

The Development of Plant Breeding at Minnesota



by Herbert K. Hayes

*Edited by Ronald L. Phillips
Foreword by A. Forrest Troyer*

DEPARTMENT OF AGRONOMY AND PLANT GENETICS
UNIVERSITY OF MINNESOTA

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In the cover photograph a University of Minnesota agronomist and student pollinate corn in early hybridization work at the Southern School and Experiment Station, Waseca, about 1920.

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Editor's Notes

Following his retirement as chief of the Division of Agronomy and Plant Genetics at the University of Minnesota in 1952, H.K. Hayes compiled a record and observations of the division's research through his tenure, and that of the successor Department of Agronomy and Plant Genetics over about the next 10 years. His manuscript was never published.

Why would a manuscript written in the 1960s and covering the previous 50-60 years be published at this time? Many "lessons learned" examples in this previously undiscovered manuscript could be applied today. The intensity of plant-breeding studies in this one department, Agronomy and Plant Genetics, often in concert with the Department of Plant Pathology, seems incredible even by today's standards. Judging from the future accomplishments of the many graduates of the program — the Who's Who of plant breeding — the intensity and value of the work must have been palpable in everyday studies at that time.

The leadership of the department believed deeply in the power of genetics; consequently, many of the graduate theses defined the inheritance of a variety of traits under study, often disease resistance. The effect of stem rust race 15B was devastating at that time and had to be overcome; lives depended on a solution. Interestingly, 70 years later we face a similar challenge with the raging Ug99 stem rust strain that Norman Borlaug realized could potentially attack nearly all wheat varieties in the world. Having such a summary of individual theses as presented in this book is indeed fortunate; many important facts buried in the papers and theses Hayes reviewed might well be overlooked today.

The application of mathematics and statistics, cytology and cytogenetics, and crop physiology were all recognized as important sciences. Amazing to me was that a cytology lab was set up in 1917 in the Division of Agronomy.

Discussion and debate served an essential part in making advances in this new field of scientific plant breeding. Often it appeared that the faculty and students went beyond debating both sides of a question by inventing a seemingly third side of the argument. Hayes reportedly said that, "If two people always think alike, then one is not needed". Respect for differing opinions seemed to reign. Several of the early faculty had been graduates of the program, something frowned upon today. Hybrid corn was new and students had to be convinced of its value; they could not believe that crossing two small-eared corn inbreds would give rise to superior types.

The plant-breeding faculty worked on many different species, including corn, wheat, barley, oats, soybeans, flax, sugarbeets, and forage crops such as alfalfa, Kentucky bluegrass, orchard grass, brome grass, fescue, sweet clover, crimson clover, white clover, sunflower, and wheat grass.

H.K. Hayes, an early faculty member (joining the faculty on January 1, 1915) who later became department head until 1952, obviously knew what was going on in his Division of Agronomy (later Division of Agronomy and Farm Management, and later Division of Agronomy, Farm Management, and Plant Breeding). Hayes became the chief of the Division of Agronomy and Plant Genetics in 1928. The Department of Agronomy and Plant Genetics was the name assigned after Hayes' retirement. Hayes understood the science of all of the research programs. In this manuscript, he discusses meiotic irregularities, races of pathogens, independent assortment and linkage of genes, parthenogenetic development of seed, apomixis, ecology, protein, oil, and other topics.

Hayes fostered collaborative research as exemplified in the interactions with the sister Department of Plant Pathology led by E.C. Stakman. He contributed significantly to international agriculture by teaching at the University of Chile as part of the Cornell program. He went to China back when it was a major effort to travel.

One could argue that H.K. Hayes exerted the most influence on the field of plant breeding of any faculty member, before or after his presence at the University of Minnesota. Immer's statistical knowledge was helpful in placing plant breeding on a scientific base; his formula for linkage analysis was used extensively. And, of course, the textbooks by Hayes and Immer and Hayes, Immer, and Smith were important in teaching plant breeding around the world. Powers also offered statistical methods for interpreting the segregation of quantitatively inherited traits.

Many techniques were utilized to measure traits of interest. Pericarp puncture tests in sweet corn were used to score tenderness of the kernels. Several cytological analyses were used, such as micronuclei as a measure of meiotic instability in wheat, detection of aneuploids in forages and corn chromosome knobs. Burnham used chromosome translocation studies

to develop his proposed *Oenothera* method of producing inbred lines of corn. Other techniques included cold tests, corn borer resistance and smut resistance measurements, and sucrose content determinations in sugarbeets.

It is amazing how one University could so dominate the field by its own work and the later work of its graduates. Many of the students have been honored by receiving the University of Minnesota Outstanding Achievement Award, the highest award given by the University to an alumnus.

This book provides a snapshot of the historical traditions of the University of Minnesota Department of Agronomy and Plant Genetics. For a more comprehensive history of the department, please see the book "Agronomy and Plant Genetics at the University of Minnesota" published in 2000 by the Minnesota Agricultural Experiment Station (Minnesota Report 247-2000).

In the concluding chapter of this book, Hayes states, "I have been impressed, in these contacts, with the enthusiasm of many staff members dedicated to furthering knowledge in biological and agricultural sciences, and the application of this knowledge to the improvement of living conditions and the welfare of people engaged primarily in agriculture. At nearly all institutions there have been numerous foreign students, and their dedication to their chosen fields has been an inspiration. These are the main reasons why, in spite of many undesirable interrelations reported vividly in the daily press, it seems the chances are very good for eventual cooperation between the emerging nations of the world and older nations and the eventual evolution of the 'One World Idea,' where there is opportunity for all."

Ronald L. Phillips, Editor
Chair Hayes Memorial Lecture
and Graduate Student Award Committee since 1973

Editorial assistance of Jean Swanson and Ginger Walker in preparation of the text and Lee Hardman and Harlan Stoehr in the publication phase is gratefully acknowledged. Their sincere interest in the project serves as another example of the pride we all have in the University of Minnesota, Department of Agronomy and Plant Genetics.

Foreword

Herbert Kendall Hayes, Ph.D., was a learned plant-breeding scholar and teacher. He was associated with the Agronomy and Plant Genetics Department of the University of Minnesota for more than 40 years while it became the world's center for plant-breeding research and training. He followed and had similar responsibilities and talents as Prof. Willett Hays, the father of American scientific plant breeding, who first identified the individual plant as the unit of selection (*J. Hered.* 94:435-441). Dr. Hayes made plant breeding more scientific as senior author of a trilogy on plant breeding methods that was translated into several languages and widely used for four decades. Dr. Hayes was responsible for 146 professional papers and reports. He was the preeminent teacher of genetics and plant breeding. During his tenure from 1915 to 1952, 225 graduate students completed advanced degrees from agronomy and plant genetics. He was advisor for 67 M.S. and 66 Ph.D. graduate degrees. Nine of his former graduate students became president of the American Society of Agronomy from 1939 to 1973.

Herbert Kendall Hayes was born (March 11, 1884) and raised on a corn and tobacco farm near Granby, Connecticut. He received the B.S. degree from Massachusetts State College at Amherst in 1908. His studies included genetics and a plant breeding courses. He received the M.S. degree in 1911 and the D.Sc. degree in 1921 from Harvard University under the guidance of Dr. Edward Murray East. He was appointed Special Agent, Tobacco Investigations USDA, in 1908; Assistant Agronomist, Connecticut AES in 1909; and Plant Breeder, Connecticut AES in 1911. He became Associate Professor of Plant Breeding at the University of Minnesota in 1915. He was Collaborator, Division of Cereal Investigations, USDA, from 1916 to 1931. He was promoted to Professor in 1918 and was made Chief of the Agronomy and Plant Genetics Division in 1928, a position he held until his retirement in 1952.

In 1932-33, Dr. Hayes was visiting professor of plant breeding at Cornell University. In 1935 he was Sprague Memorial Lecturer at Michigan State University. He spent 1936-37 in China as Research Advisor. He spent six months in 1941 in Chile as Advisor to Plant Breeders and Geneticists. After retirement, Dr. Hayes spent two years as Professor, Cornell University attached to the College of Agriculture, University of the Philippines. Then he was visiting lecturer in plant breeding at North Carolina State University, University of Florida, University of Georgia, University of Kentucky, University of Illinois, Purdue University, and Oregon State University. Beginning in 1952, he was also Emeritus Professor, University of Minnesota.

Dr. Hayes was a member of Phi Kappa Phi, Alpha Zeta, Alpha Gamma Delta, and Sigma Xi honor societies. He was decorated with the Order of Merit from the government of Chile in 1941. He was an honorary member of the Swedish Seed Association, the Agronomy Society of Argentina, the Agronomy Society of Chile and the Minnesota Crop Improvement Association. He was a member of the American Society of Agronomy from 1911 to 1972, elected Fellow in 1927, served as its vice president in 1934, and president in 1935. He was a member of the American Genetic Association. He served as a section vice-chair and chairman for the American Association for the Advancement of Science in 1936. Dr. Hayes was awarded the honorary Doctor of Science degree from the University of Massachusetts in 1948. The Agronomy Building on the St. Paul campus of the University of Minnesota was officially renamed Hayes Hall in 1994.

Dr. Hayes was instrumental in the development of hybrid corn: "After harvesting 200 bushel-per-acre hybrid corn yields in 1909 and 1910 in Connecticut, I never doubted hybrid corn's eventual success." Dr. Hayes stayed the course when Drs. Shull and East wavered. Dr. Hayes started inbreeding corn at Connecticut in 1909 and developed the Burr White variety inbreds used in the first practical corn hybrid — the Burr-Leaming double-cross hybrid. He continued inbreeding corn at Minnesota starting in 1915. He selected strong silking plants on University Farm's drought-prone soils to increase moisture stress-tolerance of corn inbreds and hybrids. Dr. Hayes encouraged Jim Holbert and Dr. Jenkins to develop inbreds and hybrids in the mid and late 1910s. Dr. Hayes was of primary importance in the early days of inbred and hybrid development of corn.

Dr. Hayes maintained and enhanced the plant breeding reputation of the University of Minnesota. Prof. Willet Hays had developed Minnesota 13 corn variety, released in 1896, when corn acreage in Minnesota was only 200 thousand acres. Minnesota corn acreage grew to two million acres in 1911 and to five million acres in 1932 largely due to Minnesota 13; this corn variety was recommended by 12 northern and/or higher elevation states in 1936 (*J. Amer. Soc. Agron.* 47:905-914). Drs. H. K. Hayes and E.C. Stakman developed Thatcher, rust-resistant, hard red spring wheat that

was released in 1934 after six years of testing. Thatcher was grown on 71 percent of the Minnesota spring wheat acreage in 1939 and reached a maximum of 17 million acres of the total spring wheat area of North America in 1941.

Dr. Hayes was asked to address the 50th anniversary of the Agronomy Society in 1957 on the developments of plant breeding during the last 50 years. He began with a short biography, and then declared that plant breeding had grown from simple selection to a science. His topics included: The Extension of Mendelian Laws; Genetic and Cytogenetic Bases of Plant Breeding; Centers of Origin; Heterosis; Disease and Insect Resistance; Applications of Statistics; Special Techniques; and Cooperation in Plant Breeding. He ended by relating a conversation with his grandfather comparing each of their 50-year views of progress and predicted the coming, future 50 years would show even more progress (*J. Amer. Soc. Agron.* 49:626-631).

Dr. Hayes believed firmly that the only way to know plant material was to study it yourself in the field and laboratory. Some of Dr. Hayes' principles from his prefaces follow: "The purpose of this book is to present fundamental principles of crop breeding and to summarize known facts regarding the mode of inheritance of many of the important characters of crop plants" (*Breeding Crop Plants*, 1921). "Plant breeding is an applied science that is carried out efficiently only through the application of other plant sciences" (*Methods of Plant Breeding*, 1942). "The primary purpose of this reference to experiences in the Philippines is to make clear that, certain principles could be applied to the solution of the problem of producing adapted double-cross hybrids for the Philippines" (*A Professor's Story of Hybrid Corn*, 1963). His primary goal was useful new varieties and hybrids with basic information important but secondary.

Dr. Hayes encouraged cooperation among projects on disease or insect resistance with plant breeding. He spread the scientific plant-breeding gospel to the programs in pre-WWII China, Chile, Argentina, the Philippines, and Taiwan, and he held brief assignments at the agricultural colleges at Cornell and Michigan State Universities before retirement and Purdue, Illinois, Florida, North Carolina, Kentucky, Nebraska, and Oregon subsequent to his retirement in 1952.

This author first met Dr. Hayes in the summer of 1956 on University Farm while harvesting sweet corn ears. "You should try some of this smaller, early variety," he said. "I'm not particular about sweet corn." I replied. "I like it all." To which he proclaimed; "I AM PARTICULAR ABOUT SWEET CORN, and this small early variety is better quality than what you are harvesting." Of course it was. It was Hayes White that had been improved for pericarp (female tissue enveloping the kernel) tenderness at Minnesota by selection with a penetrometer 20 days after pollination while the ears

were still attached to the plant. Tougher ears were harvested to eat; the more tender ears were left on the plant to mature and be harvested for planting next year, when the procedure was repeated. Hayes White sweet corn kernels nearly melt in your mouth.

In the 1950s, the Department of Agronomy and Plant Genetics contained many people vitally interested in plant breeding. They awoke in the morning and went to sleep at night thinking about it. The plant-breeding seminars included several plant pathology and horticulture plant-breeding faculty and students to total 50 to 60 people. Topics and student presenters were chosen carefully. It was scheduled on Fridays from 3:00 to 5:00 PM all three quarters. The audience was expected to absorb the presentation and ensuing discussion over the weekend and be knowledgeable about the topic by Monday. The discussion commonly lasted until 6:00 P.M. When it continued until 7:00 P.M., someone would stand up and say: It is 7:00 P.M., and everyone would stop—even in the middle of a sentence—and leave the room. Dr. Hayes sat near the front of the room and asked tough questions. He had two short sentences he sometimes drew and fired like a revolver: One was: “Never, never select against vigor.” Another was: “If you don’t have 1,200 plants, you don’t have an F_2 population.” He could be fearsome.

My responsibilities at Minnesota included planting and harvesting several yield trial locations in western Minnesota with a crew from the Morris school and branch station. I stayed there a few weeks and slept in the infirmary when not on the road. During my absence, Dr. Hayes used my office (Room 311) next door to Dr. Ernest Rinke’s office, to write “A Professor’s History of Hybrid Corn.” He accidentally broke a glass nameplate I had received for a seminar presentation. Dr. Hayes kindly asked three or four people to tell me he was sorry he broke it. Interestingly, he never told me himself.

Dr. G.C. Marten, as a neophyte teaching assistant in 1958, fondly remembers sharing Dr. Hayes’ retirement office. Dr. Hayes sometimes reminisced about illustrious international activities sprinkled with good advice. After one such oration, his parting thought was as follows: “Young man, keep one important thing in mind as you go through life—until you’ve been criticized, you haven’t done a damn thing of significance!”

Dr. James Brewbaker remembers Dr. Hayes in the Philippines in 1953 as an efficient administrator of field and office activities: “He made his presence felt; he was dogmatic and made things happen. The corn program at the University of Philippines was immediately driven to develop hybrids, long before any population improvement of corn had occurred.”

Dr. D.C. Smith states Dr. Hayes had broad interests in plants and liked to work with them. He was always a student and liked to discuss and argue as necessary. He was constantly evaluating and was critical and frank, in

a constructive fashion. He was understandably impatient when progress seemed unnecessarily slow or when coworkers unexplainably defaulted in their responsibilities. He was competitive, industrious, and persistent in following research programs to conclusions. He was fair, generous, and loyal, and for those who knew him best, friendly and warm. He inspired confidence and effort (Crop Sci.14:1-5).

J.L. Morrill, President of the University of Minnesota, states: Dr. Hayes' colleagues speak of his optimism as one of his most striking traits. Even when his co-workers are discouraged and ready to pronounce a problem insoluble, he will insist there is a solution if only they keep looking. Dr. Hayes has great powers of analysis; he has the capacity to strip away the complexities and seize upon the fundamentals. Whenever you go into his office with a problem, you come out with a solution or at least a good idea of how to find one. Dr. Hayes' dominant philosophy was his faith in cooperative effort. He believed in close working relationships from the bottom to the top.

Dr. Hayes had a direct positive influence on the training of more plant breeders than any other one person. The following generations of plant breeders trained by Dr. Hayes' students and their students probably now number the majority of plant breeders in the world.

A. Forrest Troyer
Ph.D. 1964, Department of Agronomy and Plant Genetics
2009 Siehl Prize in Agriculture

Contents

<i>Introduction</i>	1
<i>Chapter 1 – Early Developments in Agricultural Research in the United States</i>	7
<i>Chapter 2 – The State Agricultural Experiment Station Program</i>	12
<i>Chapter 3 – Early Cooperation in Minnesota before 1921</i>	16
<i>Chapter 4 – Research Studies 1921-36 Inclusive of Staff Members</i>	25
<i>Chapter 5 – Research Studies 1921-36 Inclusive of Graduate Students' Theses</i>	45
<i>Chapter 6 – Staff Research 1937-52 Inclusive</i>	70
<i>Chapter 7 – Graduate Student Research 1937-52 Inclusive</i>	90
<i>Chapter 8 – Concluding Discussions</i>	145
<i>Literature Cited</i>	163

Introduction

I joined the Division of Agronomy and Farm Management, University of Minnesota on January 1, 1915, to take charge of Farm Crops Plant Breeding in the Minnesota Agricultural Experiment Station and to take part with others in teaching genetics and plant breeding in the College of Agriculture, School of Agriculture, and Graduate School. At that time, Andrew Boss was Chief of the Division of Agronomy and Farm Management. In Boss' original letter to me in the fall of 1914, he stated that the man who was appointed to this position could develop plant breeding as seemed most desirable to him.

I was invited to Minnesota in September 1914 to see the work underway. Extensive breeding studies with farm crops were being carried out, but adequate use was not being made of Mendelian principles. Extensive breeding nurseries using the Centgener method, developed by W.M. Hays, were grown, particularly with small grains. Corn and other crop breeding was also studied.

