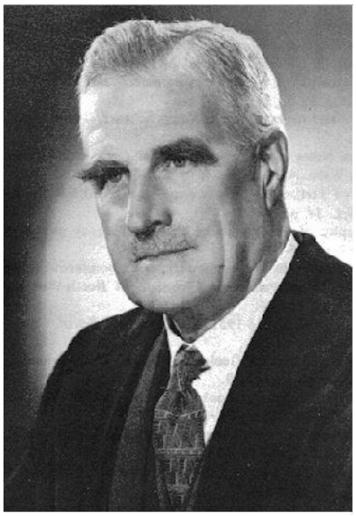
Walter Larry Waterhouse 1887-1969



By I.A. Watson and O.H. Frankel

Walter Lawry Waterhouse was born at Maitland, N.S.W. in 1887. At that time his father, John Waterhouse, was headmaster of West Maitland Boys' High School, a position he held until 1889 when he was appointed District Inspector of Schools and served in various centres throughout the State. Walter was only seven when his mother and a younger sister were drowned in an accident in Wellington Harbour. This tragedy had a profound effect on his formative years. Together with his father's periodic absences, the lack of maternal support imposed early responsibilities on the boy and his elder sister.

In 1896 John Waterhouse became headmaster of Sydney Boys' High School. According to biographical notes contributed by the Waterhouse family, "in the new environment his father's mother, with stern discipline, assisted in the management of the house". Walter attended Chatswood Public School and Sydney Boys' High School. John Waterhouse was a keen ornithologist and geologist and whilst at Maitland was associated with Professor Sir Edgeworth David during his work on the Greta Coal Seam. His father's interest in Natural History aroused similar interests in Walter. Big home gardens in country homes, and the large garden and near-by bush land at the Chatswood home aroused the boy's interest in horticulture and in native plants. After two years in a commercial office he went to Hawkesbury Agricultural College, Richmond, as a result it seems of his early attraction to agriculture and horticulture. Soon after graduating in 1907 he was appointed headmaster of the Mission Boys' High School of the Methodist Church at Davuilevu in Fiji (1908-1910). Required to include agriculture in the curriculum, he decided he needed to study in greater depth and hence joined the newly established course in Agricultural Science at Sydney University under R.D. Watt in 1911, at the age of 24.

Waterhouse had an outstanding undergraduate record. In 1913 he was awarded the first Farrer Research Scholarship for a study 'The effects of superphosphate on the wheat yield in New South Wales', which was published as a Science Bulletin. In 1914 he passed with first class honours and received the University Medal. The First World War had already broken out; and when in the next year he was awarded the 1851 Science Exhibition he declined it, and instead enlisted for overseas service with the first A.I.F. He was awarded the Military Cross for conspicuous gallantry at Pozieres in July 1916, and, severely wounded in November of the same year,was invalided back to Australia early in 1917.

In 1918 he was awarded a Walter and Eliza Hall Research Fellowship. He went to Imperial College in London and obtained its Diploma. On the return voyage to Australia via the United States he spent some time in the Department of Plant Pathology at the University of Minnesota, St. Paul. There he came under the influence of Dr E.C. Stakman, a man of dynamic personality about his own age. Stakman was in the process of building up a Department of Plant Pathology at which several Australian graduates later had the opportunity to study. He and his colleague, M.N. Levine, were both active in cereal rust research and Waterhouse repeatedly emphasised his indebtedness to both of them.

Teaching

Returning to Australia in 1921 he was appointed Lecturer and Demonstrator in three disciplines-Plant Pathology, Genetics and Plant Breeding and Agricultural Botany in the University of Sydney. This entailed a heavy teaching load in the Department of Agriculture and Veterinary Science. The preparation of new material for his three courses must have been a formidable task as he appeared before the students for one lecture each day throughout the year and for six hours of practical classes each week, for which he had to prepare most of the laboratory material himself.

