research were not always easy to find.

Another beneficial influence in determining the trend of rust research was that of Dr. Robert Newton who, in 1936, succeeded Dr. Tory as Chairman of the Associate Committee meetings and acted in that capacity until 1945. The reorganization, proposed in 1945, of the Associate Committee on Field Crop Diseases, which did not meet during the war years 1941-44, was largely based on ideas advanced by Dr. Newton. In this reorientation of the work of the Committee, emphasis was placed more on research planning than on the evaluation of work already performed or in progress. In the words of the report of that meeting, "it was generally agreed that policies and trends should be the main topics of discussion and that reports should be kept to a minimum except for those given before small sectional groups." At the same meeting (Feb. 1945) it was proposed to convert the Subcommittee on Plant Breeding into a full-fledged Associate Committee of equal standing with those of Field Crop Diseases and Grain Research. The new Committee held its first meeting in February 1946.

Apart from his influence on the general direction of rust-research activities, Dr. Newton made direct contributions to a specific field of rust research. A biochemist by training, he laid the plans for the first physiological and biochemical investigation in Canada of host-rust relationships; and he gave his support to the resumption of this type of study after the outbreak of race 15B in 1950.

In this story of rust research the outbreak of race 15B, in 1950, has been considered as the second great challenge to rust investigators. In this connection it was fortunate that several of those who had played important roles in this type of research were present at that time in Ottawa in high administrative posts of the Department of Agriculture. Since 1946, Dr. K. W. Neatby had been Director of Science Service, while Dr. J. H. Craigie had assumed direction of the Division of Botany and Plant Pathology in 1945 and Dr. C. H. Goulden had taken charge of the Cereal Division in 1948. The intimate knowledge of rust research possessed by these men was an important factor in the quick response of the department to requests for increased financial support for research. The fundamental scientific research that these men had done was in itself an assurance of sympathetic consideration for requests for more basic study in relation to the rust organism and its hosts. Without their support the response to the challenge of race 15B would have been far weaker than it was.

The Associate Committe meeting of February 1951, may be considered a landmark in the sense that it fully reflects the realization, which had been taking shape during preceding years, that rust research was inevitably a continuing problem. The basis of this realization was the fact that the rusts had demonstrated their ability, in Kenya Colony, in Australia and now, finally, in North America, of developing new pathogenic types adapted to survival on cereal varieties highly resistant to the main body of the rust population. In effect, the plant breeder and the plant pathologist were, unintentionally, directing the evolution of the rust by placing in its path immense acreages of resistant varieties that effectively blocked the action of most of the genes of pathogenicity available in the rust. It had now become clear that the periodic display by the rust of unsuspected genes for pathogenicity, brought to light by the selective action of new varieties, necessitated an energetic and continuing search for counteracting resistance genes in the host. Although the discovery of hitherto unknown genes for pathogenicity in a rust has generally resulted in a discovery of corresponding genes for resistance in its host, it is realized that there is no guarantee that adequate sources of resistance can be found indefinitely. But as the adequacy of plant breeding as a rust-control measure depends on the finding of ever-new sources of resistance it is obviously necessary to explore other means of rust control and to attempt to gain an ever-increasing knowledge of the rust-host relationship in the hope that such knowledge may eventually have practical results. These considerations have, in fact, been guiding influences in much Canadian rust research since 1951.

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