I was greatly interested in the research under way in the Division of Botany and Plant Pathology concerning breeding high quality bread wheats for stem rust resistance. This was led by E.M. Freeman, Chief of the Division and Dean of the College of Agriculture, Forestry, and Home Economics, and John H. Parker, of the U.S. Department of Agriculture. Because of my interest and training in genetics in relation to breeding, I helped plan and carry out a study of the genetic nature of rust resistance in wheat. A joint project drawn up in 1916 entitled, "Genetics of Rust Resistance in Wheat," under the leadership of Hayes, Freeman, and Parker was approved by administrative leaders in Agronomy, Plant Pathology, and U.S.D.A. This led later to an overall project entitled, "Breeding Disease Resistant Varieties of Farm Crops," to cover the cooperative phases of disease resistance with all farm crops. Although several studies were completed previously, the first cooperative outline was formulated in 1921.

The more distinctive phases of researches relating to genetics of disease organisms, their life histories, related problems, etc., were carried out by E.C. Stakman and coworkers. Studies relating to genetics and breeding of other characteristics than disease resistance were under my direction along with coworkers. In many cases with segregating generations, members in both Divisions took research data on disease reactions and classified crop characters. Project leaders in agronomy were primarily responsible for planning crosses.

The undergraduate-graduate course in genetics, the beginning course in the College of Agriculture, Forestry, and Home Economics, was taught cooperatively by agronomists and horticulturists. In 1915 and for several subsequent years, the leader in horticulture was M.J. Dorsey; I represented agronomy. In spring 1915, Dorney Valleau joined me in teaching an undergraduate course in plant breeding. J.H. Beaumont succeeded Dorsey when he resigned. When Beaumont resigned, the beginning course in genetics was transferred to the agronomy division.

In 1915, the undergraduate-graduate course entitled "Plant Breeding" was taught in cooperation with Valleau. I emphasized methodologies of breeding, particularly Mendelian principles. Intensive discussion of the effects of cross- and self-fertilization with corn was an important phase of hybrid vigor, first called "heterosis" by Shull in 1914. Since about 1905 both East and Shull made many studies of heterosis with both selfed and cross-pollinated species. The latter was new to Minnesota agricultural students and corn seed growers who, in many cases, were overly impressed with corn seed shows and the value of scorecard type.

A student in this class, Bob Hodgson, who later became Superintendent of the Waseca Agricultural Experiment Station, described this class:

I have quoted here from a letter written by Hodgson to me several years later. "Every boy who grew up on a southern Minnesota farm knew all about corn. It was as familiar as the dining room table. In the first quarter of the century, every careful farmer selected his own seed corn with great care. Each ear had to meet rigid qualifications and some growers even selected for healthy stalks, produced under competition. These extremists were either "cranks" or "the enlightened," depending on who told the story.

In the fall of 1915, a group of boys, mostly seniors at the University of Minnesota College of Agriculture, registered for a course called Plant Breeding. Previously, this course had dealt with such orthodox procedures as selection, type, and purity. Now, rumor had it, a new professor, with basic training in genetics and everything, was planning to introduce a whole new set of rules for improving our plant crops. The boys adopted a "show me" attitude.

This was the situation faced by the new prophet from the east. He was a "foreigner" to these provincial Minnesota boys. He was obviously more familiar with tobacco growing than with corn culture, particularly corn culture as these boys knew it. He held up some tiny nubbins and proclaimed that these would make better seed than the big beautiful ear beside them. This was too much to

swallow! To a boy who had spent days and weeks in the field selecting seed ears; who had taken A.C. Army's course in corn judging and had placed the samples in several county shows; who knew all about corn; this was plain heresy and anyone promoting such ideas deserved to be burned at the stake.

It must have been a frustrating experience for Professor Hayes to run head on into such resentment and active opposition in his first class at the new University. He was brimming with enthusiasm over the possibilities of a genetic attack on plant improvement and most anxious to fire his first students with the new gospel of controlled inheritance. It must have been hard to lay aside his plans for new crops with bred-in quality and go back to the ABC of genetic mechanism.

A good teacher, in addition to knowing his subject, must know human nature as it activates students. Dr. Hayes was a good teacher. He went back to the beginning and made the path plain. After he was satisfied that the fire was burning, he piled on the fuel. It was one of the most difficult and time consuming courses taken by those Minnesota boys but by spring, Dr. Hayes had every one of those lads impatient to get out in the field and try some of these new ideas. So far as I know, he won the respect and friendship of every student in that class.

When this example of that resentful group was put into a position where experimental work with plants would be possible, my first commitment was to tell Dr. Hayes, 'You may be sure that your plant breeding projects will be carried out as extensively and as carefully as my ability permits.

So Dr. Hayes' first achievement in Minnesota was not genetic in character. He won a group of Minnesota boys who knew all about corn to a rudimentary understanding of and a vast enthusiasm for the new science of plant breeding. Speaking for this member of that first class, after more than 40 years of close cooperation in field experiments and nearly 50 years of admiration, respect, and friendship for Dr. Hayes, I'm most thankful that I signed up for that first class in Plant Breeding in the fall of 1915.

Hodgson was greatly impressed with the value of plant breeding. Corn breeding by controlled pollination methods was started at Waseca in the early 1920's. Hodgson's M.S. thesis research was entitled, "The economy of corn production as affected by the use of F_1 seed of varietal crosses." He compiled data comparing the F_1 cross of Longfellow X Silver King with Silver King for ensilage purposes. The cross gave a 10-percent increase for silage over Silver King, a 12-percent increase in protein, ether extract of 22.5 percent, nitrogen-free extract of 8.3 percent, and about a 5-percent decrease in crude fiber.

P.J. Olson, an assistant professor in the agronomy division, attended the class in plant breeding as a visitor. Olson was greatly interested in teaching and gave vigorous lectures. He said, "I became convinced that biological knowledge of the field covered is at least as important as methods of teaching."

Perhaps the writer may digress at this point. During the last year he attended the ceremony and accompanying dinner at the University of Minnesota in honor of Dr. Manuel Carreon, of the Philippines, who in 1923 earned the Ph.D. degree specializing in Educational Psychology, and who in

1962 was given a University Citation for his leadership in Education. During these ceremonies, and because the writer had been in the Philippines with a Cornell University group at the College of Agriculture in 1952-54, and perhaps because of the apparent agreement on principles, the writer had several discussions with Dr. Carreon. At the evening dinner in reviewing his educational background and experiences Dr. Carreon said somewhat as follows, "Education seems to me to be a two-way street. Unless the teacher gains new viewpoints and inspiration from his students, as well as inspiring them, the method of teaching is probably not on a sound educational foundation."

An undergraduate-graduate course in "Horticultural Crop Breeding" has been taught throughout the years by members of the Horticultural staff.

Few graduate students were in agronomy and plant breeding in those early days or in other divisions in the College of Agriculture. Harry V. Harlan majored in agronomy with Boss as adviser. Harlan earned a Ph.D. degree in Minnesota in 1914, using studies with barley as his thesis problem (Harlan, 1914). In 1915 Harlan's large barley breeding nursery was grown at University Farm independent of the agronomy breeding nursery. In summer 1915, Harlan grew numerous barley crosses in F_2 and F_3 segregating generations and I aided in classifying segregating characters. Although Dr. Harlan soon transferred his major barley nursery to Aberdeen, Idaho, where growing conditions were very favorable for the barley plant, these early studies led to several cooperative researches with barley completed in Minnesota (Harlan and Hayes, 1920; Hayes and Harlan, 1920). One related to inheritance of spike density and another to inheritance and production of *Hordeum intermedium* Krke. from crosses of 6-rowed, *H. vulgare* L. with *H. distichon* L.

The following is quoted directly from Harlan's autobiography (Harlan, 1957).

My Minnesota days were enriched by friendships with Tom Cooper, Andrew Boss, H.K. Hayes, and E.C. Stakman. With the latter two the connections were official as well as personal. To the outsider we must have seemed bitter enemies. We were never on the same side of any question except by accident, and then somebody made a quick shift. If we were all three present at the same time, we managed to find three sides to a question. Stakman and I commenced to argue while he was still in the hall. I hope the others look back upon these days with as much pleasure as I do.

In the Graduate School of the University of Minnesota, seminar courses in genetics and plant breeding were conducted cooperatively by the Divisions of Agronomy and Farm Management and Horticulture. Genetics seminars reviewed basic genetic and cytogenetic problems, although plant genetics and cytogenetics were featured more than animal. Plant breeding seminars concentrated primarily on basic problems of farm and horticultural crops.

A 1921 publication, *Breeding Farm Crops*, by Hayes and Garber utilized much of the knowledge gained at these weekly seminars on genetics and plant breeding.

In the early 1920's graduate students in plant breeding could select plant breeding as a major; the title of the Division was changed to read Agronomy, Farm Management, and Plant Breeding. In 1928 this Division was reorganized. Boss and coworkers in farm management joined the agricultural economics staff, and Boss took over the part-time position of vice director of the Agricultural Experiment Station. The Division of Agronomy and Plant Genetics was set up with myself as chief and continued under this leadership until my retirement on July 1, 1952. Will M. Myers was then named head and Division was changed to Department. This was a desirable change since the Department of Agriculture was given a new title, The Institute of Agriculture.

Recognition is made of the leadership in teaching and research in genetics and plant breeding of various workers in both divisions, including coworkers in plant genetics, in about the order of their period of activity; P.J. Olson, Ralph J. Garber, Fred Griffee, H.E. Brewbaker, F.R. Immer, I.J. Johnson, R.P. Murphy, E.H. Rinke, LeRoy Powers, F.J. Stevenson, W.M. Myers, C.R. Burnham, H.K. Shultz, Carl Borgeson, Y.S. Tsiang, Emmett Pinnell, and H.L. Thomas.

Various members of USDA who have been headquartered in the Division of Agronomy and Plant Genetics included Karl Quisenberry, O.S. Aamodt, E.H. Ausemus, A.H. Moseman, and J.O. Gulbertson. Ausemus and Gulbertson also held appointments as professors at the University. In the Division of Horticulture, major leaders in plant breeding were M.J. Dorsey, Richard Wellington, J.H. Beamont, F.J. Krantz, A.N. Wilcox, and Troy Currence.

In the Graduate School I taught an "Advanced Genetics" course for many years until Burnham joined the staff in 1937 to take charge of the Cytogenetics Laboratory. At that time he took over the responsibility of graduate courses in genetics and cytogenetics. Until my retirement, I also taught a graduate course in "Methods of Plant Breeding." Most graduate students interested in horticultural plant breeding, plant genetics, and plant breeding took this course. Plant pathology students interested in disease resistance also attended. After graduate work in plant breeding was well underway, a laboratory course given in summer was developed in which most of plant genetics Staff participated.

After my retirement the course in "Methods of Plant Breeding" was taught by Myers, head of the Department of Agronomy and Plant Genetics. In recent years Rinke has taught both the graduate and undergraduate courses in plant breeding.

This history was written to:

1. Present the development of teaching and research in genetics and plant breeding at Minnesota.
2. Emphasize the extent and nature of cooperation that was carried out, with particular reference to disease resistance.
3. Point out relationships that were developed between graduate student researches and the carrying out of Agricultural Experiment Station projects.

My experiences in foreign fields have been presented in order to show the value of cooperative research methods as developed at Minnesota and their application to similar research problems in newly emerging nations.

My appreciation is expressed to all who have aided me, particularly to the late J.J. Christensen and M.F. Kernkamp, Plant Pathology; C.R. Burnham, E.H. Ausemus, D.C. Rasmusson, and Herbert W. Johnson, Agronomy and Plant Genetics; and especially to H.J. Sloan, former Director, Minnesota Agricultural Experiment Station, and to his successor, W.F. Hueg.

The first and final copies of the manuscript were typed by Mrs. Julia Thomas. In so doing she made very valuable suggestions that helped to clarify certain reviews. My wife, Rachel R. Hayes, greatly aided me in checking the typed manuscript and proofreading the final copy. Both my wife and son, H. Kendall Hayes, read the completed manuscript and made helpful suggestions.

Chapter 1

Early Developments in Agricultural Research in the United States

The following quotation from *State Agricultural Experiment Stations. A History of Research Policy and Procedure* (Knoblauch et al., 1962) is pertinent to this discussion of University of Minnesota research related to breeding disease resistant varieties of farm crops. "In 1962 we will commemorate the signing by Abraham Lincoln on May 15, 1862 of 'An act establishing the United States Department of Agriculture,' and on July 2, 1862, of 'An act donating public lands to the several States and Territories' which may provide colleges for the benefit of American agriculture and the mechanic arts." These two acts were essential to the development of agricultural teaching and research in the United States.

Agricultural research has greatly modified agricultural production. After World War II, the assistant chief of the Bureau of Agricultural Economics stated that the breeding of disease resistant varieties, the development of hybrid corn, and mechanization had greatly helped win the war.

The information in the following two paragraphs was supplied by Dr. E. Fred Koller, Professor of Agricultural Economics, University of Minnesota.

Changes in farm production and efficiency have been great. In 1910 the number of persons supported by one farm worker was about 7, in 1951, about 15, and in 1961, 27. The ratio of farm population to total population has also greatly changed. In 1920, the total population was about 106 million with about 30 percent farm population. In 1950, the total was over 151 million with 16.5 percent farm population, and in 1960 over 180 million and 11.4 percent farm population.

Comparisons of people engaged in all occupations and in agriculture also give a striking picture of changes that occurred. In 1870, of nearly 12 million workers, 53 percent were engaged in agriculture; in 1920, of over 42 million, 27 percent were engaged in agriculture; in 1940, of over 56

million, only 17 percent were engaged in agriculture; and in March 1960, of over 70 million, only 6.4 percent were engaged in agriculture. The actual round numbers of persons engaged in agriculture in 1870, 1920, 1940, and 1960 were 6,850,000, 11,449,000, 9,540,000, and 4,565,000, respectively.

These gains in efficiency were largely due to results of research. The development of the State Agricultural Experiment Station research programs was of equal importance to that of USDA. Because both were made possible through federal support, cooperation has been fostered between these two agencies.

The first State Agricultural Experiment Station originated in Connecticut and is still functioning in New Haven. It is one of the few state stations not connected directly with a land-grant institution. S.W. Johnson was responsible primarily for its creation. When he failed to obtain support for initiating an agricultural station in Connecticut, he presented a plan for such a station to a prominent New York State society. Until 1887 Johnson and others worked tirelessly to gain support for the State Agricultural Experiment idea. He and colleagues developed a center for teaching research methods in agricultural chemistry at Sheffield Scientific School in New Haven where advanced students were training.

During my first year, 1909, at the Connecticut Station, I worked directly with E.M. East and gained from him great inspiration for a life work in genetics and plant breeding. On completing work for the M.S. degree in 1911, I was given charge of the work at Connecticut. During 1905, studies with corn and tobacco at the Connecticut Agricultural Experiment Station were supported largely by the Adams fund. E.H. Jenkins, director of the station, and East both believed that a trained research worker should have a free hand to conduct investigations. From them I learned the importance of an enthusiastic vital interest in research and the equal importance of individual freedom to conduct studies without being hampered by directives.

W.O. Atwater was also an outstanding advocate of the State Agricultural Experiment Station. With Johnson's aid the first State Agricultural Experiment Station was set up at Wesleyan University, Middletown, Connecticut, where Atwater was professor of chemistry. The Connecticut State Legislature granted \$2,800. Orange Judd, a farm paper publisher, gave \$1,000. Atwater was placed in charge.

Because of administrative difficulties, Atwater and coworkers drew up a new plan. In 1877 the Connecticut Agriculture Experiment Station was created to be governed by a board of control and financed by a continued appropriation of \$5,000 from state treasury funds. This board appointed Johnson as director and leased temporary quarters at Sheffield in New Haven. In 1882 the legislature authorized purchase of a small private estate

in New Haven. The Connecticut Agricultural Experiment Station is today located in the same headquarters.

Six other states launched Agricultural Experiment Stations prior to the Hatch Act in 1887. These included: Tennessee, 1882; Wisconsin, 1883; Kentucky, 1885; New York Geneva Station, late 1880's; New York Cornell Station, 1879; and Massachusetts, 1883. University trustees in California in 1875 encouraged a station movement and gave broad authority (by 1880) to a station director.

Even though experiment stations were not set up, experimentation was started early at most land-grant colleges. Either by charter provision or separate enactment, college governing bodies were directed to initiate and maintain agricultural experimentation.

Because of lack of direct federal support for the Agricultural Experiment Station idea, each state carried out experimentation according to the desires and research viewpoints expressed at different land-grant institutions. Unfortunately, when state legislatures authorized State Agricultural Experiment Stations, they were set up independently of land-grant institutions. Therefore, there was lack of coordination between early research at land-grant institutions and at stations. These difficulties were largely surmounted when Congress passed the Hatch Act as amended in 1887.

"In the winter of 1885-86, the committee on presidents," (land-grant institutions) "assiduously cultivated the Congressional chairman of the agricultural committees, William H. Hatch in the House and James Z. George in the Senate." These two chairmen were strong supporters of the station bill. Although Hatch encountered no great difficulty of obtaining support for the measure, two divergent viewpoints were expressed in Senate debates. George considered experiment stations to be extensions of USDA since both were to be financed by the federal government. Senator Joseph H. Hawley, Connecticut, took an opposite view. He proposed a substitute measure in which no reference would be made to USDA. Hawley was interested primarily in a plan whereby a state legislature could use Hatch Act funds for an experiment station which was not connected with a land grant institution.

Amendments to the Hatch Act as passed are summarized as follows (Knoblauch et al., 1962):

"They made legislative assent a necessary component in the creating of a college station; they enabled the legislature to supply funds to an independent station; they removed the requirement that a station must operate a farm; they deleted the obligation of the Stations to aid the Department of Agriculture; they excised all phrases intimating that the Commissioner had powers beyond those of aiding and assisting the State

stations.”

This compromise was relatively satisfactory to both George and Hawley and permitted passage of the amended Hatch Act on March 2, 1887. The precedent set up furnished a satisfactory basis for cooperation in agricultural research between USDA and State Agricultural Experiment Stations with each organization having equal responsibility for planning and carrying out research.

To complete this brief survey of agricultural research before the Hatch Act, reference is made to Kansas (Call, 1961) as an example of what was occurring at land-grant institutions.

The Kansas legislature on March 3, 1863 passed an act relating to the government of the Kansas State Agricultural College. This act required the Board of Regents to report annual progress relating to “Experiments,” their cost and results accomplished, as one of its duties. So it was recognized from the beginning that agricultural experimentation would take place. Prior to the Hatch Act, one major difficulty was the lack of buildings, including both laboratories and barns, that were necessary for carrying out agricultural research. Suitable experiment station fields were needed. The cost of machinery and other apparatus, horses for work purposes, livestock to use, etc., greatly inhibited progress in those early days when little money was available.