Although his main interests were in plant diseases he taught on a wide range of subjects and his personality was infused into all his lectures and demonstrations. The lectures were delivered in the laboratory amidst specimens of botanical interest about which he spoke, but the academic robes, the scholarly and stimulating addresses all helped to create an atmosphere that will long be remembered by all students who were part of the audience. Practical classes were conducted with split second timing. The demands made on the students in his three subjects often interfered with their attention to other work and the impasse was a constant source of trouble both for the students and for the Dean.

Waterhouse had the capacity to dramatise his lectures so that situations were depicted in a most realistic way. Students became disturbed to learn of immense personal losses that were being suffered by some farmers following plant disease epidemics. After these lectures one was left with a sense of urgency. There seemed to be no alternative but to become involved in research dealing with these problems.

All classes were conducted under a set pattern as Waterhouse was a very strict disciplinarian. Students were given some rein but there was never any familiarity. Most students had few opportunities to get to know the real Waterhouse, and it was unfortunate that even senior undergraduates came to know almost nothing of the nature of the research in which he was engaged. Nevertheless he had a fine sense of humour which was very refreshing on the appropriate occasions. Biometry classes included a short penny tossing exercise to show frequency distributions and he would always ask some responsible student to watch Science Road in case the Vice-Chancellor should arrive and question the activities in progress. In other classes students reporting lack of progress in their Drosophila mating experiments would be queried in a most dignified voice, 'Well, do you expect anything to happen when two females are together?'.

He always maintained a keen interest in the subsequent careers of his former students and had an open door for any who returned to the Faculty.

In 1929, Waterhouse received the first award of the degree of Doctor of Science in Agriculture. In 1937 he was made Reader, and in 1946 Research Professor in Agriculture, a status held until his retirement in December, 1952, when the title of Emeritus Professor was conferred on him.

Waterhouse served on many committees concerned with the advancement of science. He was a member of the committee of the National Research Council and of the State Committee of CSIRO, and president of the Linnean Society of New South Wales, the Royal Society of New South Wales, and Section K of ANZAAS.

Honours

Dr Waterhouse was awarded the Farrer Memorial Medal (1938 and again 1949), the Clarke Memorial Medal (1943), the Medal of the Royal Society of New South Wales (1948), the Medal of the Australian Institute of Agricultural Science (1949), and the James Cook Medal (1952). He was the first recipient of the Elvin Charles Stakman Award in 1956. For his contributions to agricultural science he was made a C.M.G. in 1955, and elected a Fellow of the Australian Academy of Science in 1954 and of the Australian Institute of Agricultural Science in 1960.

Family life and retirement

In 1924 Waterhouse married Dorothy Blair Hazlewood. Her grandfather, Rev. David Hazlewood of Fiji, reduced the Fijian language to a written form in the *Dictionary and Grammar of the Fijian Language,* published in 1872. Waterhouse's home life was an extremely happy one. His wife and three daughters showed sympathy and support for his scientific studies. Ruth, now a lecturer at Macquarie University, was of considerable assistance in the preparation of his later manuscripts and to her, in part due to her early disabilities, he was particularly attached. Apart from his research and duties associated with scientific societies, his family was practically his whole life.

His main hobbies were gardening and photography. He showed considerable skill in illustrating his research work, particularly with the equipment available in the early years of his investigations.

In many respects Waterhouse was somewhat austere. He frequently chose not to accept methods associated with technological advancement. For example, his Sunday afternoons were devoted to writing longhand to various scientific colleagues and farmers with whom he co-operated.

Upon his retirement Waterhouse devoted a good deal of time to bean and pea breeding, and to writing up of research work which had been considerably impeded by ill-health following a serious heart attack in 1942. In his last years he became dependent on his family for the communication of the written word. He died on the 9th December, 1969.

Rust research

When the early basic studies on members of the genus *Puccinia* began in 1921 there was great speculation throughout the world as to the cause of pathogenic variability. It was known that new and dangerous strains of most plant pathogens arose from time to time but their origin was often obscure. Marshall Ward in England had received some support for his proposals that pathogenicity may be increased as a result of organisms growing on a 'bridging' host. Such a 'bridge' would allow a pathogen to acquire the ability to attack a host plant which was previously resistant to it. The United States workers, led chiefly by Stakman, had refuted these proposals and claimed that new strains arose largely by mutation and/or hybridization.

The information available on Puccinia graminis was at this stage not at all clear. It was suspected that the alternate host of this fungus played some role because it had been known for a long time that there was a connection between the barberry plant and the cereal stem rusts, barberry eradication programmes in both Europe and North America being successful in reducing rust damage in cereal crops. However, apart from providing early spring inoculum, the real significance of barberry was not appreciated in the early 1920s.

In Australia it was known that species of barberry were introduced as early as 1859; but prior to 1921 it was widely accepted that the local wheat stem rust organism had lost the ability to infect them. This belief was quickly dispelled by Waterhouse who was able to show that the basis for the confusion lay in the variability within the organism itself. *P. graminis* f. sp. *tritici*, the rust attacking wheat, was found to comprise six strains which were characteristically Australian. They had not been found elsewhere. These strains could be separated as dikaryons by their ability or inability to attack a group of 12 different wheats, but Waterhouse showed that as monokaryons there were also differences. One strain which he called race 43 was avirulent on barberry plants; others such as 45 and 46 grew normally on it. This was the first evidence of differentiation at the monokaryotic level and some 25 years later a similar happening was reported from Canada.

During these early days when strains of the stem rust pathogen were recognised, these questions were repeatedly asked-where do they originate and how do they breed? In the early experiments wheat stems showing the black stage of a rust strain whose identity had been established, were used to infect barberry plants. The aeciospores recovered from the latter were used to reinfect wheat but although these spores represented the sexual progeny there was nothing exciting about them. For the first four years of these experiments the parental strain only was recovered after passage through the alternate host. Race 46 only gave race 46 in its progeny and although this was not apparent at the time, hindsight tells us that it was apparently homozygous for the genes for virulence and avirulence on the wheat seedlings which were used. In the fifth year - 1925 - he repeated the work using his race 45 and from the barberry he recovered progeny dissimilar from the parent. This, from information we now have, was a very significant finding but for some reason Waterhouse withheld the information. Apparently the differences between parent and progeny were not sufficiently large to impress him.

In the spring of 1928 the real advance was to be made, because he took yet another rust - race 34 - which when used to infect barberry gave rise in its progeny to two new races, 11 and 56 outstandingly different from the parent which of course was also recovered. Race 34 was apparently heterozygous for the genes for virulence on the wheats Einkorn and Mindum and hence segregation had occurred. In 1929 in a short paper to the Linnean Society of N.S.W., Waterhouse made this dramatic announcement about the role of the barberry plants in the life cycle of *P. graminis*.

The excitement in three leading rust laboratories at the time, St. Paul, Winnipeg and Sydney must have been intense. The work of Craigie (1927) in Winnipeg had shown clearly that the structures developed within the haploid infections on the barberry were functional and this stimulated further work in North America. Workers in that area were doing experiments similar to those being done in Sydney and they also obtained new strains from barberry inoculations. Like Waterhouse they found some races were homozygous for their genes for virulence while others were heterozygous. In their work however, they were dealing with a multiplicity of races because infected barberries could be found within a short distance of the laboratory. Under these circumstances and with the method of culturing available it was not always easy to distinguish between artificially produced races and those occurring naturally. Waterhouse on the other hand was working in isolation away from natural infection of barberries, so it was much easier for him to obtain irrefutable evidence that the new races had arisen from self fertilisation on barberry of a heterozygous race.

This discovery, which was later confirmed at a no. of different laboratories, underlined the significance of the barberry eradication programme in the United States and Canada. In Australia no action was taken to remove the barberries in Tasmania which have been allowed to grow even to the present day undisturbed over widely separated areas in that State. Having established the important role for barberries in relation to *P. graminis* it was only a short step for Waterhouse to show, again for the first time, that species of Thalictrum served the same purpose in the life cycle of *P. recondita*, the organism causing leaf rust of wheat, as Berberis did for *P. graminis*.