However, prior to 1887 numerous investigations were carried out. Winter wheat variety tests were undertaken, five varieties being grown in 1879; in fall 1887, 51 varieties of winter wheat were sown. Variety tests of both dent and flint corn were also studied. Other crops studied included: alfalfa, sorghums, barley, oats, rye, flax, millet, buckwheat, castorbeans, cowpeas, sugarbeets, and mangoes. Fertilizer investigations were made largely with stable manure and gypsum. Due to the cost of application and its value, general manuring was not recommended; instead it was suggested that manure be applied to easily accessible fields.



Dr. Andrew Boss, Chief, Division Agronomy and Farm Management, Vice Director of Minnesota Agricultural Experiment Station, and a life-long leader in Agriculture.

Horticultural investigations were rather extensive. E. Gale reported in 1871 that there were 2,100 apple, pear, peach, cherry, and plum trees in the orchard; in 1873 there were 1,000 varieties of apples, chiefly in nursery rows. Forest and shelterbelt studies were extensive; 34,489 trees were in the experimental forest and 2,072 in the shelterbelt in 1872. Studies were carried on with flowers, vegetables, and shrubs. A total of 40½ acres of land were used by the horticulture

department.

In these early years, livestock investigations consisted mostly of purebred stock and distribution of these by sale to farmers. Feeding experiments were undertaken with pigs in 1880; the value of winter shelter for mature pigs was also investigated. Various feeding studies were carried out prior to the Hatch Act, including studies of the value of whole milk for young pigs, cooked versus raw corn for fattening, alfalfa and orchard grass for hog pasture, corn and corn and cob meal for beef production, and warm drinking water for milk cows.

Investigations were carried out also in chemistry. Soil samples, taken in nearly all counties, were compared for organic matter and a few were minutely analyzed. Sugar content of different sorghum varieties was determined and desirability of varieties for producing sugar was studied. However, work was limited because of insufficient financial support.

Other investigations included studies in entomology, botany, zoology, and meteorology. In 1872 approximately 800 species of insects had been collected. By 1871 the mineral and fossil collection consisted of about 2,000 specimens. Twenty-seven species of wild grasses were placed in the botanical collection in 1872.

As this description of Kansas activities shows, extensive studies were undertaken at land-grant institutions before the Hatch Act. These were believed essential to a sound development of education in agriculture and mechanic arts. Studies of a similar nature were conducted at State Agricultural Experiment Stations not connected with land-grant institutions. In each state the nature of the studies depended upon needs and wishes of the agricultural clientele. When the Hatch Act was passed in 1887, a sound background of knowledge already existed upon which to build agricultural research.

Chapter 2

The State Agricultural Experiment Station Program

*E*ssential to an understanding of “The Development of Plant Breeding at Minnesota” is some knowledge of the support given to the State Agricultural Experiment Station. For this reason, a brief summary follows.

Because State Agricultural Experiment Stations are supported by both state and federal funds, both agencies were responsible for the development of agricultural research at the state level. However, states differed widely in their resources and the importance of agriculture and agricultural businesses to other phases of livelihood. Therefore, funds available from state appropriations for agricultural research varied greatly from state to state. Federal funds for Agricultural Experiment Stations also differed from state to state, depending at least partially upon size of rural population.

The original Hatch Act as amended furnished \$15,000 per year to each state. In states that had no stations, the money was to be used to develop experiment station work in connection with the land-grant institution. If a state already had both a land-grant institution and a separate station, the state could apply benefits from the Act to both. Furthermore, a state could use the Hatch Act funds to support agricultural research that seemed desirable to the state legislature.

A full report of operations and expenditures had to be submitted annually to the governor of the state or territory. A copy also had to remain in the station files, another copy had to be sent to the Commissioner (now Secretary) of Agriculture, and another copy had to be sent to the U.S. Secretary of the Treasury. To secure some uniformity in these reports, the U.S. Secretary of Agriculture had to furnish forms for tabulation of results and generally give advice and assistance.

Accomplishments in agricultural research were of such great value that the state stations soon were faced with more problems than they had

facilities for solution. Many problems were solely of local importance. And, in many cases, funds were not sufficient for carrying out the more basic researches. This situation led in 1906 to the Adams Fund Act for original researches. Five thousand dollars were made available to each state for the first year and \$2,000 additional were available each succeeding year until the annual amount paid to each state was \$15,000.

The U.S. Secretary of Agriculture administered the Act for the purpose of original research. By mutual agreement between the Secretary and station personnel, administration consisted of a fiscal review of each Adams Fund project and consideration of expenditure of funds and research accomplished. Thus, for example, members of the Office of Experiment Stations carefully reviewed Adams Fund projects and all other agronomy projects, whether supported from state or federal funds or both. This review led to a careful outline of the research and experiment program prior to execution and a yearly summary of results. Suggestions for the final summary of the project, as originally outlined, and the formulation of a new project to cover new phases, were made by a reviewer who often had aided in such reviews at other stations.

The Purnell Act of 1925 gave added financial support for state station research. Starting in 1930, \$60,000 were appropriated annually for experiment station research in each state. The appropriation could be used for research and experimentation on production, preparation, manufacture, use, distribution, and marketing of agricultural products, particularly for the establishment and maintenance of a permanent and efficient agricultural industry. Economic and sociological investigations involving the development and improvement of rural life also were authorized.

Further extensive federal support for agricultural research was furnished by the Bankhead-Jones Act of 1935. As originally outlined, "the sum of \$1,000,000 was appropriated for the fiscal year beginning after the enactment of this title, and for each of four fiscal years thereafter \$1,000,000 more than the amount authorized for the preceding fiscal year, and \$5,000,000 for each fiscal year thereafter."

Forty percent of the Bankhead-Jones appropriation was for USDA investigations, although 2 percent of this could be used for administering state experiment stations appropriation. This USDA appropriation was available for the prosecution of research already established, except on written approval of the Secretary.

Sixty percent of the Bankhead-Jones appropriation was available for experiments, similar to those conducted by USDA, by state agricultural experiment stations. The Secretary was responsible for implementing these allotments.

In order for a state or territory to obtain its allotment under this Act,

no payment could be made in excess of this amount of state funds provided for the fiscal year of agricultural research and maintenance of necessary facilities for that research. Further provisions were made for use of funds from any money in the treasury not otherwise appropriated to make more complete endowment and support of land-grant colleges.

In 1946, Congress passed an “amendment to the Bankhead-Jones Act to provide for further research into basic laws and principles relating to agriculture and to improve and facilitate the marketing and distribution of agricultural products.”

The amendment outlined purposes in rather great detail. It covered broadly what seem to be all phases of research relating to the maintenance of a sound agricultural and rural life. Appropriations consisted of \$2,500,000 for the fiscal year ending June 30, 1947 and additional yearly increases in appropriations until on June 30, 1951 and thereafter for each fiscal year a continued appropriation of \$20,000,000. Not less than 97 percent of total appropriations for experiment stations was allotted to Puerto Rico, each state, and territory. The remaining 3 percent was available to USDA for administering their research.

Appropriations were also made to carry out further research on utilization and associated problems of development to application of present, new, or extended uses of agricultural commodities.

Total additional funds appropriated, starting with \$3 million for the fiscal year June 30, 1947 and each subsequent fiscal year and continuing with an equal added appropriation of \$3 million for each of 4 additional years, made \$15 million additional available for each year subsequent to 1951. This part of the Act was administered by the Secretary of Agriculture. He could contract with public or private organizations when the work authorized could be carried out more advantageously than if performed by USDA.

An additional appropriation was made available for cooperative research by USDA and state experiment stations or other appropriate agencies as mutually agreeable to USDA and the experiment stations concerned.

An appropriation of \$1,500,000 for the fiscal year ending June 30, 1947 was made to be continued in each subsequent fiscal year. Similar additional amounts were appropriated for each of 3 succeeding years making \$6 million available for each fiscal year after that ending on June 30, 1950.

A further amendment was made in the Act on July 31, 1947. This required that not less than 20 percent of all additional funds made available by the amendment of the Bankhead-Jones Act of 1946 should be used for marketing research projects approved by USDA. The Secretary of Agriculture was given broad powers to administer this Act in relation to all phases of marketing problems for “agricultural products.” These included,

“agricultural, horticultural, viticultural and dairy products, livestock and poultry, bees, forest products, fish and shellfish, and any products thereof, including processes and manufacturing products, and any or all products raised or processed on farms and any processed or manufactured product thereof.”

An Act of 1955 consolidated the Hatch Act and laws supplementary to it relating to appropriation of federal funds for support of agricultural experiment stations. The Act reaffirmed Congressional policy to continue agricultural research as had been conducted under the various acts previously reviewed. The primary purpose was, “promoting the efficiency of such research by a codification and simplification of such laws.”

Chapter 3

Early Cooperation In Minnesota Before 1921

On January 1, 1915, I joined the staff of the Division of Agronomy and Farm Management of the Department of Agriculture, University of Minnesota. I took charge of farm crops plant breeding research in the Minnesota Agricultural Experiment Station and cooperated primarily with the Division of Horticulture in teaching genetics and plant breeding in the College of Agriculture and Graduate School. This review deals chiefly with research and teaching programs at Minnesota that were pertinent to the development of plant breeding.

Boss, the division chief, had said that I would have charge of plant breeding research and experimentation with farm crops and a free hand to develop this work. The Graduate School's procedure was that each staff member would deal directly with the Dean of the School concerning graduate student problems. This did not interfere with a sound administration of subject matter research in the division concerned; the division chief was the administrative leader of both teaching and research as carried out in his subject matter area.

Although plant breeding research in farm crops was to be under my direction, all problems in this connection were not easily solved. At first, some intradivisional problems remained such as deciding what phases of farm crop research were legitimately covered by plant breeding. One professor was conducting simple selection with both flax and soybeans but he contended that improvement by simple individual plant selection was not breeding. He also had underway a study of first generation varietal crosses in corn, but did not consider this to be plant breeding.

Boss concluded that these problems should be decided largely by the division staff. After many meetings it was concluded that all phases of selection, whether individual plant or mass, were plant breeding. Varietal corn crosses were included. But final variety tests—whether the new variety

was bred in Minnesota or elsewhere—were considered to be crop production investigations and were not included in the plant breeding program. This decision removed from the breeder's hands the pleasure of conducting the final comparison of a new breeding production. However, some give and take were essential in cooperative research efforts. Eventually, about 1930, final varietal trials of individual crops became part of the project leader's work in breeding researches.

In these early days, in connection with project reports, each leader of a project was required to prorate his time in teaching and research. If connected with several projects, he had to determine the time given to each. This was necessary as funds for salaries came from several sources.

I was asked to join in a basic study relating to breeding of stem rust resistant spring wheats of high quality for bread making. The project of breeding wheat for stem rust resistance was originally started in 1908 by Freeman and E.W. Johnson of USDA. Disease resistance also had been considered by Hays in agronomy. Hays was an early leader in the United States who emphasized breeding new varieties. He made many outlines of research relating to basic principles of heredity with particular reference to plant and animal breeding. He was a leading early theorist who enjoyed outlining research programs. But he did not have the interest, or ability, or perhaps time to carry out research for their solution.

An early bulletin, *Wheat, Varieties, Breeding, Cultivation*, was published in 1899 by Hays and Boss. In 1901, USDA published a bulletin, *Plant Breeding*, written by Hays. In outlines for wheat breeding, one column was headed "Rust Resistance." Boss soon became a leader in farm management; except in the administrative field, he gave little subsequent intensive attention to plant breeding research and experimentation.

When I joined the Minnesota staff, breeding for stem rust resistance in wheat was being conducted by Freeman and Parker. I was asked to join in a basic study of the "Genetics of Stem Rust Resistance in Wheat," under the joint leadership of Hayes, Freeman, and Parker. This cooperative research was set up in project form in 1916. Although Freeman had many other duties he cooperated in planning the research program relating to breeding rust resistant spring wheats and the more basic study in genetics. The actual work of carrying out the latter study was left largely to Parker and myself.

At this early period, Parker was greatly interested in genetics in relation to plant breeding. He had an excellent grasp and appreciation of the individual characters of farm crops and their importance.

After careful consideration of the problem relating to the basic study, it was decided to make an intensive study of several crosses. Large numbers of plants were to be used in the early segregating generations of crosses of durum X vulgare and emmer X vulgare where the desirable bread wheat

variety Marquis usually was the vulgare parent. In previous studies Freeman and Parker grew many crosses but often less than 100 F_2 plants of each.

During summer 1916, Parker and I studied segregation of wheat characters under rust epidemic conditions. Two types of crosses—White Spring Emmer X Marquis and Kubanks, and Lumillo durum X Marquis—were used in studies of stem rust resistance. These were grown under artificially induced epidemics by methods then used in plant pathology. Breeding nurseries were grown in short rows of parents and hybrids with plants individually spaced in rows. Plots were surrounded on the edges by rows of susceptible wheats. Rows of susceptible wheats also were planted at intervals with the hybrid material.

A collection of rust spores was obtained by growing and inoculating seedling plants in the greenhouse, making a water suspension of spores, and spraying nurseries at heading time with this suspension. Inoculum for the F_2 and F_3 generations and parents consisted of a water suspension of rust spores from a single source. Barberry bushes were removed from the vicinity of the rust nursery to eliminate, as far as possible, lack of homogeneity of rust material. Before presenting results, a brief review will be made of studies of the stem rust organism that were conducted largely by plant pathologists.

Leaders in plant pathology and plant breeding felt it was important to study the stability and genetics of disease organisms. The value of such knowledge in relation to the breeding of disease resistant varieties of crop plants is self-evident.

Stakman (1914) summarized many of these researches and carried out, under Freeman's direction, an original research "A Study of Cereal Rusts: Physiological Races." The biological forms used were those identified previously as:

Puccinia graminis tritici (stem rust of wheat) on wheat and barley.

P. graminis hordei (stem rust of barley) on barley, wheat, and rye.

P. graminis secalis (stem rust of rye) on rye and barley.

P. graminis avenae (stem rust of oats) on oats.

The following quotation is from Stakman's bulletin: "Pole Evans has found that a hybrid wheat produced by crossing rust-immune and rust-susceptible wheats may rust quite badly and be capable of causing infection of the immune parent and a more severe attack of rust on the susceptible parent variety than rust from that variety itself will cause."

In Stakman's extensive researches, no results were obtained of this striking nature. In one study, however, he used Minnesota 163, a susceptible wheat, and Einkorn 2433, one of the most resistant *Triticums* to the wheat stem rust. After the wheat stem rust was cultured for 1 year on Einkorn,

with successive transfers at 3-week intervals, the rust “seemed to be much more virulent than the original rust had been.” Einkorn plants, when inoculated with rust that was cultured on Einkorn for a year, were compared with Einkorn plants inoculated with rust taken directly from wheat.

Both sources of rust gave 100 percent infection but the virulence differed. Rust pustules from Einkorn sources were larger and more numerous than those from wheat sources. Wheat plants were inoculated from rust cultured for a long time on Einkorn in comparison with wheat plants inoculated with rust from wheat. In this comparison, rust from wheat sources was more virulent.

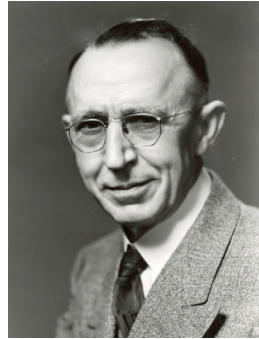
Stakman wrote, “The conclusion then is justified that by confining *Puccinia graminis tritici* to Einkorn for successive generations throughout a year or more the rust adapts itself somewhat to its new host and loses, at least to a slight degree, its power to infect its original host.” He went on to say, “It would no doubt require a very long period of time to fix this character in the plant to such a degree as to make it a new biological form.”

Stakman’s early interest in basic problems relating to disease resistance is evident. Stakman, like Freeman, has been recognized as a world leader in problems relating to agriculture, especially in the field of plant pathology.

Stakman and Piemeisel (1917a) discovered physiological races of stem rust. Stakman, Piemeisel, and Levine (1918) studied the stability of biological forms with particular attention to *secalis*, *tritici*, and *avenae* after culture for a period of time on many host plants. Such a change, as reported by Evans, whereby cultures of the disease organism on a susceptible hybrid of a cross between resistant X susceptible parents could then infect the resistant parent, was called bridging. The host plant, leading to a change in parasitic capabilities, was called a bridging host. Extensive studies were made without obtaining evidence of bridging. In relation to disease resistance, one conclusion was of basic importance to the breeder: “Biological forms seem to be roughly analogous to pure lines. Plus and minus fluctuations occur, but there is always a tendency to return to normal” (Stakman, Piemeisel, and Levine, 1918).

Physiological races of stem rust of wheat cannot be differentiated except by their manner of reaction on wheat species and varieties used as differential hosts. The number of different races that can be identified is greatly dependent upon the number of differential hosts available.

Stakman and Piemeisel (1917b) discovered a new biological form, which



Dr. E.M. Freeman, Chief of the Division of Plant Pathology and Botany, Dean of the College of Agriculture, Forestry and Home Economics.

they named *Puccinia graminis tritici-compact*, by means of differentiation of reaction on differential wheat hosts. Melchers and Parker (1918) found another strain to which Kanred and two other winter wheats were susceptible while these wheats remained immune to *Puccinia graminis tritici*, the normal form. Levine and Stakman (1918) found a third biological form of *Puccinia graminis tritici*.

The differentiation of races within *Puccinia graminis tritici*, on the basis of reaction to selected species, varieties, and strains of wheat, is still important research as a basis for disease resistance breeding. However, the problem has become more complex through the years; today more than 300 strains have been identified as physiological races. Within some physiological races, plus and minus deviations indicate the race is genetically not homozygous. Fortunately, in many cases a single genetic factor may condition reaction to many forms. Today, most disease organisms probably are composed of physiological races that can be differentiated by using differential hosts. Therefore, these physiological forms of disease organisms are not exactly analogous to pure lines of crop plants.

Stakman, Parker, and Piemeisel (1918) studied whether stem rust on wheat could change rapidly enough to interfere with breeding for rust resistance. They found no evidence that the culture of stem rust on hybrids, either on resistant or susceptible plants, appreciably affected the parasite; no evidence substantiated the idea of a bridging host. Rust resistance seemed to be a permanent hereditary character, not broken down by changes in the host or parasite.