In the early days of rust research there were insufficient data to assess whether or not Australia's geographical isolation offered any protection against cereal rust inoculum entering the country from overseas. While the initial studies showed the six original races to be unique, race 34 which was used in the barberry experiments was isolated from Western Australia in November 1925. Such a race is widespread throughout the world and although Waterhouse speculated as to its origin, this has not yet been determined. Genetic evidence eliminates the possibility that race 34 arose from the pre-existing races since they carried several recessive genes for virulence whereas in 34 the corresponding genes were dominant. His suggestions about an overseas origin cannot be dismissed as it seems very likely that rust spores may enter Australia from time to time and if they fall on a congenial host they begin to colonise it. A new race, 21, was found by him on *Agropyron monticola* on Mt. Kosciusko in 1948 and this could have been brought in as spores carried by wind; other unusual races found in 1954 and 1969 provide further evidence. Spore movement from Australia across the Tasman Sea is well established but more documentation is necessary before we can be certain that new material is entering Australia from the west across the Indian Ocean.

The elegant studies that had been made by Waterhouse on sexual hybridisation on barberries explained racial diversity in North America but it did not explain variation in Australia where except for Tasmania, barberries were rare. On the mainland new races were arising to coincide with the cultivation of new resistant wheats. While he conceded that foreign spores may enter occasionally from outside, he was not convinced that introduction or sexual hybridization could account for the variation in virulence occurring in the cereal rusts of Australia. He had earlier observed in the glasshouse mutation both for spore colour and virulence in *P. graminis tritici*but in 1942 he had his first clear demonstration of the importance of mutation in this organism in the field.

About 1940 there was great satisfaction with the contribution that wheat breeders had made towards a solution of rust control. Thatcher, a hard spring wheat, was thriving in North America and Macindoe had released Eureka in New South Wales in 1938. It was commonly accepted that stem rust was no longer to be feared. Waterhouse had released his wheats Fedweb and Hofed, yet while their resistance was still effective, he was always on guard for the fungus to attack any wheat that was currently resistant. The blow fell in 1942 when a rusty crop of Eureka was found near Narrabri, N.S.W. This material was collected by Mr J.A. O'Reilly who was the Agricultural Instructor stationed at Gunnedah. O'Reilly gave Waterhouse extremely valuable help during the whole of the time he was active in wheat breeding in northern N.S.W. He collected widely, he was enthusiastic about the new resistant wheats Eureka, Fedweb and Hofed and the wheat growers accepted with confidence the advice that was given. This close association over a long period with the University programme was in no small measure responsible for the success it achieved because as Waterhouse once wrote, 'There is no other N.S.W. Department of Agriculture officer who has had such a wide experience of rust and who has such a respect for it!'

The unexpected rust on Eureka required some explanation and there was widespread speculation among those who had had long experience with wheat; some blamed the time of sowing, others the unusual temperatures, while still others claimed the direction of sowing could have accounted for the result. Perhaps they can be excused for being wrong because this was a new experience for them. Resistant varieties had not previously 'broken down'. The real explanation came some months later when Waterhouse and Watson showed that the fungus had changed, a new strain had arisen which, except for its ability to attack Eureka, was identical with that against which Macindoe had obtained resistance. It was a stepwide mutation in the fungus for virulence on plants with Sr6, the gene for resistance in Eureka.

The unexpected change in the resistance of Eureka was the forerunner of a series of events that Waterhouse was to observe over the next 10 years with monotonous regularity. It was an event which was to demonstrate forceably the futility of basing resistance on single genes and there was no difficulty in convincing him of the value of the broadly based genetic resistance which has, since 1947-48 given excellent protection to the Australian wheat crop in the rust liable areas. Macindoe naturally was disappointed at the turn of events as he had based his hope on what he thought was the field resistance of Eureka. He claimed that the use of seedling reactions and undue attention to physiologic forms of rust could retard breeding work by at least a decade. Since Waterhouse assessed his material both as seedlings and in the field it is not surprising that considerable rivalry developed between these two breeders as a result of the different techniques used. Each was ready to search for deficiencies in the varieties developed by the other but undoubtedly both men made outstanding contributions to our knowledge of rust resistant wheats.

Most of the changes that have been observed in the virulence of *P. graminis* involved single gene mutations in which a particular host gene for resistance became ineffective. From time to time, however, Waterhouse believed that some sort of vegetative hybridisation may take place between strains. He visualised the possibility of nuclear exchange between the + and - nuclei when two different strains were present in a given host. Such an exchange could bring together recessive genes and so make possible the expression of virulence which otherwise was masked by dominant genes for avirulence.

We now know that certain strains of rust when mixed on a compatible host will hybridise as dikaryons and the process has been reported in several species. While the exact mechanism involved is not yet understood, artificial culturing of *P. graminis* on agar may provide the answer. Waterhouse predicted that some day these obligate parasites would be cultured on agar and it is appropriate that the building at the University of Sydney in which this was first done in 1966 in only a short distance from the one in which he worked. From William's work with *P. graminis* it appears that monokaryotic diploids arise from dikaryons from time to time when the latter are grown on artificial media and presumably they also arise in the host.

Waterhouse was always interested in the total pathogenic ability of the rust strains. He concerned himself mainly with those occurring on the small grain cereals wheat, oats, barley and rye. It was realised early in the work that there were wide taxonomic differences between these crops, nevertheless the plant pathogens were able to seek out certain biochemical affinities between them *P. graminis* f. sp. *tritici* could attack wheat and barley but not oats or rye. *P. graminis* f. sp. *secalis* could attack barley and rye but not oats or wheat. *Dactylis glomerata* was susceptible to *P. graminis* f. sp. *avenae* and *P. graminis* f. sp. *lolii*. Waterhouse studied these relationships and his work on the rusts attacking wild grasses in Australia is being appreciated more now than when he was actively engaged doing it. One or two examples of the ramifications of his studies will suffice, and these should be viewed in the light of present day efforts to conserve the wild species.

Agropyron scabrum is a native Australian species and was shown in these early studies to be a host for both *P. graminis tritici* of wheat and *P. graminis avenae* of oats. It was probably an essential species for the stem rust organism before the cultivation of wheat. Unlike *A. elongatum* and *A. intermedium* it has never been used as a source of resistance to stem rust but there is a tremendous range of variability from plant to plant in the field; some are resistant. The finding by Waterhouse that the species is susceptible to more than one *forma specialis* is very important as such a host species provides the opportunity for somatic hybridisation between two groups of rusts when members of each group are capable of attacking it.While it .is now extremely rare to find *P. graminis avenae* on *A. scabrum*, *P. graminis tritici* and *P. graminis secalis* are commonly found associated on this species in Queensland together with a range of strains that are somatic hybrids between them. These hybrid strains possess many genes for avirulence; some have come from *P. graminis tritici* others from *P. graminis secalis* and hence they may be unable to attack either wheat or rye but for the most part they are virulent on *A. scabrum*, the host from which they came. While Waterhouse assumed this species to be important in the perpetuation of wheat rust from season to season, we can now commonly find situations where the grass is heavily rusted along fence lines but wheat on either side is unaffected. In Europe these hybrid strains would probably be called *P. graminis* f. sp. *agropyri*.

The wild species of Avena were also studied by Waterhouse in relation to their reaction to rust diseases, the species *A. ludoviciana*coming up for detailed consideration. The resistance and susceptibility between ecotypes that he observed in this material is characteristic of the wild species and in *A. sterilis*, a close relative it is now known that valuable resistance to oat stem rust can be found. The relationships between the genes for resistance in the wild species and those in the cultivated oats has not yet been determined in detail but they are known to carry different genes.

In studying these rusts of wild and cultivated grasses Waterhouse recognised four formae speciales of *P. graminis* - *tritici*, *avenae*, *secalis* and *lolii*. These are still valid but he realised that they are inadequate to describe the variation since not only is there a rust attacking mainly *Agropyron* spp. but also others specific for a genus such as *Dactylis*, *Phalaris* or *Deyeuxia* *P. graminis* is now thought of as a species comprising a huge pool of genes from which combinations of genes may flow to give the various *formae speciales*. The rate of flow will be accelerated when a common wild grass host allows somatic recombination to occur.