An early study by Barrus (1911) with the bean anthracnose organism demonstrated physiological specialization. Barrus isolated two strains, *Alpha* and *Beta*, that differed only in parasitic ability. The value of such information was evident from the work of McRostie (1921). White Marrow was resistant to the *Alpha* strain but susceptible to the *Beta* strain. Robust was susceptible to *Alpha* but resistant to *Beta*. In the F_2 crosses of White Marrow X Robust, where only a single strain caused infection, ratios of 3 R: 1 S were obtained. But when both strains were present, a ratio of 9 R: 7 S occurred; on the average, 1 out of 16 bred true for resistance to both strains.

After discussing the stability of disease organisms, let us return to the early studies in Minnesota of "genetics of stem rust resistance in wheat."

Hayes, Parker, and Kurtzweil (1920) stated that, "There is every reason to hope that the stem rust problem can be solved by barberry eradication and the development of resistant wheat varieties." They reported studies of stem rust reaction in two types of crosses, varieties of *Triticum vulgare* with varieties of *T. durum* and *T. dicoccum*, respectively. They used the Marquis variety of bread wheat, then grown widely, as one parent.

The F_2 generation of these crosses was grown in 1917 under rust

epidemic conditions. The epidemic was induced by spraying with a water suspension of rust spores in a nursery of wheat surrounded by barberry bushes. The F_3 generation, produced by growing families of all F_2 plants that produced viable seed, was grown in 1918. The epidemic that year was produced with a known racial strain of the biological form, *Puccinia graminis tritici*, Erikss. and Henn. Parent varieties and other check varieties were included. Barberry bushes were removed from the vicinity before the wheat was planted.

Results of these studies need not be reported in great detail. Two types of reciprocal crosses were grown using as parent varieties: Marquis, susceptible to stem rust, in crosses with Kubanka and lumillo, durum, resistant to rust; and Marquis, in crosses with White Spring Emmer, resistant.

Classifications for wheat characters and rust reaction classes were made in F_2 and checked by F_3 breeding behavior. Reciprocal crosses gave similar results so data for the two generations were combined.

For parent varieties and F_1 crosses grown in 1918, with the F_3 generations, the following percentages of rust were obtained: Marquis, 40-70 percent; Kubanka, 20 percent; lumillo, 15 percent; Emmer, 0 percent; Marquis X Kubanka F_1 , 40-70 percent; Marquis X lumillo F_1 , 40 percent; and Marquis X Emmer F_1 , 10 percent. In crosses of resistant durums X susceptible Marquis the F_1 was susceptible. F_1 crosses of Marquis X Emmer were somewhat more resistant than durum varieties; Emmer, in these studies, showed no infection.

F_2 classifications for botanical type of head and rust reactions were checked in F_3 progenies. Results of these two generations of study were combined into one table representing F_2 characteristics and rust reaction, as determined by F_3 breeding behavior. Head types were determined by using those characters that usually are used to separate durum and common wheats. In durums, glumes are prominently and sharply keeled; in common wheats, outer glumes of spikelets are only slightly keeled.

In the F_1 there was an intermediate development of the keel. Condition of the collar also was used as an aid in final classification. In most durums the collar extends around the neck of the culm. In common bread wheats it extends only part way around. Emmer wheats in the segregating generations threshed like emmer and resembled the White Spring Emmer variety used as a parent. These may have included plants belonging in the *Triticum spelta* group.

Bearing in mind that these data are combined for both crosses of durum X Marquis and that both F_2 and F_3 data were used to classify the hybrids in groups, refer to Table 1 for a summary of results.

The segregation ratio here was 1 R : 9.7 S. This ratio indicated the

possibility of two recessive complementary genes that conditioned resistance. These genes were presumably responsible for conditioning rust resistance under field conditions to the biologic race of *Puccinia graminis tritici* used to produce the epidemic. Parents and a few selected F_3 lines were tested—through the kindness of M.N. Levine—in their seedling reaction to this same biologic form of rust. There was excellent agreement between seedling reaction and mature plant reaction under field conditions.

Later information bore out the suggested ratio of 1 R : 15 S. Deviation from this ratio in the durum X common crosses, Marquis X durum in this experiment, could have resulted from the wide cross of a 14= n variety of durum X 21= n Marquis variety because of chromosome behavior in crosses between species differing in chromosome numbers where partial sterility was involved in the segregating generations. This suggestion seems logical because later pure selections of the common wheat derivative selected from a F_3 common, resistant, vulgare plant of the cross of lumillo X Marquis was shown to carry two recessive factors for rust resistance in the mature plant stages to many physiologic races under field epidemic conditions.

Table 1. Botanical classification, on the basis of spike characteristics, and rust reaction of F_2 generation plants and F_3 progeny trials of crosses of Marquis X lumillo and Marquis X Kubanka.

Botanical Classification	Rust Reaction		
	Resistant	Susceptible	Total
Durum	24	109	133
Near Durum	45	267	317
Intermediate	22	322	344
Near Common	7	205	212
Common	2	126	128
Emmer	6	1	7
Total	106	1,030	1,141

Another interesting result was that durum X common crosses led to production of emmer and probably spelt types of wheat, in addition to pure breeding forms of durum and common wheats. Results were in agreement with studies of Vilmorin (1880, 1883) and Tschermak (1913).

It is pertinent to the present study that Peterson and Love (1940), in crosses of lumillo durum X various varieties of common wheat, obtained pure breeding common wheats that under field conditions were immune or resistant to a collection of races. However, they were susceptible to certain of these races in the seedling stage. Waddell (1940), in durum crosses in which lumillo was one parent and a susceptible variety was the other parent, found some lines that were susceptible to certain races in seedling stages but resistant to these same races in mature plant stages. This proved that lumillo from the genetic standpoint carries:

1. Genes for seedling resistance that also condition a similar reaction to the same physiologic race of rust in the mature plant stage.
2. Genes for "mature plant" resistance to races to which it is susceptible in seedling stages.

Waddell's study, apparently carried out largely at the Dominion Rust Research Laboratory in Winnipeg, was the basis of a thesis submitted in the Division of Plant Pathology and Botany, University of Minnesota. In "Acknowledgements," Waddell thanked Immer and Ausemus in the Division of Agronomy and Plant Genetics as well as Stakman in Plant Pathology and Botany.

These early studies of Stakman and others at Minnesota illustrated the desirability of obtaining further information on the stem rust organism before breeding rust resistant wheats. At this time World War I had a marked effect on agricultural research. Although the rust nursery was grown each year, cooperative work of USDA with the Minnesota Agricultural Experiment Station was curtailed. For several years Leonard Melander, who had charge of barberry eradication, was also in charge of making the rust epidemic. Later generation progenies of the F₃ plant 186-16-5 and two sister individual plant selections continued to be resistant under field conditions in the nursery to artificial epidemics of black stem rust of wheat. A sister selection, eventually named Marquillo, was also grown. It continued to be moderately resistant through the years until stem rust race 15b appeared.

It is pertinent to this story that the research of E.S. McFadden in South Dakota in breeding for rust resistance in wheat, was interrupted due to curtailment of USDA support in war time. Nevertheless, McFadden continued his studies on his own farm. He successfully completed the transfer of resistance to the bread wheats Hope and H44 from crosses of White Spring Emmer X Marquis.

A note regarding rust resistance in timothy by Hayes and Stakman (1919) is one of the early phases relating to breeding for disease resistance in Minnesota. Selections obtained from C.H. Myers at Cornell were compared with Minnesota selections under artificial epidemic conditions. A high percentage of the plants from the Cornell selections were rust resistant, although a few plants were susceptible. In Minnesota selections, only a few plants were resistant while most were highly susceptible. These results were obtained before 1921 when a formal project was formulated by Stakman and myself. At this time Stakman was head of the Section of Plant Pathology in the Division of Plant Pathology and Botany and I was of the Section of Plant Breeding, Division of Agronomy, Farm Management, and Plant Breeding.

Two other cooperative researches were completed before the organization in 1921 of the cooperative project for the breeding of disease

resistant varieties of farm crops. Stakman, Hayes, Aamodt, and Leach (1919) discussed "Controlling flax wilt by seed selection." They included brief review of early studies of breeding for disease resistance with particular reference to the pioneer work of Bolley (1901, 1903, 1909) at North Dakota.

The writers emphasized that, under wilt infestation conditions, lines and varieties were obtained immediately that bred true for resistance. In some cases, continuous selection through several progeny generations seemed to give a progressive change in resistance. Both mass and individual plant selection were studied, but individual plant selection gave more uniform progeny.

Tests of resistant selections isolated in North Dakota indicated segregation for wilt reaction. Whether these were due to mechanical mixtures or, as Bolley suggested, because varieties tended to lose their resistance when grown on nonwilt-sick soil was not determined.

Chapter 4

Research Studies 1921-36 Inclusive of Staff Members

Cooperative studies for breeding disease resistant varieties of farm crops were outlined in project form in 1921 by myself for the Division of Agronomy, Farm Management, and Plant Breeding and by Stakman for the Division of Plant Pathology and Botany. This project was reorganized about 1953.

In describing results from 1921 through 1952 the presentation will be subdivided into two periods; 1921 through 1936 and 1937 through 1952. Each period will be presented separately; one chapter devoted to studies of staff members and another to thesis researches and subsequent work of graduate students.

The Ph.D. thesis problems discussed will be primarily for students majoring in plant genetics. However, several students majoring in plant pathology who had research problems or subsequent research primarily concerned with breeding for disease resistance and several students majoring in agronomy who subsequently specialized in crop improvement will also be mentioned. A few M.S. plant genetics majors who made important contributions will be included also.

BASIC STUDIES IN PLANT PATHOLOGY

The most important type of plant pathological research of value to breeding disease resistant varieties during 1921-36 inclusive concerned the knowledge of physiological races. It soon became apparent that many physiological races were within a biologic form such as *Puccinia graminis tritici* E & H. Stakman and Levine (1922) reported that 37 physiological races had been identified. Reaction to individual races were studied in seedling stages of the host plant in the greenhouse. Reaction to a collection of races in the mature plant stages, from heading to maturity of the host plant, were carried out under artificially induced epidemic conditions in the field. Known races of rust were used to produce the epidemic.



The writer, Dr. H.K. Hayes, who was a member of the University of Minnesota staff from January 1, 1915 to June 30, 1952, and Chief of the Division of Agronomy and Plant Genetics 1928-52. Now Professor Emeritus.

A brief general summary of results of plant pathology researches in Canada and the United States is desirable. Although individual rust races apparently were highly stable, new forms were produced by crossing on the barberry. The reddish uredospores borne in uredia on wheat or the host plant reinfected the host plant throughout the season. During this stage each cell was binucleate or dicaryotic. The two haploid nuclei originated in distinct haploid uninucleate thalli on the barberry. Uredospores over-wintered in the south but not in the north.

As the wheat plant approached maturity, telia containing two-celled thick-walled spores developed and could overwinter on the wheat plant. When the telia spore germinated in the spring, true fusion of two haploid nuclei took place. Reduction division occurred before the haploid sporidia infected the barberry. Fusion of two haploid nuclei on the barberry led to production of dicaryotic aeciospores that were wind borne to the grass host or wheat plant.

Newton and Johnson (1932) in Canada described the production of physiologic races of *Puccinia graminis tritici* on barberry. For example, when race 9 was selfed (on the barberry) only race 9 was produced. When crossed with race 15, only race 9 resulted. But when this hybrid race 9 was selfed, races 9, 15, 57, and 85 were obtained. Race 53 when selfed produced 18 other races. These data showed how new races were produced by recombination of factors on barberry. This seems to be the main source of new physiologic races of stem rust of *Puccinia graminis tritici* E & H.

Stakman and Christensen (1926) and Christensen and Stakman (1926) demonstrated the existence of physiological races of *Ustilago zaeae*. They gave conclusive evidence that some forms mutated rapidly on culture media. This led to studies of the probable importance of physiologic races of corn smut in relation to breeding for smut resistance.

Intensive and extensive investigations were made by plant pathologists of life histories, reactions to environments, and host plants. This material was essential to the study of effects of disease organisms, their stability and mutability, and normal causes of heritable variations.

The knowledge that red rust spores of the organism responsible for stem rust of cereals can overwinter in the south, and that even after the elimination of the alternate host—the barberry bush for *Puccinia graminis tritici*—epidemics of stem rust can occur by the transfer of red rust spores by the wind from south and north, gave further impetus to breeding for

resistance. Although new rust races may arise by mutation, these do not seem more frequent than the small percentage of such mutations in higher plants.

Before there was much information regarding the mode of inheritance of resistance to pathogenic diseases, numerous observations and researches were reported regarding the probable causes of resistance, effects of environmental conditions, and stability and variability of disease reactions. Stakman's (1914) study of stem rust focused attention on many problems of stem rust reactions. These included stability of disease causing organisms, the effect of environmental conditions on the extent and degree of infection, and probable causes of resistance. He clearly found that reaction to rust in the seedling stages resulted from incompatibility between protoplasm of the wheat plant and rust mycelia after infection. This antibiosis has been classified as physiological.



Dr. E.C. Stakman, Chief of Division of Plant Pathology and Botany for many years, and who with the writer organized the cooperative project, "Breeding of Disease Resistant Varieties of Farm Crops," that was carried out as a cooperative project from 1921 to 1953 inclusive. Now Professor Emeritus.

Hursh (1924) and Hart (1929, 1931) studied probable causes of rust resistance. Hursh concluded that physiological resistance resulted from partial or complete lack of ability of a race of rust to cause severe infection in a particular variety of wheat, even though the rust entered the host tissue.

Hursh's studies focused primarily on the internal morphology of the wheat plant. He used a series of known resistant and susceptible varieties as determined from previous data. With these two variety groups resistant and susceptible, respectively, entrance of rust into the host plant was accomplished in both cases. On the susceptible group the rust organism grew vigorously. However, on the resistant group there was only a low to moderate development of rust that in many cases did not greatly inhibit the wheat host.

Hursh found wide differences in proportion of schlerenchyma to collenchyma in stems and other organs of different wheat varieties. In general, stem-rust resistant varieties such as Vernal emmer and Kota had heavier bands of schlerenchyma tissue surrounding the stem than did susceptible varieties such as Marquis and Little Club. This kind of resistance was called morphological.

Hart (1929, 1931) also compared resistant and susceptible varieties. Her 1931 research consisted of investigations relating both to morphological and functional causes of resistance. She corroborated the work of Hursh on morphological causes of resistance and gave added evidence. It seems

logical to accept morphological explanations as one probable cause of “mature plant” resistance.

Hart’s evidence was equally definite that time of opening of the stomata differed rather consistently between the two groups of wheats, resistant versus susceptible. She used the same varieties as studied by Hursh as well as several other resistant and susceptible varieties. Of special interest was the addition of Hope and Marquillo to the resistant group because of the importance of these two sources of “mature plant” resistance.

It was evident from previous studies, as corroborated by Hart, that germ tubes of rusts enter through the stomata. This fact led to intensive comparisons of the time of opening, extent of opening, and length of time that stomata remained open for wheat varieties belonging to resistant and susceptible groups. Susceptible varieties were characterized by opening of stomata shortly after sunrise; the stomata remained open throughout the day. With the resistant group, the stomata opened slowly after sunrise and closed relatively early in the day. This difference Hart found definite and consistent in the varieties studied. This led to the postulation of a third cause of resistance called functional.

SOME STUDIES IN PLANT GENETICS

An early study of the inheritance of spike and kernel characters of crosses between varieties of *Triticum vulgare* is of interest in relation to wheat breeding (Hayes, 1923).

In crosses of Preston, a bearded variety and Marquis, an awnless variety, the F_1 had longer tip awns than Marquis. In the F_2 , there was a ratio of 1:2:1; that is a ratio of 1 like each of the two parent awn types to 2 of the F_1 type. Many lines, each from an individual plant of the preceding generation, were grown in generations F_3 to F_5 , inclusive.

Length of seed per plant was computed by first selecting 10 average seeds from a plant and then measuring their length, using vernier calipers. This method’s reliability was determined by independently repeating the process and observing any deviations. It was learned by studying later generations, such as F_5 , that practically all gradations in kernel length between that of the two parents Preston and Marquis could be obtained that seem to be homozygous or nearly so. Moreover, the presence of the awn markedly affected length of kernel, plumpness of kernel, and kernel weight. In other words, bearded spike plants usually produced longer, plumper, and higher weight kernels than did awnless spike plants.

A mixture of soft and corneous endosperm in the kernel, called yellow-berry, was found to result from both inheritance and environment. Such variation in kernels of a homozygous type could result solely from environmental causes. With comparable material of the cross of Preston,

bearded X Marquis, awnless, the homozygous bearded lines in 1918 and 1920 favorable seasons, yielded an average of 7 and 8 percent more, respectively, than homozygous awnless families. In the unfavorable growing season of 1919, bearded plants excelled the awnless in yield by nearly 17 percent.

Hayes and Aamodt (1927) studied winter hardiness and growth habit in crosses of Marquis with Minhardi and Minturki winter wheats. These winter wheat varieties were two of the more winter hardy selections produced from crosses of the very winter hardy variety Odessa with the Turkey winter wheat variety. The crosses that produced Minhardi and Minturki were made in 1902. Yield trials of these selections were made and seed of Minturki was increased and distributed to seed growers.

These two varieties were described in considerable detail by Hayes and Garber (1919). Minturki, Minn 1507, was not only very winter hardy but also superior in grain texture and milling and baking quality to its parent Odessa. However, it was not equal to spring wheat variety Marquis in grain texture and milling and baking quality.

F₁ crosses of Marquis X Minturki and Minhardi when planted in the spring headed as early as Marquis; there was complete dominance of the spring wheat habit. In this case, all 12 plants from fall sown seed from each cross were winter killed. Minturki often showed considerable resistance under field conditions to rust attacks from *Puccinia graminis tritici* although not the equal in this respect to that of Marquillo or Thatcher.

To obtain comparable hardiness index values the F₂ generations of both crosses were grown in large, individually spaced plant plots of about 1,000 plants each. Individual plants were placed in three classes: strong, weak showing some injury, and dead. A hardiness index value was calculated by multiplying the number of strong plants by 4, the weak by 2, and the dead by 0. Results were placed on an index value with 100 as a perfect score. The hardiness index of F₃ and F₄ lines, each the progeny of a single plant, was determined from an average of 4 replications of 25 plants each.

In these studies hardiness indices of Minhardi and Minturki, where numerous row trials were grown, ranged from 45 to 99, that of F₂ from 29 to 49, and of F₃ and F₄ generation lines from 0 like Marquis to the higher values obtained for the winter wheat parents.