Although the cereal rust studies included a very broad field, Waterhouse concentrated on the stem and leaf rusts of wheat and many of the principles that he established emanated from host-pathogen studies of the strains within these two species. In these studies he sought to examine the impact that resistant cultivars had on the variability of the organism and hence the structure of the whole rust population. In the initial attempt to breed rust resistant wheats the six races originally present were arranged in two groups of three. By crossing parents which were resistant to races of group one with those resistant to races of group two, Waterhouse was able to combine the genes and so to develop a wheat resistant to all races. This approach did not reach fruition, as the arrival of race 34 in 1925 nullified several years of work since it attacked all parents, regardless of the group to which they belonged. Race 34 clearly had new genes for virulence and this alone could have explained the manner in which it so dramatically dominated the Australian rust scene for the next 15 years. Waterhouse found, however, that this new rust also brought in genes for greater aggressiveness because in competition with the original six races, under conditions equally congenial to all, race 34 quickly overran the others. This was important because it meant that during the 1930s one was breeding for resistance against only one strain.

The ecological relationships between host and pathogen which first showed up with the release of Eureka (gene Sr6) wheat in 1938 was studied by Waterhouse in detail for the next 15 years. As Eureka became increasingly popular, the mutant strain of 1942 specific for it increased in prevalence until finally the variety was so susceptible that farmers rejected it in favour of Gabo, a wheat with a different gene for resistance (Srl1). The almost complete withdrawal of Eureka from cultivation finally resulted in the disappearance of the recessive gene in the pathogen that enabled it to attack plants with Sr6 in 1942. Gabo quickly replaced Eureka as the most popplar variety in the north but it also fell to two new stem rust strains in 1947-48.

These classical studies soon attracted the interest of fungal ecologists abroad. The question was asked whether those pathogens which accumulate genes for virulence maintain fitness equal to that in the original strains. Are genes for virulence in the fungus which are not necessary for survival lost from the population? These questions posed nearly 30 years ago still remain largely unanswered. Van der Plank in South Africa has argued, largely from the Australian work, that a loss of fitness is associated with an accumulation of genes for virulence. If so, plant breeders could take solace from the thought that as more and more genes for resistance are built into the host varieties, poor survival ability of the fungal strains attacking them, will give added protection. There is some evidence to support Van der Plank but on the other hand, substantial evidence also can be found to show that fitness is not related to an accumulation of genes for virulence. The concept of 'strong' and 'weak' genes still needs further study before it can be accepted unreservedly.

Wheat breeding

The international recognition that Waterhouse enjoyed for many years, came as a result of his more theoretical studies conducted in the laboratory, in his rather primitive glasshouses and on a small patch of land adjoining the Veterinary School at Sydney University. At Hawkesbury Agricultural College, Richmond, however, association with an old friend the late E.A. Southee, Principal of the College, enabled him to test allegedly rust resistant wheats in a more typical environment. The agronomic worth of these wheats developed from his own hybridisation programmes became apparent to him and he was encouraged to seek facilities further afield to broaden the scope of his studies. The grim determination with which he undertook this field programme in the face of almost insuperable difficulties is a lesson to many of us in modern times. His university facilities were appallingly primitive, he had virtually no assistance, his field areas apart from those at Richmond were non existent and yet he undertook to develop rust resistant wheats for northern N.S.W. and Queensland. The seemingly hopeless situation was not helped by the fact that he had practically no time to conduct field studies in the country since he had a heavy teaching commitment. About October each year during the 1930's, he made a tour of three days and this allowed him to see field problems for himself. He travelled by train to Bathurst, thence to Cowra and finally to Dubbo where contacts at each point showed him the latest in rust resistant cereals.