One hundred and five Marquis X Minhardi F₂ plants had sufficient seed to plant both in fall and spring. These were classified for growth habit and hardiness with the following average results:

<u>Growth Habit</u>	<u>Hardiness Index</u>
Homozygous, winter	46.5
Heterozygous, winter	31.7
Heterozygous, intermediate	15.1
Heterozygous, spring	11.1
Homozygous, spring	4.1
Marquis	0.0
Minhardi	70.3

Both growth habit and hardiness showed wide segregation; results were explained on a multiple factor basis. In F_4 lines, sown both in fall and spring, average differences in the hardiness index of the homozygous winter for growth habit and the homozygous for spring habit was not great. However, all of the homozygous lines for spring habit of growth and a rather high winter hardiness index headed later than the Marquis parent.

Using wheat varieties and hybrids developed by breeding for resistance to rust and other diseases, Hayes, Immer, and Bailey (1929) studied milling and baking qualities. They were particularly concerned with inheritance of quality. These varieties and strains were grown in yield trials at University Farm and at other Minnesota Agricultural Experiment Stations. Milling and baking data were obtained in Bailey's laboratory in the Division of Agricultural Biochemistry.

Strains used in the studies were selected for grain of desirable agronomic type. Therefore, strains of undesirable quality of grain were eliminated before the milling and baking tests were conducted.

There was a general tendency for positive interannual correlations between results of different seasons for protein content, loaf volume, flour percentage, and color and texture of the cut loaves after baking. There also was a tendency for positive correlations between loaf volume, color score of loaf, and texture score of loaf, but these relationships were not consistent under all conditions.

Milling and baking studies reported by Ausemus et al. (1938) were continuations of studies of the inheritance of milling and baking qualities and were completed shortly after 1936. The material consisted largely of samples taken from border rows of three-row plots of spring wheat grown at four state experiment stations: University Farm, Waseca, Morris, and Crookston. Similar samples of winter wheat were also grown at University Farm and Waseca. Some data were included from 1/40 acre plots. Wheat varieties and strains consisted of standard check varieties, parents, and hybrids that were under trial for disease resistance comparisons and agronomic desirability. Strains distinctly undesirable for milling and baking quality were usually discarded after 2 years consecutive trial.

Both interannual and interstational correlation coefficients were calculated (see Table 2).

All relationships were relatively small, except color score of loaf and test weight. Total flour, texture, score of loaf and loaf volume were correlated sufficiently to be of importance.

Average values for interstational correlations were all significant. The largest average r value was 0.49 for color score of loaf; the lowest was 0.29 for loaf volume and adsorption.

Table 2. Average values for interannual correlations*

Characters Correlated	Interannual correlation coefficients		
	Rod Rows		1/40-Acre Plots
	Spring	Winter	Spring
Test weight	0.33	0.52	0.46
Total flour	0.37	0.20	0.40
Crude protein	<u>0.20</u>	<u>0.13</u>	0.54
Adsorption	<u>0.03</u>	0.13	0.15
Loaf volume	0.32	0.39	0.39
Color score	0.75	0.74	0.55
Texture score	<u>0.25</u>	0.37	Crumb texture 0.27
Grain score	<u>0.19</u>	<u>-0.06</u>	Crumb grain 0.12

*Nonsignificant values are underscored.

Protein and loaf volume were correlated in all three trials: spring wheat rod rows, winter wheat rod rows, and 1/40 acre plots. Values of r ranged from 0.16 to 0.34. In this respect, results differed from those reported by Hayes et al. (1929) in previous studies.

There was a consistent and important relationship, on the average, for the intercharacter correlation values between loaf volume, loaf color score, leaf texture score, and loaf grain score. In the studies here reported, the chief lack in Marquillo from a milling and baking standpoint was color score. Marquillo was a new variety selected in the cooperative Minnesota breeding program from a wide cross of Marquis X Iumillo durum.

COOPERATIVE STUDIES OF DISEASE RESISTANCE

Standard procedures for determination of resistance versus susceptibility to rusts in small grains were developed for seedling reaction in studies of physiological races and of disease reaction inheritance. Studies of reaction under field conditions, from heading to maturity, were also carried out and compared with seedling reaction. In many cases, field reaction was taken in percentages where low percentages of leaf and other infected were considered as a resistant reaction. Although many variations in types of reaction were considered, and some varieties seemed more tolerant than others to rust infections, excellent agreement generally existed between extent of infection under field conditions and yielding ability.

Knowledge of the following types of reaction in the seedling stages is essential to an appreciation of results obtained in the various reported researches:

Resistant Group (as seedlings):

0 = immune

0; = immune, with no rust pustules but with small flecks of light green or colorless areas

- 1 = very small pustules, often surrounded by necrotic areas
 2 = somewhat larger pustules, often with necrosis
 X⁻ = mostly small pustules, with a few larger ones with or without necrosis

Susceptible Group (as seedlings):

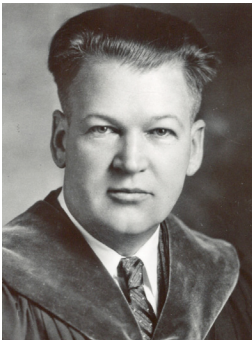
- 3 = moderately sized numerous pustules, with or without necrosis
 4 = large confluent pustules
 X⁺ = mostly large pustules with a mixture of a few smaller ones

Varieties, strains, or hybrids placed in the resistant group, by seedling reaction to a known race of rust, generally are resistant from heading to maturity to the same rust race under field conditions. A strain of wheat classified as susceptible in the seedling stage to a race of rust carries genes for susceptibility to that race in the mature plant stages.

However, some wheat varieties that are susceptible to a particular race as seedlings may have a resistance to all or nearly all races in the mature plant stages from heading to maturity.

In Wheat

Waldron and Clark (1919) at North Dakota discovered a *Triticum vulgare* variety that they named Kota. It was more stem rust resistant under field conditions than any other known variety of common wheat. However, Kota did not yield equal to Marquis and lacked strength of straw under humid conditions.



Dr. O.S. Aamodt completed work for the Ph.D. degree with a major in Plant Genetics and minor in Plant Pathology. For many years he represented the U.S. Department of Agriculture with headquarters at U. Farm, St. Paul Campus and was in direct charge of the cooperative wheat breeding nursery.

Hayes and Aamodt (1923) studied crosses of Kota by Marquis to determine the genetic basis for Kota's rust resistance. They also studied if reaction to individual races of rust in the greenhouse could be used to predict reaction to a collection of races under normal field growing conditions. Eleven physiologic forms were made available by Levine who was cooperating with Stakman in studies of physiological races. Race 19, to which Marquis gave reactions 1 and 2 while Kota reacted to give 3 type pustules in seedling studies in the greenhouse, and Race 27, to which Marquis gave 2+ reactions and Kota gave the immune or 0 reaction, were selected for the studies. From a total of 372 F₃ lines studied, 3 lines were as resistant to race 19 as Marquis and were immune to form 27 like the Kota parent.

A field epidemic was induced using 11 races,

1, 3, 9, 17, 18, 19, 21, 27, 29, 32 and 34. In one group of 206 randomly selected F_3 lines, 28 lines were as resistant as Kota. The study of seedling reaction to races 19 and 27 did not prove to be a satisfactory means of isolating F_3 or later generation lines that had the field resistance of Kota to the 11 races used in the study.

Harrington and Aamodt (1923) in crosses of durum wheat varieties studied seed color and reaction to physiologic races. Mindum, with amber colored seed, was immune to race 1 and susceptible, with X+ or 4 types of infection, to race 34, while Pentad with red seed was susceptible to race 1, X- to 4 type infection, and resistant, 0 to X- infection, to race 34. It is noted that the two parent durum varieties reacted in a reciprocal manner to the two rust races.

The Mindum durum variety was selected originally at University Farm from an individual plant found as a mixture in common spring wheat. It appeared desirable and was named Hedge Row. It is one of several varieties of wheat grown in centgener plots since the early 1900's. It was later grown in yield trials, renamed Mindum, and released by the Minnesota Station. At the time of its release in about 1917 it was known to excel in macaroni quality.

In the Pentad X Mindum cross there was evidence of a single main pair of allelic factors for reaction to physiologic race 1 and some evidence that a separate pair of allelic factors conditioned reaction to race 34. Although no definite conclusion was reached for reaction to race 34, six out of 110 F_3 lines were highly resistant to both races and of these six lines two were homozygous for white seed color.

It is evident that in crosses of Mindum X Pentad that it is relatively easy to combine amber colored seed (white) with resistance to two races to which the parent varieties reacted in a reciprocal manner.

Stakman and Hayes from Minnesota, Bolley from North Dakota, and Dickson from Wisconsin attended by invitation the Second Cereal Rust Conference, held at Winnipeg, Manitoba in September 1924, under the joint auspices of the Federal Department of Agriculture and the Research Council of Canada (see Anonymous, 1924). Among the leaders from Canada were Dr. R. Newton, Biochemist, Dr. D.L. Bailey, and Dr. G.R. Bisby, Plant Pathologists, and Dr. W.T.G. Weiner and Dr. J.B. Harrington, Plant Geneticists. All of these Canadian research leaders had received a part of their graduate training in Minnesota. The research leaders with Dr. E.C. Stakman as Chairman, together with Dr.'s W.P. Fraser, H.T. Gusson, and W.P. Thompson, drew up a brief report of the phases of the cereal rust problem that they thought should be studied cooperatively by investigators in Canada and the United States. These consisted of (1) epidemiology studies, (2) biological specialization, (3) physiological and ecological studies, and (4)

The delegation attending the Second Cereal Rust Conference held in September 1924 at Winnipeg, Manitoba, Canada, under the joint auspices of the Federal Department of Agriculture and the Research Council of Canada.



breeding for rust resistance.

The latter phase included genetical, cytological and histological studies, field trials of hybrids for disease observations, yield trials, and milling and baking studies.

It was apparent that the type of cooperation desired, and approved by the conference, should consist of a free exchange of materials and ideas with the hope of obtaining adequate support for each research leader to conduct investigations as he wished. Laboratory, field and greenhouse facilities as needed would be provided.

Aamodt (1927) at a Plant Breeding Symposium of the American Society of Agronomy held in November, 1926 discussed, "Breeding Wheat for Resistance to Physiologic Forms of Stem Rust." This discussion included the combined viewpoints of Aamodt, Stakman, and myself. Aamodt had completed graduate work with a major in plant genetics and a minor in plant pathology at Minnesota. He was an associate pathologist, Office of Cereal Crops and Diseases, USDA. His headquarters was at Minnesota in the Agronomy division where he cooperated with Stakman and myself in the production of disease resistant varieties of spring and winter wheat.



Aamodt in his summary referred to the papers of Hayes, Parker, and Kurtzweil (1920), Hayes and Stakman (1922), and Hayes, Stakman, and Aamodt (1925). He was able to show that the mature plant resistance from heading to maturity, to a collection of races of rust that Hayes and others (1920) transferred from *Iumillo durum* to a common wheat variety, was dependent upon the interaction of two recessive genes in the homozygous recessive condition. He showed also that these appeared to be independent in inheritance from a dominant gene obtained originally from Kanred winter wheat that conditioned resistance of Kanred to 11 races of rust, both in seedling stages and under field conditions.

Aamodt also presented an outline of a later step in the cooperative program to combine the rust resistance of H44, obtained by McFadden (1930) from Vernal emmer, by crossing the better Minnesota selections from the Minnesota double crosses with H44 and studying reaction in seedling and mature plant stages to all known races.

So at this early date the more important sources and types of resistance to black stem rust appeared to be:

1. A combination of mature-plant resistance, found in Marquillo and

two sister selections from a cross of lumillo, durum X Marquis dependent on 2 pairs of recessive homozygous factors, with physiological resistance to 11 races dependent upon a single dominant pair of factors inherited from Kanred winter wheat. Numerous selections, called Double Crosses, of this origin were tested for many years and one of these was named Thatcher and was grown very widely.

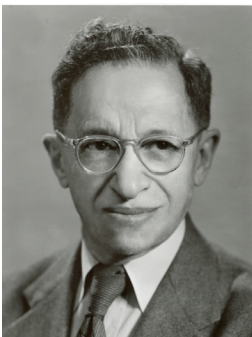
2. Hope and H44, as parent varieties, were obtained by McFadden in South Dakota from crosses of Emmer X Marquis that carry genes for mature plant resistance to a collection of races and also genes for physiologic resistance to some races.

Aamodt also summarized various types of evidence regarding mature plant resistance. The evidence was conclusive that certain wheat varieties such as Marquillo, certain of its derivatives such as Thatcher, and sister selections referred to as double crosses, were resistant in the stages from heading to maturity to a collection of physiologic races, to some races of which the wheat varieties in question were completely susceptible in the seedling stages.

Correlated reaction in wheat was studied by Hayes, Ausemus, Stakman, and Bamberg (1936) to stem rust, leaf rust, bunt and black chaff in F_3 progenies from random selections of F_2 plants.

Epidemics of stem rust, leaf rust and bunt were created artificially while black chaff developed naturally in the rust nurseries. Bunt was studied in a separate nursery and the epidemic was induced by dusting the seed with bunt spores just before seeding.

The crosses studied were between H44 and H35, selected by McFadden, which are susceptible to black chaff but resistant to stem rust, leaf rust and bunt with Double Cross II-21-28, that has the resistance of Kanred to 11 individual rust races of stem rust and field resistance to a collection of races, and with Kota X Marquis. II-19-167, that reacts similarly to II-21-28 in field reaction. Both II-21-28 and II-19-167 were resistant to black chaff. Parents and random F_3 lines were studied.



Dr. M.N. Levine, Research Leader, U.S.D.A. with headquarters in Plant Pathology, University of Minnesota, for many years. Cooperator in Disease Resistance Problems, particularly stem rust of wheat.

The mature-plant type of stem rust resistance of the H44 parent appeared to be due to a single factor difference and dependent upon factors not allelic to those determining moderate resistance of the mature type found in Double Cross II-21-28 or Kota X Marquis II-19-167.

Resistant types were obtained in F_3 for each of all four diseases although the number of factor pairs was not determined. Independence of

reaction was indicated for stem rust and bunt, leaf rust and bunt, leaf rust and black chaff and black chaff and bunt. Stem and leaf rust resistance were linked in inheritance and stem rust resistance and black chaff susceptibility were linked. However, there seemed to be a good probability that resistance to all diseases studied could be combined in a single variety.

Various studies have been carried out in replicated rod-row yield trials of small grains to determine by means of correlation coefficients the importance of mode of reaction to various diseases, together with agronomic and botanical character differences in their relation to yielding ability. Studies conducted were made during seasons in which the growing conditions were favorable and the material in the trials seemed of greatest interest. They included rod-row yield trials of hard red spring wheat and winter wheats at Waseca by Hayes, Aamodt and Stevenson (1927), rod-row trials of oats by Immer and Stevenson (1928) and rod-row trials of hard red spring wheat at Morris by Bridgford and Hayes (1931).

The results were analyzed by partial and multiple correlation coefficients and where desirable tests were made for linearity of regression. The information obtained had a very direct relation to a determination of the relative importance of various characters and their influence on yielding ability. All three studies referred to will be discussed together although the study of Immer and Stevenson was with strains of oats. The studies made were similar to earlier studies of Goulden and Elders (1926) in Canada.

For the rod-row trials at Waseca (Hayes, Aamodt and Stevenson) the characters studied included date of heading, leaf rust reaction, stem rust reaction, height of plant, bearded or awnless spikes, percentage plumpness of grain, winter injury in the winter wheat rod-rows, and yield. In these and other studies there were three replications and data were averaged for the 3 plots.

The spring wheat rod-rows included 6 selections of Marquis X Preston or Marquis X Bluestem that were susceptible to stem rust but not severely injured by leaf rust, 24 selections of Kota crosses that were rather resistant to stem rust and that differed in reaction to leaf rust, 15 selections of Marquis X Kanred that varied in reaction to both stem and leaf rust and several parent check varieties.

The bearded strains, on the average, excelled the awnless in percentage plumpness of grain in both spring and winter wheat. Simple product moment r values for percentage plumpness of grain in spring wheat was correlated with yield to the extent of $+0.51$ while in the winter wheat trials the r value was $+0.62$.

The multiple R coefficient for yield in relation to the five variables mentioned was $+0.65$ in spring wheat and when winter injury was included with the same five values in winter wheat the R coefficient became $.90$. Both

of these R values were significant at the .01% point.

In the studies of Immer and Stevenson with oats where 280 strains were grown, plumpness of grain, date heading, crown rust reaction, height of plant, and lodging each showed a direct relation with yield. A multiple R value of .82 for the five character expressions and yield was obtained. As with wheat, plumpness of grain was rather closely associated with yield.

In the studies of rod row trials of hard red spring wheat, at Morris by Bridgford and Hayes, 61 strains were grown with the data being taken in 1929 which was a satisfactory year for spring wheat at this station. A rather extensive list of characters was studied including plumpness of grain, weight of 1,000 kernels, heads per row and kernels per spike that make up yield, height of plant, date heading, leaf rust infection, stem rust infection and yield.

The material included selections of Kota crosses that excelled in kernels per spike and lacked stooling ability: Minnesota Double Crosses, that were selected from (Marquis X Kanred) (Marquis X Lumillo durum) that in general excelled in stooling ability, i.e., heads per row in these studies, and standard parents. In this study again there was a very direct positive relationship between percentage plumpness of grain and yielding ability. The multiple R value for yield with the plumpness, weight of 1,000 kernels, date of heading, height of plant, number of heads per row and kernels per spike was $.81 \pm .05$.

These studies seemed to the writer to have much the same purpose as those of Grafius who has emphasized the desirability of measuring yield components and planning a breeding approach through hybridization methods that are based upon the combination of those relationships that make up total yield.

Powers (1936) used statistical methods to determine, in F_1 , F_2 and F_3 generations, the relation in barley of genes for black vs. white glumes, *deficiens* vs. *vulgare* spikes, and normal vs. brachytic type of growth, to yield of seed and other similar characters of a quantitative nature. The genes for brachytic and *deficiens* type of spike were of the nature of physiologic defectives and affected markedly such quantitative characters as yield, while those for color of glumes seemed to be of the non-defective type. More favorable environmental conditions for growth led to a wider range in performance of segregating generations than the same comparisons made under less favorable conditions.

The most important accomplishment resulting from breeding studies with spring wheat, during the period from 1921 through 1936 inclusive, was the introduction of Thatcher wheat in 1934. (See Hayes, Ausemus, Stakman, Bailey, Wilson, Bamberg, Markeley, Crim and Levine (1936).)