The first impact of Waterhouse's applied researches were to be made in the north-western part of NSW where Mr C.H. Beeson, an old mate from Hawkesbury College, was farming at 'Leyburn', Gunnedah. Mr Beeson offered to provide land and labour for sowing and harvest. The varieties Hofed and Fedweb, were never widely grown as they had been developed without adequate yield testing, but they demonstrated in 1935-36 what could be expected from resistant varieties and paved the way for the ready acceptance of Eureka, a variety which was more widely adapted. By 1938 other material showing great advances was ready for trial. This had come from crosses in which Waterhouse had attempted to transfer the rust resistance of the tetraploid wheats Khapli Emmer (*T. dicoccum*) and Gaza (*T. durum*) to hexaploid wheats. He had been particularly attracted to the vigour of material in which Gaza (2n-28) had been backcrossed to a special accession of Bobin received from Mr J.T. Pridham, a former assistant to William Farrer. This accession is not unlike Gular, a wheat of good quality and quite unlike the Bobin grown commercially. It is less surprising then that Gabo, which was derived from this cross, has been so widely acclaimed.

Selection for rust resistance and agronomic characters were made in the first instance at Hawkesbury College. Successful lines were then assessed at Cunnedah on Mr Beeson's property. During the 1930s Waterhouse was approached by Dr Erasmus Bligh of North Sydney who owned a property at Brookstead Queensland, on the Darling

Downs. Waterhouse provided seed of his most resistant lines and thus began a long association between Dr Bligh's son John and the University of Sydney. He was the first to grow Gabo in Queensland, and since he had excellent irrigation facilities and could grow wheat in the summer very successfully, he undertook a rapid multiplication programme for the more recent University wheats.

Expansion of the work to Gunnedah, N.S.W. and to Brookstead, Queensland was so encouraging that Waterhouse sought additional help to handle the material. In May 1938, I.A. Watson was appointed as Assistant Lecturer with instructions to be prepared to take over lectures at any time, but as Waterhouse was seldom absent from the University, there was no opportunity to give them.

The main purpose of Watson's appointment was to promote the field work at Gunnedah where the new wheats were showing such promise. More assistance was also needed at Sydney University and at Hawkesbury College and in 1941 Waterhouse appointed E.P. Baker as his Graduate Research Assistant. Both these new appointees were trained as plant breeders, Watson with Hayes and Stakman at Minnesota, and Baker with the N.S.W. Department of Agriculture and at the University of California. In 1946. N.H. White was appointed to assist in teaching but he was given no formal lecturing work in the areas in which he was qualified Waterhouse was unwilling to delegate these responsibilities to others.

From preliminary testing it became evident that among the hybrid wheat progenies some exceptionally high yielding material was available. Dough ball tests carried out according to the Pelshenke method indicated a potential for high quality also, but this test was by no means infallible. There was concern about a reliable assessment for quality and, knowing of this, Mr Henry Marcroft, manager of Brunton's Flour Mill, Gunnedah, during the course of a visit to the 'Leyburn' plots, suggested that the cereal chemist of the company might be able to help. The cereal chemist happened to be Mr Eric Bond, now Director of the Bread Research Institute of Australia. Bond quickly saw in some of these lines the possibility for a marked improvement in the quality of northern wheat. He accompanied Waterhouse to the Gunnedah plots in 1941, offered his services in the work, but in doing so he almost certainly did not realise the key role he would have in the improvement of Australia's hard wheat over the next 30 years.

From this humble beginning, Brunton's Mill at Granville virtually became the headquarters for the assessment of quality in the wheat breeding programrme, and Mr Bond, backed by the resources of Brunton's, became an indispensable member of the team. When he subsequently moved to North Sydney to direct the Bread Research Institute, he agreed to contine the quality testing of all the breeding lines. The Institute was enlarged and moved to North Ryde and the support given to the University programme was further expanded. This association between the Bread Research Institute and the University of Sydney has been outstandingly successful in the development of prime hard wheats.