In the Foreword of this bulletin on Thatcher wheat, Director W.C. Coffey, Minnesota Agricultural Experiment Station, and Dr. M.A. McCall, in charge of the Division of Cereal Crops and Diseases, U.S. Department of Agriculture, wrote in part,

“Thatcher is, in a real sense, a cooperative institutional product, involving not only a long period of investigation supported by state and federal appropriations but also numerous investigators who have each contributed to the final result.”

“Thatcher wheat is a great step forward in spring wheat breeding, but, because it is a biological product, it is by no means the final solution of the important problem of black stem rust of wheat.”

Thatcher wheat was produced in Minnesota from a wide cross. One parent was a selection from Marquis X Kanred that carried the immunity of Kanred winter wheat to 11 physiological races of stem rust. This parent also bred true for spring habit of growth and also appeared to excel in vigor of growth and performance. The other parent was a selection from lumillo, durum X Marquis that carried the chromosome number of vulgare wheats, $n=21$, and that was moderately resistant as far as tested from heading to maturity under field conditions to all known physiological races of rust then prevalent. Thatcher selected from crosses of these two parents, excelled in many agronomic characters and in milling and baking qualities.

Unfortunately Thatcher proved rather susceptible to leaf rust and perhaps for this reason did not prove especially desirable in Minnesota after subsequent tests. In 1949, many years after Thatcher was released, Bayles and Clark (1954) reported that Thatcher was grown on 3,370,823 acres in the spring wheat area of the United States and on 15,336,900 acres in the Prairie Provinces of Canada. In 1962 Canadian reports stated that Thatcher was grown on 62.2 percent of the acreage in Alberta, 49.1 percent in Saskatchewan and on 2.1 percent in Manitoba.

In Oats

The studies of Garber (1922) as a part of the Ph.D. thesis work were completed at West Virginia although the data were taken when he was an Assistant Professor at Minnesota in the Division of Agronomy and Farm Management. They will be reported in greater detail in discussions of graduate student thesis problems.

Open-panicked, rust resistant high yielding strains, selected by the pedigree method from Garber's crosses, were described by Hayes (1932). Anthony, obtained from the cross of Victory X White Russian, and Minrus, from the cross of Minota X White Russian were rather extensively grown in Minnesota and nearby states.

Selections from crosses, Anthony X White Russian, II-18-2 (Anthony)

and from Minota X White Russian, II-18-4 and II-18-37, that bred true for open panicle, and stem rust resistance, and that gave good yields, were crossed with Black Mesdag, that was rust susceptible but resistant to smut caused by both *Ustilago avenae* and *Ustilago levis*. In certain of these crosses correlated studies were made (Hayes, Griffee, Stevenson and Lunden, 1928) of reaction to stem rust and smuts and to other differential characters.

The F_1 generation crosses were grown in the Washington greenhouse and harvested under the direction of T.R. Stanton, agronomist in charge of oat investigations. This permitted the cross and F_1 generation to be produced the same year.

F_3 progenies of F_2 plants were grown in Minnesota and segregation studied for color of glume, rust reaction, awn development and pubescence on rachilla. Random selections were made of approximately equal numbers of F_2 plants in each of 4 groups, black glumes resistant to rust, black glumes susceptible to rust, white glumes, resistant and white glumes, susceptible. Each such F_2 plant became the parent of an F_3 line and 75 seeds were inoculated in an envelope with about a teaspoonful of smut spores. Lines which were susceptible to smut were not tested again but bunt free lines were again tested in F_4 by harvesting the F_3 in bulk for growing F_4 progenies.

The data will not be discussed in detail. Black vs. white glumes and rust resistance vs. susceptibility segregated in 3:1 ratios. Two crosses II-18-2 and II-18-4 X Black Mesdag approximated a ratio of few hairs on the rachilla of the second spikelet to many hairs of 3:1 while in the cross of II-18-37 X Black Mesdag there was a greater proportion of few-haired segregates than expected on a 3:1 basis. The Black Mesdag parent was heavily awned and the other parents had few weak awns. In the F_2 of II-18-37 X Black Mesdag 66 F_2 plants were awnless while 378 were heavily awned. As far as tested, weak awned types bred true for the awnless character but the strong awned F_2 plants showed various types of breeding behavior in F_3 with no clear evidence of the number of genes involved.

Of a total of 378 lines that were studied for smut reaction there were 47 lines that produced no smut under infection conditions as tested from F_3 to F_5 . Some lines appeared to be highly resistant with only a small percentage of infection. Other lines were somewhat susceptible under the conditions of the test. The suggestion was made that the Black Mesdag parent carried two genes for resistance, I for immunity epistatic to R with R conditioning a high degree of smut resistance.

All possible associations were studied for segregation of glume color, hairs on rachilla, awn development, reaction to stem rust and to smuts. In rust comparisons independence of inheritance was evident although there was a slight tendency for loose linkage between genetic factors for hairs on rachilla and for glume color although the linkage, if any, was very loose.

In Barley

Christensen (1922) made a comprehensive study of the parasitic capabilities of *Helminthosporium sativum*. He found that "leaf spot, root rot, foot rot and seedling blight of wheat, barley, rye and numerous grasses" result from attacks of this organism. Its reaction on the heads, foliage and roots of barley have been termed spot blotch.

Degrees of infection were greatly modified by environmental conditions. The tests for reaction were made by growing a 5 foot row, planted with 5 grams of seed, on infested soil. The varieties, and selections studied, at about heading time were sprayed, at intervals of a day or two, by spore suspensions of *H. sativum*, three to five sprayings being made. The sprayings were carried out largely by Christensen.

The degrees of infection taken separately on three parts of the plants, i.e., the spike, culm and leaves together and root were denoted by figures, trace = 10, light- = 9, - - - medium - heavy + = 1, were added together. Yield as a rule was determined from replicated rod-row trials.

The studies of Hayes, Stakman, Griffee and Christensen (1923) were reported in two parts. Part I Varietal Resistance, Part II, Inheritance studies in a cross between Lion and Manchuria.

The writer has a vivid picture of these studies. Often all four worked together and there were many arguments regarding classification for spot blotch reaction and other characters. This close association of workers often has proven very desirable as a means of becoming interested to a greater extent in cooperative research.

Thirty-nine purified smooth awn selections were under yield trials during 1921-22, and were also tested in 5-foot rows under an artificially created epidemic for spot blotch reaction for each of the 2 years. Average spot blotch reaction was correlated with average yield. As the smooth awn lines were selected from crosses of Lion, that is rather susceptible to spot blotch, with Manchuria, that is usually resistant, the unselected material was excellent for the studies made. Results are presented in the form of a correlation 'surface'.

		Average Yield					
		42	45	48	51	54	Total
Spot blotch reaction	12	1					1
	15	1	3	1		1	6
	18	2	1	4	2		9
	21		2	8	6	2	18
	24		1	2		2	5
		4	7	15	8	5	39

$r = .46 \pm .09$

As the infection in the rod row yield trials was a natural one and the spot blotch classification made in a special plot where a row of each of the 39 selections were grown there seems to be definite evidence of the importance of the spot blotch disease.

Also a correlation coefficient was calculated for the average *Helminthosporium* reaction under artificial infection for two years 1921-22 and average yield in replicated row trials for a 3-year period 1920-22 for 17 strains of 6-rowed barleys. The r value in this case was $.58 \pm .11$.

Studies were made also of the degrees of infection of different strains in separate years, and for spike, foliage and root infection. The following summary presents the more valuable results.

These calculated values led to the conclusion that the average reaction of spike, foliage and root was a relatively desirable method of classifying varieties and strains for spot blotch reaction. In 1922 when conditions were favorable there was rather excellent association, under artificial infection conditions, of degrees of infection in the three separate areas for the 70 strains under test.

Characters correlated	Number strains	Years of study	r values
Degrees of infection	49	1920-1921	$.50 \pm .07$
Degrees of infection	67	1921-1922	$.62 \pm .05$
Spike infection	63	1921-1922	$.49 \pm .07$
Root infection	66	1921-1922	$.30 \pm 0.8$
Foliage infection	65	1921-1922	$.54 \pm .06$
Spike infection with root infection	70	1922	$.71 \pm .04$
Spike infection with foliage infection	70	1922	$.71 \pm .04$
Root infection with foliage infection	70	1922	$.78 \pm .03$

Studies of inheritance of awn condition, glume color and spot blotch reaction were made in the cross of Lion X Manchuria. Rough vs. smooth awn and black vs. white glume color segregated on a single factor difference basis.

A random sample of 124 F_3 lines of the cross were studied for spot blotch reaction. Lines that appeared as resistant as Manchuria and as susceptible as Lion were retested in F_4 and on these bases 8 lines were selected out of the 124 that were as susceptible as Lion and 6 as resistant as Manchuria. The correlation coefficient for F_3 and F_4 of 36 lines, for spot blotch reaction, under artificial infection was only $.26 \pm .11$. These same 36 lines were tested for root infection in greenhouse trials. The r values for 1922 field reaction with root infection in the greenhouse was $.43 \pm .09$. The spot blotch reaction segregations required more than a single factor difference to explain inheritance.

A greater proportion of resistant F_3 and F_4 lines had rough awns and

colorless glumes than susceptible lines; however, within the 124 lines grown, all combinations of resistance and susceptibility, smooth and rough awn and black and white glume color were obtained.

Although smooth awn is recessive to rough, there were different degrees of smooth awn ranging from as smooth as the Lion parent to a much greater part of the awn with teeth. Intermediate smooth of different grades bred true in F_3 in several cases. These were explained as the result of modifying factors inherited from the rough awn Manchuria parent.

Powers and Hines (1933) studied reaction to stem rust *Puccinia graminis tritici* in crosses of Peatland, the resistant parent with Glabron and Minn. 462, the two latter being smooth awn selections from Manchuria X Lion. These research workers studied inheritance in barley crosses of reaction to forms 17, 38 and 49 of *Puccinia graminis tritici* under an artificial epidemic in the field. Resistance was dominant to susceptibility and a single factor pair (Tt) was involved. Rust reaction was inherited independently of the factor pair (Rr) for rough vs. smooth awns.

In Flax

H.D. Barker (1923), Research Assistant in Plant Pathology, made, "A Study of Wilt Resistance in Flax," under the supervision of E.C. Stakman and the writer, as one phase of cooperative investigations of Plant Pathology and Agronomy.

The purposes of the study included the determination of whether the results, "could best be explained by the pure line theory," and whether resistance was due to "a peculiar quality possessed only by certain varieties." The research also had as one purpose to determine whether resistance, as expressed when a resistant variety was grown on wilt-infested soil, was gradually lost when the resistant variety was grown on wilt-free soil as Bolley believed to be the case.

It was very evident that time of planting greatly affected the expression of resistance. Later planted resistant selections on wilt infested soil were much more severely injured by wilt than when the same selections were planted earlier on the same soil.

Under wilt infection conditions highly resistant plants bred true in some cases for high resistance. Moderately resistant plants similarly selected led to the production of varieties that were moderately resistant. It was concluded also as a result of extensive studies that,

"Constant association with the disease does not change the degree of resistance of selected genotypes."

"A wilt-resistant strain does not lose its resistance when grown on clean soil."

"There is some evidence that there are several physiologic races of

Fusarium lini," Bolley.

These results of Barker have been substantiated by further research studies and the investigations of Barker were of basic importance in the continued breeding studies of wilt-resistant varieties that excelled also in other characters.

Dr. Barker has retired. At the time of retirement he was a research leader in cotton investigations, U.S.D.A.

In Corn

Hayes, Stakman, Griffee and Christensen (1924) and Garber and Quisenberry (1925) found under artificial infection conditions in field smut plots that smut infection* of different inbred lines of corn often was localized to certain parts of the plant such as below the ear, ear infection, and tassel infection. Hayes, Stakman, Griffee, and Christensen (1924) concluded that smut infection of F_1 crosses was intermediate between that of the parents and that F_1 crosses of resistant lines were as resistant, or more so, than their inbred parents. It proved to be relatively easy to isolate resistant lines from various sources. Immer and Christensen (1925) presented further data that corroborated that of previous studies but were unable to determine how many genes were concerned with smut reaction. In relation to studies of smut resistance it may be worth mentioning that Jones (1918) made one of the early studies of smut reaction in selfed lines.

Christensen and Johnson (1935) studied a representative group of 5 varieties and 95 selfed lines of corn under natural field conditions when inoculated by mixing chlamydospores with fresh barnyard manure as a means of inducing an epidphytotic. Collections of smut were made from as many as 26 localities in 12 states east of the Rocky Mountains. Studies of infection to each collection under field conditions were made separately. They write, "Lines of corn resistant to local smut collections were equally resistant to smuts obtained from widely different sources." They found also that lines of corn had a tendency to become infected at definite plant locations irrespective of collections of smut used. This answered a question that Immer previously discussed. The writers concluded also that the resistant lines grown in this test "possess some type of resistance to the pathogen other than the physiologic."

* J.J. Christensen (1963) published a comprehensive review in monograph form entitled "Corn smut caused by *Ustilago maydis*," previously usually referred to as *U. zeae*. This review covers many phases of the life history and stability of the pathogen, the effects of smut on the corn plant and methods of control. The review here of Minnesota studies and the conclusions reached are in agreement with conclusions reached by Christensen.

Chapter 5

Research Studies 1921-36 Inclusive of Graduate Students' Theses

INTRODUCTION

The research of the plant breeding staff with particular attention to cooperative studies of disease resistance has been summarized in a previous chapter. The results of these studies may be described in the same words used in the Thatcher wheat bulletin by Coffey and McCall: "Thatcher is a landmark in a continuous and permanent program of improvements of wheats and other crops to meet the changing demands of time – a program essential to the future prosperity of agriculture."

GRADUATE STUDENTS' STUDIES AND LATER WORK

Research problems carried out by individual students often are closely correlated with faculty studies. In many, if not most, cases the student makes an intensive study of a single phase of research that often can be completed in a few years. From the research viewpoint it would be more desirable to summarize the faculty and student investigations together. When discussed separately, however, there is a better opportunity to emphasize the student's contribution.

The two first graduate students to obtain advanced degrees with the writer as their adviser were Carl Kurtzweil and Fred Griffee. Both received M.S. degrees in 1921.

Kurtzweil has been mentioned previously in connection with the studies of wheat species crosses by Hayes, Parker, and Kurtzweil. He died a few years after obtaining his degree.

Griffee's thesis study, "Comparative vigor of F_1 wheat crosses and their parents," consisted of three types of crosses:

1. Within vulgare wheats, including the compactum type Little Club that reacted in crosses in the same manner as varieties of *Triticum vulgare*
2. Vulgare-Emmer crosses

3. Vulgare-Durum crosses

The F₁ crosses and parents were grown in the greenhouse, two plants to a 7-inch pot.

A comparison was made of the immediate effect of foreign pollen on seed weight. Within each pure line progeny of each of the parent varieties "intercrossed seed" produced by emasculation and subsequent pollination from within the line, was compared with cross pollination between different pure lines.

Within the vulgare group 1, there was on the average a definite increase in seed weight due to the immediate effect of pollen of the male parent. There was no very great effect in groups 2 and 3 as far as immediate observable weight of seed except in the cross of Velvet Chaff X Mindum where the cross gave a reduction of $-4.0 \pm .8$ as compared with the seed weight of the female parent Velvet Chaff.

F₁ crosses and parents were compared for grain yield per plant. All crosses in group 1 exceeded the parental average, six out of eight exceeded the better parent. The highest yield was from the cross Marquis X Bobs which exceeded the better parent, Bobs, by 10 percent. The average increase of the crosses over parental average was 23 percent.

This early study deserved special mention because of recent reports by Wilson and Ross (1961, 1962) on the value of heterosis and the utilization of cytoplasmic male sterility and the pollen-restoring character in hybrid wheat; and a study by Suneson (1962) regarding the promise of great increases in the yield of hybrid barleys.

Griffee completed work for the Ph.D. degree in 1924, studying "Correlated inheritance of botanical characters in barley and manner of reaction to *Helminthosporium sativum*" with a plant genetics major and a plant pathology minor.

The major cross studied in barley by Griffee (1925) was Svanhals, 2-rowed, rough awn, early heading, white glumes, resistant to spot blotch with Lion, 6-rowed, smooth awns, late heading, black glumes, susceptible to spot blotch. Disease reaction in this case seemed to be conditioned by inheritance but was greatly affected by environment. The thesis study was carried out in greater detail than the previous study by Hayes et al. (1923) in which Griffee was one of the research workers.

Each of the three character pairs, with the exception of disease reaction, was due to a single pair of allelic factors. The rather clear-cut segregation for date of heading into two groups is not the usual expectation for heading date. Heading date and the factor pair for row number were linked or associated. The remaining three botanical character pairs were independently inherited.

Of greatest interest were the facts that, on the average, 6-rowed were

more susceptible to spot blotch than 2-rowed: black glumed plants were more susceptible to spot blotch than white glumed; and smooth awned plants were more susceptible than rough awned. Griffiee concluded that resistance and susceptibility were definitely inherited and that either could be combined with combinations of 2-rowed versus 6-rowed, rough versus smooth awns, or black versus white glumes.

The method here outlined led to the conclusion that at least three major genes, or groups of genes, were responsible for spot blotch reaction. This method of deciding how many genes, or groups of genes, and their linkage relations, were concerned in quantitative character inheritance, was presented separately by Griffiee (1923) and Sax (1923) on a program of the Genetics Society of America.

Chromosome analyses were essential to basic research in plant breeding. A small laboratory with the necessary equipment was started in the plant breeding section in the experiment station at Minnesota about 1917, and Griffiee was the first to carry out plant breeding research in this laboratory. For his thesis he studied root tips of Svanhals and Lion and found each to have $n=14$ chromosomes. He said that as far as he could learn, these were the first determinations of barley chromosome numbers made in the United States. Griffiee later determined that Marquillo and Thatcher spring wheats had chromosome numbers of $n=21$.

Ralph J. Garber received an M.S. degree in agronomy in 1917 and at that time was an assistant to Professor A.C. Arny. He later asked to be transferred to the plant breeding staff to aid the writer and to continue graduate studies leading to the Ph.D. degree. His thesis problem was "Inheritance and yield with particular reference to rust resistance and panicle type in oats" (Garber, 1922). Garber majored in plant genetics with a minor in plant pathology.

Two open-panicked, pure lines of oats, Minota and Victory, which were susceptible to stem rust but agronomically desirable were crossed with a side-panicked pure line of White Russian which was relatively resistant to stem rust. Segregation in F_2 and F_3 , for both panicle type and rust reaction, was found to be dependent in each case on a single factor pair with rust resistance and open-panicle dominant. The two character pairs were independently inherited.