The 1941 season was the last that Waterhouse spent in the field and he was denied the opportunity of seeing the broad acres sown to Gabo when it became so popular. Early in 1942, with a deterioration in the war situation, all University personnel were required for air raid duty around the buildings. This extra chore, superimposed on his many other responsibilities, placed a big strain on him and he suffered a heart attack which necessitated his being away from lectures for the whole of Lent term. He made an excellent recovery, but withdrew from many of his former activities. The wheat breeding programme was left entirely to his two younger colleagues Watson and Baker. Although he could no longer participate actively in the field aspects of the breeding programme he followed it closely till his retirement. He had approved the acquisition of sites for experimental work at Curlewis in northern N.S.W. and at Castle Hill near Sydney. He saw in these facilities the opportunity for greater independence and some assurance that the foundations for a continuation of the work had been laid.

Gabo, the wheat that will be remembered best and which evolved from Waterhouse's early studies, was registered in 1945. It presented a no. of new characters to the farmer. It had short straw, it was early, yielded well and was rust resistant. Farmers found it easy to harvest, but unfortunately it had several serious defects such as low bushel weight, unattractive grain appearance and a marked susceptibility to weather damage. Nevertheless, the grain gave a well balanced dough and for the first time in Australia there was available a wheat variety from whose flour alone an excellent loaf of bread could be made. By 1950 it was the standard of quality and has essentially been the basis of the prime hard wheats that are so successfully grown in the north and which at present are so readily saleable.

The success of Gabo however, was not confined to one area of the State, it became popular elsewhere in the country and at one stage was the leading wheat in Australia. In other countries also Gabo had considerable success. When the Rockefeller programme began to develop in Mexico, introductions from the United States and Canada were rust resistant but matured too late for commercial production. Among many wheats that had been sent to Dr Borlaug, Gabo had shown its superiority in rust resistance, earliness and yielding ability. It was first commercially multiplied in 1951 but had to be replaced on account of a marked susceptibility to stripe rust, the arrival of race 15B of stem rust in the early 1950s finally sealing its fate.

An important feature of this Australian variety was its contribution of a gene for insensitivity to daylength. This was quite accidental but its use as a parent in the breeding programme allowed the Mexican material to be assessed during different seasons of the year regardless of day length. The wide adaptability of many of the current Mexican lines can be attributed to the presence of this insensitivity gene which first became important in Gabo. It is seldom that a single wheat variety contributes so much in so many different environments. Gabo and its sib, Timstein, were both widely used in the pedigree of the Mexican wheats and Cajeme, Mayo, Nainari and many others can be traced back to them.

During the 25 years that Waterhouse and his colleagues had worked in northern N.S.W. definite progress was made in deriving a wheat that could be grown with confidence in the rust liable areas. In 1970, Mr Fish of the Victorian Department of Agriculture reported that 'The continuous attack on stem rust of wheat over an 80-year period has been a remarkable contribution to plant disease control and to the welfare of Australia'. From 1930 until 1947-48 it was not unusual for one third to one half of the northern wheats to be ruined by rust. At that time good years were synonymous with rusty years but this situation has been progressively changed. Unfortunately we cannot say that Waterhouse solved the cereal rust problem, because in no country in the world has the menace been completely eliminated; a lot was learnt, however, as soon as rust resistant wheats became available. Single genes for resistance quickly became obsolete, narrowly based combinations of genes being effective but still not adequate for lasting protection. The broadly based resistance of the modern varieties Timgalen, Gamut and Gatcher, each with at least 4 resistance genes, has given excellent protection in northern N.S.W. These wheats together with their predecessors, have reduced rust losses to insignificant proportions for the past 25 years. Waterhouse's work laid the basis for this success and his students developed and improved on his methods, techniques and facilities. In places where the lessons he taught have not been learnt, losses from rust disease continue to occur. They were serious in southern N.S.W. in 1955, in Western Australia in 1963 and again in southern N.S.W. and South Australia in 1969.

The wheat growers of N.S.W. did not allow to pass unnoticed the work of Waterhouse and the University in the northern part of the State. When the Wheat Research Act was passed in 1957 and they decided to establish their own Research Institute at Narrabri, the University of Sydney was asked to administer it and direct its research. Professor McMillan gladly accepted the honour on behalf of the University and the work at Narrabri has flourished since the place was established in 1958. One of the buildings there has been named in honour of W.L. Waterhouse.

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