Previously Miss Allen (1921) concluded that stem rust reaction of Kanred wheat, immune to a group of physiologic races, was due to small stomatal apertures which prevent the entrance



Dr. Ralph G. Garber, coauthor of "Breeding Crop Plants," 1921, 1927 McGraw-Hill Book Co., New York. Fellow Amer. Soc. Agron., 1933. President 1939.

of rust. Garber, however, found that stomatal openings of Victory, the susceptible parent, were much smaller than those of White Russian.

Yield in F_2 and F_3 was affected by rust. In the Minota-White Russian F_2 the average percentage reduction in yield because of rust was 12 percent in the open-panicked plants and 34 percent in the side-panicked plants. In the F_2 cross, Victory X White Russian, average reduction because of rust was 37 percent in the open-panicked plants and 24 percent in side-panicked plants. These same groups in F_3 gave yield reductions due to rust of 24, 14, 37, and 30 percent, respectively. Garber made numerous studies of genetics and breeding of small grains, corn, and grasses and with the writer was author of the book "Farm Crops Plant Breeding," 1921, 1927, McGraw-Hill Book Company, New York.

J.A. Clark (1923) completed work for the M.S. degree with a major in plant genetics and a minor in agricultural biochemistry. He was a leader of coordinated research between the U.S. Department of Agriculture and the state experiment stations. His thesis problem, "Correlated inheritance in a cross between Kota and Hard Federation wheats," was one of the earlier publications on spring wheat. Added data and much of the thesis studies were published in 1924.

The stem rust resistance of Kota was discovered independently by Clark and Dr. L.S. Waldron of North Dakota. It is from an introduction of Professor H.L. Bolley in 1903. Although Clark states that previous to 1918 stem rust resistance had not been reported in hard red spring wheat in the United States, previous reviews make plain that studies for this purpose were carried out. Hard Federation is a variety of white endosperm wheat. It was developed about 1908 by J.T. Pridham at the Cowry Experiment Station in New South Wales.

Clark found susceptibility to stem rust to be a dominant over resistance. Segregation was on the basis of 15 susceptible to 1 resistant. An interesting feature was that no lines from resistant F_2 plants bred true in F_3 , although Clark states, "Evidence was shown that strains homozygous for resistance could be obtained in F_4 ."

Color of kernel segregated according to a 15:1 ratio with red color dominant, while awn development was conditioned by the interaction of two factors. The presence of awns and rust resistance both were of importance in relation to yield.

J.B. Harrington (1925) completed studies for the Ph.D. degree in 1924 with a major in plant breeding and minor in plant pathology. His thesis problem consisted of studies of crosses between the durum varieties Kubanka 8 X Pentad and Mindum X Pentad.

Pentad, selected at North Dakota, was known to have high resistance

to stem rust but produced red seed color of low macaroni quality. Kubanka 8 and Mindum were less rust resistant on the average, produced amber colored grain of desirable macaroni quality, and had good yielding ability.

Studies of reaction to rust were made principally under greenhouse conditions to individual races of rust. In studies of the cross Mindum X Pentad, Mindum was nearly immune to Race 1 while Pentad was intermediate susceptible; to the recently acquired Race 34, however, Mindum was susceptible and Pentad was resistant. Race 21 became available in 1924; Mindum and Pentad reacted as they had to Race 34.

Studies of reaction to Race 1 were made on 166 randomly selected F_3 lines and 23 families of each parental variety, while 23 F_3 lines were selected representing various types of infection and F_4 progeny reactions were studied.

The reactions were explained on the supposition that Mindum carried a gene for high resistance to Race 1 while Pentad carried an independently inherited gene for slight resistance with the factor for high resistance epistatic to that for slight resistance. The recessive condition for both genes produced wheats more susceptible than the Pentad parent.

In another series of studies Mindum was susceptible to Race 34 while Pentad was moderately resistant. These two parental varieties were found to react in the same manner to Race 21. Random F_3 lines also were used to study reaction to Race 34. Pentad was resistant and Mindum was susceptible. Parental types were recovered in F_3 and in F_4 , although the number of genes responsible for reaction to Race 34 was not determined. Tests of a limited number of families were made to Race 21, and these reacted in the same manner as to Race 34.

Reactions were studied under field epidemic conditions in a rust nursery where Races 1, 9, 17, 18, 19, 21, and 34 were used to produce an epidemic. Of 27 random F_3 lines of Mindum X Pentad one was as susceptible as Mindum, but none were as resistant as Pentad. Over 200 F_4 lines were studied, each the progeny of an F_3 plant. In this case numerous resistant, susceptible, and segregating progenies were obtained. The number of genes responsible for field rust reaction was not determined. There was no relation between seedling rust reaction to Races 34 or 21 and reaction under field conditions to a mixture of nine races.

Other plant characters were studied including plant height, erectness of plant, and time of heading. There was a slight tendency for these characters of the hybrids to be associated with rust reaction under field nursery conditions in the same manner as the parents.

Harrington later made extensive contributions to plant breeding methodologies and published numerous papers in plant genetics and plant

breeding. In 1952 he published an excellent paper on "Cereal Breeding Procedures" when connected with the staff of FAO.

C.H. Goulden (1926) completed studies for the M.S. degree in 1923 and the Ph.D. degree in 1925 with a major in plant breeding and a minor in plant pathology. His thesis problem was "A genetic and cytologic study of dwarfing in oats."

The Kota X Marquis cross studied by Hayes and Aamodt, previously discussed for stem rust reaction, segregated dwarf plants in F_2 . By studying these generations and backcrosses to both parents, and using goodness of fit trials, Goulden decided that Kota carried dominant genes ID , where I is an inhibitor of D and D is a dominant factor for dwarfing, while Marquis carried both factors in a recessive condition. The segregation ratio in F_2 was 13 normals to 3 dwarf. Similar results were found from a Chul X Marquis cross obtained from Dr. W.P. Thompson of the University of Saskatchewan.

Although the agreement with expectation on the basis of the above hypothesis was good, there were wide deviations from expectation in a few cases. Pollen mother cells from various stages showed instances of lagging chromosomes. Goulden discussed possible explanations of deviating ratios on hypotheses suggested by Winge in 1924. This may be illustrated on the basis that deviations in gamete formation might be obtained because of affinities between a pair of chromosomes in set A that had pairing relations with a similar pair of chromosomes in set B, and that A and B sets of seven chromosomes each arose originally from the same ancestral set of seven chromosomes. Thus ID/id might pair in such a way as to give equal frequency for combinations, ID , id , Id , iD and $ID id$ Li and Dd . The Li and Dd combinations might be lethal. Other possibilities resulting from similar types of chromosome affinities were discussed.

Goulden made important contributions to disease resistance researches and field experimental methods and was author of the well known book, "Methods of Statistical Analyses," John Wiley and Sons, Inc., New York, 1939.

Earl S. Quisenberry, Ph.D. 1925, majored in plant breeding with a minor in plant pathology. The thesis research was carried out when Quisenberry was junior agronomist at the University of West Virginia. The thesis, "Correlated inheritance of quantitative and qualitative characters in oats," was published in 1926.

The characters studied in crosses of Victor and Sparrowbill were as follows:

Victor	Sparrowbill
1. Grain long	1. Grain short
2. Grain black	2. Grain white
3. Grain awned	3. Grain awnless
4. Panicle open	4. Panicle side

Detailed studies of the length of grain of the parents were made in 1923 and 1924. Measurements were taken on the primary grain of the main panicle. Measurements were recorded from 10 grain samples distributed throughout the panicle in a random manner—a method which appeared to be a highly reliable measure of grain length.

The parents were grown on soil of both high and low productivity. The average length of grain in millimeters of Sparrowbill was 13.3 for 1923 and 12.2 for 1924. Average grain length of Victor was 17.9 for 1923 and 16.9 for 1924.

Inheritance studies were carried out for grain length, where the grain length of parents, F_1 and F_2 generations, were summarized in frequency tables for the two years. The progenies of 75 F_2 plants each of reciprocal crosses were studied in F_3 . The correlation for length of grain of F_2 plants and the mean of their F_3 progenies was $r = 0.71 \pm 0.03$, showing the character length of grain to be very stable and highly heritable. The results were explained on the basis of three factor pairs. When each was in a dominant homozygous condition, there was an increase of 1.6 mm. in grain length; when heterozygous, an increase of 1.2 mm.

Color of grain was clearly dependent upon a single factor difference, with black dominant to white. As in similar cases, degree of awn development was difficult to classify. The F_1 generation was nearly as heavily awned as Victor, which produced heavy, twisted, geniculate awns. F_2 and F_3 generations were studied. There was excellent agreement between awn development of F_2 plants and their F_3 progenies.

In F_2 , only 14 plants out of 998 produced no awns while 35 Sparrowbill plants were placed in the 0 class and 19 in class 2 with one awn per panicle. In F_3 some lines bred true for awnless and a greater number of lines bred true for heavily awned. The number and nature of factors were not clearly determined.

Panicle type in this study gave good agreement with a ratio in F_2 of 15 open : 1 side, indicating duplicate factors. Grain color and panicle type appeared to be independently inherited.

Length and color of grain appeared to be independent in inheritance; length of grain and panicle type showed association, the side type of panicle in F_2 producing shorter grains, on the average, than open panicles. The conclusion was reached that each of two different factors for awn type were linked with a factor or group of linked factors for length of grain.

Quisenberry concluded there were three linkage groups of factors: one containing the pair for grain color with the possibility of a factor for awns, a second group containing one of the factors for panicle type together with a factor or group of factors for length of grain and a factor for awns, and a third group containing the other factor for panicle type and a factor or group of factors for grain length.

While at Minnesota, Quisenberry, the writer, and Dr. E.C. Stakman worked closely together in spring and winter wheat breeding with particular attention to breeding for diseases resistance and related problems.

Quisenberry published extensively in genetics and improvement of wheat and other cereals.

George Stewart completed work for the Ph.D. in 1926. When Stewart first inquired about graduate work, he described a study he had under way with wheat. Intensive phases of study were repeated after selecting progenies of individual parents and using so-called "pure lines" parents for subsequent studies of parents and their crosses. Varietal crosses made previously and the parents and certain of their progenies were used in studies of yield and of reaction to stem rust.

Three varieties were used as parents: Dicklow, a spring wheat commonly grown under irrigation; Federation, a new variety from Australia; and Sevier, a variety discovered in Sevier County, Utah.

In studies of yielding ability and rust reaction pure lines of Dicklow and of Sevier and relatively homozygous selections from varietal crosses were utilized.

When grown as spring wheat under irrigation in 3-row blocks with four replications, some recovered lines from the cross of Dicklow X Sevier yielded far superior to Dicklow in 1924. As dry-farm winter wheat, there was a wide range in yields both for the hybrids and for pure lines of Sevier.

Marquis, Dicklow, Sevier, G40, and G149 were tested in the greenhouse for rust reaction in the seedling stage to 19 physiologic races made available by Stakman and Levine. The Dicklow parent lines mostly gave reactions in class 4, very susceptible; Sevier showed mostly class 3 reactions, susceptible. G149 and G40 selected from varietal crosses Sevier X Dicklow gave evidence of a moderate degree of resistance to most races of rust. Stewart gives data on rust reaction for 1925 at six widely distributed stations for several wheat varieties compared with G40 and G149. Both of the latter selections were moderately resistant under all conditions tested and were equal or slightly superior in this respect to Kota, Marquillo, and Ceres, the latter produced by Waldron at North Dakota from crosses of Kota X Marquis.

The genetic studies of characters were made from pure line crosses of Dicklow X Sevier. Studies were made of methods of taking data and the methods used were found to be reliable. The parents and characters studied were:

The characters of parents, F_2 crosses, and F_3 progenies of individual plants were taken in a systematic manner. F_3 rows of approximately 40 plants each from progenies of individual plants were grown to determine breeding behavior. Individual rows of parents were grown at intervals with the F_3 generations.

There were four classes for awn characters in F_2 : class 1 like Federation,

awnless; class 4, awned like Sevier; class 2, tip awns in upper head like the F_1 ; and class 3, intermediate between classes 2 and 4. In class 3 awns were variable in length with awns on upper part of head nearly as long as the Sevier parent and short apical awns on lower half of head.

The extensive studies in F_2 and F_3 were explained on the basis of two loosely linked pairs of genes where Sevier carried the factors *AATT* and Sevier *aatt* and gametic production in F_2 was on the basis of 1.8 *AT* : 1.0 *At* : 1.0 *aT* : 1.8 *at*; i.e., a crossover value of 35 percent. Linkage of these genes had not been found by previous research workers.

For spike density the parents overlapped when individual plants were studied. The F_2 showed wide transgressive segregation with a range in length of internode from 1.75 mm to 7.75. Using the coefficient of variability to separate homozygous F_3 lines from heterozygous, 59 F_3 lines bred true for denser heads than any of the Sevier parent rows, and 65 F_3 lines bred true for lax headed types with about half that had higher mean values than any of the 24 Federation parent rows. There were 123 rows that gave greater variability for head density than any parent rows, with means ranging from more dense than Sevier to as lax as the grand mean for all 24 Federation rows.

The above F_3 ratios in themselves approximate the ratio of 1 homozygous dense : 2 heterozygous : 1 homozygous lax, but the head density of the Sevier parent type was not recovered. It was suggested that in addition to a major factor there are several minor modifying factors.

While segregation for squareheadedness occurred in F_2 , most of the lines did not have a higher coefficient of variability than the parents. No Factor hypothesis was attempted.

Correlations of characters were studied by calculating coefficients of correlation and the correlation ratio. Because the two characters of spike density and awn classes were definitely inherited and because of the nature of the segregation, the conclusion was reached that, "there is a strong suggestion of linkage between the genes for these two characters."

Stewart was an extensive contributor to plant genetics and breeding, and to agronomic practices including irrigation, dry farming, range management, and agricultural planning.

Characters studied	Federation	Sevier
Awn development	Awnless	Awned
Spike density (per row)		
Length of internode in mm	4.25-5.25	3.25-4.75
Squareheadedness (per row)		
Ratio of number of internode in middle third of head to number in upper third	.99-1.17	.78-1.08
Length of tallest culm in mm (per row)	93-105	114-126

H.E. Brewbaker (1925) completed work for the Ph.D. majoring in plant breeding with a minor in plant pathology. His thesis, "Studies of self-fertilization in rye," did not have a close relation to disease resistance problems. He found some plants, in selfed lines and in the variety Minnesota No. 2, were highly resistant to *Puccinia graminis secalis* but no strain available appeared uniformly resistant.

Undesirable recessive abnormalities occur in commercial varieties. Self-fertilization was utilized to produce lines that approached homozygosity and bred true for uniformity of plant and grain characters.

Most plants were rather highly self-sterile, producing only a few seeds under controlled self-pollination. Other self-pollinated lines were rather highly self-fertile.

Certain inbred strains appeared outstanding in vigor and self-fertility, seemingly more vigorous than comparable self-pollinated lines of corn. The utilization of such inbred lines of desirable seed color and vigor was considered to be an advantageous means of producing synthetic varieties.

It is of interest that Brewbaker used material from selections for seed color under open-pollinated conditions that were initiated by the writer in 1916. Brewbaker's material later was used partially to develop the desirable variety Emerald, which bred true for bluish-green seed color and was released by the Minnesota Agricultural Experiment Station. It was grown extensively in Minnesota for several years.

L.E. Kirk (1927) completed this Ph.D. studies with a major in plant breeding. The data were taken at the University of Saskatchewan field husbandry experimental plots. Except for studies of methodologies in plant breeding, the study has little or no relation to breeding for disease resistance.

Kirk's thesis, "Self-fertilization in relation to forage crop improvement," furnished a comprehensive idea of the problems studied with alfalfa, bromegrass, and red clover.

With alfalfa the selfed lines studied were from material selected originally in Minnesota by Wendelin Grimm and two Saskatchewan strains that had been improved by mass selection for winter hardiness and vigor over a 12-year period.

The correlation between forage yield and seed production of both first and second generation selfed lines was $r = 0.49 \pm 0.07$, which indicates considerable relation between vigor of growth and seed yields in early generation selfed lines. Certain inbred lines were relatively vigorous under inbreeding, although in general there was a marked reduction in vigor as a result of self-pollination. It was shown that for both seed setting and hardiness there was a considerable degree of inheritance when first and second selfed generations were compared. Selfed lines of alfalfa exhibited many seedling

abnormalities of a recessive nature.

With awnless brome grass, *Bromus inermis*, the most striking result of the effects of self-fertilization where spaced plant progenies were grown was the reduction in spread of plants from selfed seed lines. In individual plant yields in selfed lines the relation between yield and spread of plant gave a calculated r value of 0.96 ± 0.01 . Some rather vigorous selfed lines were obtained.

Two varieties of red clover, a strain of Minnesota origin and Altaswede, were used in the studies of the effects of self-fertilization. A comparison was made of the number of seeds per head resulting from self- and cross-pollination (normal). Many self-pollinated heads produced few or no seeds although as many as 48 seeds were obtained from one selfed head of each variety. Marked reductions in vigor were obtained when selfed lines were compared with the varieties. Seedling abnormalities were frequently obtained in selfed line progenies.

Kirk discussed the effects of self-fertilization on different crops. He noted that most selfed lines of maize, red clover, and alfalfa are markedly reduced in vigor, while a greater proportion of selfed lines of brome grass and timothy were relatively strong and productive. He expressed the viewpoint that controlled self-fertilization, with selection in selfed lines, was a logical method to use in the systematic breeding of many cross-pollinated plants.

Kirk has been an extensive contributor to plant breeding, plant genetics, and field husbandry.

Arthur F. Swanson completed work for the M.S. degree in 1928 with a major in plant genetics. Part of the data used were from joint studies of Swanson and Dr. J.H. Parker of the Kansas State Agricultural College. Swanson's thesis was entitled "Seed-coat structure and inheritance of seed color in sorghums."

The following is a brief summary of major results and conclusions:

"Pigmentation may occur (1) in the epidermal and hypodermal cells of the pericarp, (2) always in the nucellar layer when this structure is present, or (3) in both regions at the same time. The nucellar layer does not occur in all varieties."

A single gene *B* was assumed to be responsible for the development of the nucellar layer and its associated pigment, while *b* determined the absence of the nucellar layer or pigment.

S was assumed to condition development of a vestigial mesocarp, while *s* conditioned a well developed, starchy, opaque mesocarp. This type of mesocarp masks nucellar color and colored pericarp due to *B*.

R determined coloration in the epidermal and hypodermal cells of



Dr. F.R. Immer, Professor of Agronomy and Plant Genetics, Vice Director of the Minnesota Agricultural Experiment Station and Joint Author with the writer of, "Methods of Plant Breeding," McGraw-Hill Book Co., 1942.

the pericarp, while *r* led to absence of color. The effects of *R* were intensified by the presence of *B* and *S*.

Swanson made extensive contributions to plant breeding and genetics of sorghum, winter wheat, winter barley, and improvement of grain sorghums for industrial starch and other uses.

F.R. Immer (1927) completed undergraduate work at Minnesota and obtained the Ph.D. with a major in plant breeding and a minor in plant pathology. His Ph.D. thesis, "The inheritance of reaction to *Ustilago zaeae* in maize" was published as Technical Bulletin 51 of the Minnesota Agricultural Experiment Station.

A smut epidemic was induced artificially under the direction of J.J. Christensen in plant pathology who joined with Immer (1925) in a study of inheritance and reaction of selfed lines and their crosses to smut infection.

Studies were made in F_2 under field conditions of smut reaction and genes in known linkage groups. Independence was found for smut reaction and for normal vs. shrunken endosperm in the "C" linkage group, the *Prpr* factor pair located in the "R" linkage group, the sugary factor pair *Susu* in the "su" linkage group, the factor pair for purple vs. green plant color, the factor pair *Yy* in the "Y" linkage group, and the factor pair for brown vs. colorless aleurone in the "Bn" linkage group.

The factors for smut reaction were found to be linked in inheritance with the factor pair for liguleless vs. ligulate plants in the "Bn" linkage group, and the factors for brachytic vs. normal plants and red vs. colorless pericarp, both located in the "P" linkage group.

Immer was joint author with the writer of, "Methods of Plant Breeding," McGraw-Hill Book Co., 1942, and held various positions in Agronomy and Plant Genetics from 1917 through 1946. At the time of his death in 1946 he was Professor of Agronomy and Plant Genetics and Vice Director of the Minnesota Agricultural Experiment Station. He was widely consulted on problems of Applied Statistics and was the author of numerous bulletins and research papers in plant genetics, breeding, and research methods.

D.W. Robertson completed work for the Ph.D. degree in 1928 with a major in plant genetics. His thesis research, "Linkage studies in barley," was carried out largely from data obtained at the Colorado Agricultural Experiment Station (Robertson, 1929). From that time until the present he has been one of the leaders in studies of linkage relations in barley, although

he has been active in the field of agronomic research also.

Robertson found the following factor pairs in barley segregated in a 3:1 ratio: black vs. white glume color (Bb), hoods vs. awns (Kk), covered vs. naked seed (Nn), non-six-rowed vs. six-rowed (Vv), long vs. short-haired rachilla (Ss), green vs. white seedlings ($A_c a_c$) found originally in Colsess, green vs. white seedlings ($A_1 a_1$) found originally in Trebi, and green vs. xantha seedlings ($X_c x_c$) found also in Colsess.

In crosses between Colsess, a six-rowed barley, and *H. deficiens nudideficiens* Minn 90-5, Robertson explained segregations for spike characters on a two-factor difference in a similar manner to that previously used by Harlan and Hayes. The genotype of Colsess was considered to be $uvll$ and that of Minn 90-5 was $VVii$.

Independent inheritance was found between the following character pairs: black vs. white glumes, hoods vs. awns, covered vs. naked seed, non-six-rowed (2-rowed or *deficiens*) vs. six-rowed, and long vs. short-haired rachilla.

Two probable linkage groups were found for chlorophyll abnormalities and other character pairs:

(1) Green vs. white seedlings $A_c a_c$ and green vs. xantha seedlings $X_c x_c$ and possibly hoods vs. awns Kk .

2) Green vs. white seedlings $A_1 a_1$ and black vs. white glumes Bb .

H.H. Flor with a major in plant pathology and minor in plant physiology received the Ph.D. degree in 1929. Because of the importance of his subsequent work relating to disease resistance in flax, a brief review is included.

Numerous researches on breeding flax varieties resistant to disease have been published. Flor (1935) described physiologic races of stem rust of flax. A summary paper in 1955 entitled "Rust Resistant Flaxes" gives an excellent idea of the accomplishments resulting from many years of research by Dr. Flor.

The more important research of Dr. Flor in crop improvement consists of the genetics and breeding of varieties of flax resistant to rust caused by *Melampsora lini* from 1935 to the present time. Genes from rust resistance sources were added to commercial varieties largely by the method of backcrossing.

As the rust parasite reproduces sexually on flax, Flor discovered that the development of new races often occurred by hybridization and genetic recombination. Natural and induced mutations have been observed. The following is quoted from the 1955 review in the Agricultural Research magazine:

“Flor developed the gene-for-gene concept of the host-parasite relationship – that for each gene determining virulence in the parasite there is a gene determining resistance in the host. This research led also to the finding of evidence of the nature of physiologic resistance of plants to disease.”

LeRoy Powers completed studies for the Ph.D. degree in plant genetics in 1931. His thesis problem, “Cytologic and genetic studies of variability of strains of wheat derived from interspecific crosses,” had a direct relation to the cooperative rust resistance breeding studies of the Minnesota Agricultural Experiment Station and the United States Department of Agriculture.

The germinal stability of Marquillo – developed at Minnesota from a cross of *Iumillo durum* with Marquis – and Minnesota 2303 – later named Thatcher, obtained from a selection of a cross of a sister selection of Marquillo with an F_3 selection of Marquis X Kanred – were compared with the standard spring wheat variety Marquis. Marquillo and this sister selection and Thatcher carry mature plant resistance to many races of stem rust under field conditions from heading to maturity. Thatcher in addition carries a factor for immunity to many races of rust to which Kanred is immune.

Cytological studies of chromosome counts and occurrence of micronuclei in 42 chromosome plants, were made on immature microspores still grouped together in tetrads. Other related studies were made of irregularities, non-orientation of bivalents, non-conjunction, i.e., univalent condition of both members of a chromosome pair that are usually conjugated, and behavior of univalent chromosomes.

The number of chromosomes for 32 plants of Marquillo grown in 1929, and 27 plants of Marquis grown in 1932 was 42, except for two plants of Marquillo which had 41 chromosomes.

The occurrence of micronuclei in plants of Marquillo, Thatcher, and Marquis was studied. On the average, about 500 microspores per plant were studied. (See Table 3.)

Table 3. Average percentage of micronuclei

Variety of wheat	Number of plants	Microspores	
		Total	Average micronuclei
Marquillo	30	18,644	2.8 ± .16
Marquis	27	15,844	0.8 ± .06
Thatcher	30	20,944	0.8 ± .04

It is evident that Marquillo shows more cytological irregularities than Marquis or Thatcher. In general other cytological irregularities were greater in Marquillo than Marquis.

Powers studied percentage of natural crossing in progenies of individual

plants of Marquillo surrounded by Ceres. In this study Marquillo was resistant in the seedling stages to Race 21 of black stem rust while Ceres was susceptible. Seed from covered and uncovered spikes of Marquillo were used to study reaction to Race 21. Seed from covered spikes produced seedlings 0.04 ± 0.11 which were susceptible to Race 21, while seed from uncovered spikes produced seedlings with 3.6 ± 0.50 of susceptible type. It was expected that the susceptible seedlings resulted from natural crossing. Therefore, these data indicate that natural crossing was high in Marquillo.

Progenies of individual plants of Marquillo that had been studied previously for cytological irregularities were grown under field conditions to determine fruitfulness of outside florets, number of spikes per plant, weight of seed per plant, and plant height. There seemed to be a direct positive correlation between frequency of cytological regularities and variability of progeny.

Thatcher was as stable as Marquis. In addition to the frequency of occurrence of micronuclei, Thatcher later was found to be as stable cytologically as measured by nonorientation and nonconjunction as standard varieties.

H.L. Thomas completed work for the Ph.D. degree in 1931 with a major in plant genetics and a minor in plant pathology.

His study consisted primarily of linkage relations of a glossy seedling character (gl_3). The first glossy seedling was discovered by Brunson in 1921 in a yellow dent.

Hayes and Brewbaker (1928, 1929) made rather extensive studies of numerous glossy seedlings from different sources. From studies of 14 unknowns three different glossies were differentiated: gl_1 , gl_2 , and gl_3 . These writers found gl_2 to be linked with factors in the *B-Ig* group and that *F1 f1* flinty floury also was in this group. Gene order appeared to be *v4-F1-sk-gl₂-Ig*.

Thomas (1932) studied the linkage relations of gl_3 . In F_2 crosses of normal vs. glossy, gl_3 seedlings gave as vigorous plants as did normal plants with about the same yield.

He found gl_3 to be linked with *su* with a crossover value of 23 to 27 percent and a crossover value with *Tu* of about 11 percent. An average crossover value of *su* and *Tu* of about 29 percent had been obtained previously. It was concluded, therefore, that the order of genes was *su-gl₃-Tu*.

In these studies, largely of F_2 crosses in the repulsion phase, F_2 populations of from 1,300 to 4,600 plants were grown. To facilitate studies of linkage relations in F_2 generations Thomas used tables compiled under Immer's directions.

Since 1944, Thomas has been an associate professor in Agronomy and Plant Genetics at the University of Minnesota. He is the author of research papers and several books.

K.W. Neatby (1931) completed work for the Ph.D. degree with a major in plant genetics and a split minor in plant pathology and agricultural biochemistry.

His thesis research was entitled, "Factor relations in wheat for resistance to groups of physiologic forms of *Puccinia graminis tritici*." In a study of particular crosses he attempted (1) to determine the reaction in the seedling stages to as large a group of physiologic races as possible to find how many could be included in the same reaction group, (2) to determine to what extent a group identified in one cross might be found intact in a different cross, and (3) to learn the importance of such groups in relation to rust reaction under field conditions.

Three crosses were studied: Marquis X H44, Marquillo X H44, and Garnet X Double Cross. The Double Cross parent was a homozygous line from (Marquis X Kanred) X (Marquis X lumillo) previously described.

The hybrid material was obtained by taking one plant at random from each of 1,000 F_3 lines of each cross. Seed of each plant was divided into three lots, one lot used to study reaction to Race 36, one lot to Race 21 and the other to be increased under field conditions. The method used was to eliminate, as far as possible, F_3 lines that segregated for reaction to particular races used, in this case Race 21 and Race 36. On this basis 116 lines were selected from the Marquis X H44 cross, 228 from Marquillo X H44, and 114 from Garnet X Double Cross to be used in the studies.

Because of the complexity of the results a detailed summary will not be attempted.

SEEDLING REACTION

In the cross of Marquis X H44 the reaction in the seedling stages to the 15 races was explained by A and B factor pairs, or groups of closely linked factors, where both together conditioned reaction to Races 35, 36, 49, 52, and 57, while A alone was responsible for reaction to Races 27, 33, and 50, and where B was responsible for reaction to Races 14, 15, 21, 29, 30, 48, and 53. In many instances there were a few deviations from expectation which Neatby concluded were probably due to occasional natural crosses or to mistakes in classification.

Based on later studies of Martinez et al. (1963) for leaf rust reaction to a series of different leaf rust races, it is possible that these major factors A and B may represent, in some cases, closely linked factors. This would explain the many cases of Neatby where a few lines differed in reaction from expectation.

In the cross of Marquillo X H44 also two pairs of genes or groups of closely linked genes rather satisfactorily explained the results of seedling reactions. Neatby was unable to determine how many factor pairs were involved in reaction to groups of races. At least three factor pairs operated to govern reaction to 10 races placed in Group II.

In the cross of Garnet X Double Cross the Double Cross parent was immune to 9 of the 11 races used in the study. Two other major genes or groups of genes were considered to be involved.

FIELD REACTIONS

All 15 races were used to create the field epidemic. Neither the A nor B factor pairs were effective in controlling the field reaction of selections from the cross Marquis X H44. In the cross of Marquillo X H44 the A set of factors had a marked effect on field reaction. However, the relationship between greenhouse reaction to individual races or groups of races and field reaction was not complete and a knowledge of greenhouse reaction had little practical value as a means of selecting for field reaction.

For the Garnet X Double Cross selection there was an excellent positive relation between greenhouse studies and field rust reaction when the effect of the Kanred gene for immunity was ignored. The field data, after eliminating F₄ lines carrying the Kanred gene for immunity, were not extensive, however.

E.R. Ausemus completed work for the Ph.D. degree in 1932 with a major in plant genetics and a minor in plant pathology. At that time he was associate agronomist, Division of Cereal Crops and Diseases, EPI, USDA, and was working with the writer and Dr. Stakman on a disease resistance breeding subproject with wheat. Ausemus studied correlated inheritance of reaction to stem rust, bunt, black chaff, and other characters in triangular wheat crosses.

The results of these studies have a direct relation to the Minnesota cooperative project. The characters of the parent varieties studied were:



Dr. E.R. Ausemus, since 1950 Coordinator, Spring Wheat Region of the United States Department of Agriculture, Professor of Agronomy and Plant Genetics, Institute of Agriculture, University of Minnesota.

Character	Parental varieties		
	Hope	Marquillo	Supreme
Stem rust	Highly resistant	Moderately resistant	Susceptible
Bunt	Resistant	Semi resistant	Susceptible
Black chaff	Susceptible	Resistant	Resistant
Awn conditions	Awned	Awnleted	Awnless
Coleoptile color	Purple	Green	Green

Reaction to stem rust was studied in the field under rust epidemic conditions using 17 available different physiologic races to produce the epidemic. Reaction was studied in the greenhouse to Race 36, one of the races used to develop the field epidemic.

Reaction to bunt was studied using spores of a collection made available by R.H. Bamberg. A small spoonful of spores was placed in an envelope with 25 seeds and shaken before planting. With black chaff, natural infection only was used.

Previous studies at Minnesota had showed the type of field resistance of Marquillo to be recessive to susceptibility and dependent upon the homozygous recessive condition of two pairs of factors. Neatby and Goulden (1930) in crosses of Marquillo X Susceptible varieties obtained only a very few resistant plants in F_2 and thought three or more factors must be responsible for conditioning resistance in some cases. In most previous studies the stem rust resistance of Hope under field conditions was explained on the basis of two pairs of factors. Where Hope or H44 were used as parents in crosses with susceptible varieties, there usually was dominance or partial dominance of resistance over susceptibility.

The important conclusion of Ausemus would seem to be that factors for the near immunity of Hope and those for the moderate resistance of Marquillo are not allelic. In the cross of Hope X Marquillo there is at least one dominant factor for resistance of Hope and at least two recessive complementary factors for the moderate resistance of Marquillo. These and the factor for high resistance from Hope could be combined in the same variety.

In the Marquillo X Supreme crosses in F_2 there were 110 plants like Marquillo, or approaching it in resistance, and 415 completely susceptible. It was relatively easy to recover the type of resistance of Marquillo but because of difficulties in classification, the number of factor pairs concerned was not determined.

In crosses of Hope by Supreme the stem rust resistance inherited from Hope appeared to result from two duplicate dominant factors.

In relating the greenhouse reaction to Race 36 with field reaction to a collection of races there was no evidence of close relation.

Reaction to bunt was definitely conditioned by inheritance in the triangular crosses where the Hope parent was highly resistant, Marquillo less resistant, and Supreme more susceptible. Results, however, were highly variable.

For black chaff, Hope was susceptible, and Marquillo and Supreme were resistant. Where Hope was one parent, definite segregation occurred in its crosses with the preponderance of plants resistant. This, however,

also was the condition in the Hope parent itself where only 20 plants were moderately to heavily infected, and 96 had little or no infection.

Most character differences were found to be independent in inheritance, although there was a strong tendency of association between resistance to stem rust and black chaff susceptibility in Hope crosses.

Hart (1929, 1931) had suggested that resistance was due to "functional resistance" or the degree of opening of the stomata. Peterson (1931) in studies of hybrid selections was unable to find such a relationship.

Ausemus compared the parent varieties and F_4 resistant and susceptible lines of Hope X Marquillo and Hope by Supreme, and F_4 semi-resistant and susceptible lines of Marquillo X Supreme for extent and time of stomatal opening. He found no significant differences between stomatal behavior of resistant and susceptible segregates or between different parents.

Shortly after Ausemus completed work for the Ph.D. degree, Dr. M.A. McCall, at the time head of Cereal Crops and Diseases, USDA, visited University Farm. On a trip to the Waseca Station with Dr. McCall I mentioned the fact that it was now my intention to retire from active participation in the wheat breeding work and turn over the plant genetic phases to Dr. Ausemus. McCall replied that this greatly pleased him as they were considering sending Ausemus to some other station where he would have full charge. Ausemus has continued to make his headquarters in the Division of Agronomy and Plant Genetics and for many years also has had an appointment as Professor of Agronomy and Plant Genetics, University of Minnesota. In this capacity he has taken part in the activities of Agronomy and Plant Genetics Staff, aided in seminars and acted as adviser of graduate students.

Ausemus has been one of the active leaders in developing intensive studies of inheritance and linkage relations in wheat and in developing resistant varieties.

R.F. Peterson completed studies for the Ph.D. degree in 1933 with a major in plant genetics and a minor in plant pathology. At Minnesota he was the writer's assistant in studies of maize genetics. His thesis problem was a continuation of the rye inbreeding studies entitled "The improvement of rye through inbreeding" (1934). The primary purpose was to determine the value of selection in inbred lines of rye with special reference to increasing seed setting and seed weight.

Lines that differed in degrees of self-fertility were isolated. Progenies of crosses between highly self-fertile lines showed a higher percentage of seed set in F_1 , F_2 , and F_3 than their parents. Plants of crosses between lines of high X low self-fertility were variable in self-fertility when studied under self-pollination conditions in later generations, while plants of crosses of low



Dr. D.C. Smith, Chairman Department of Agronomy, University of Wisconsin 1941-____. Co-author with the writer and Dr. F.R. Immer of the 2nd edition, "Methods of Plant Breeding," 1955.

X low were for the most part like their parents. A small proportion, however, were rather highly self-fertile. Seed of crosses with parents (one or both) of high self-fertility was plumper than from crosses of low X low.

As most of the inbred lines came from Minnesota No. 2, synthetic varieties using lines of high self-fertility were compared with Minnesota No. 2 for seed setting and 1,000 kernel weight. Two of the synthetics significantly exceeded No. 2 in seed setting and one significantly exceeded it in seed weight.

Peterson has held various positions for the Canadian Department of Agriculture in cereal research and breeding investigations.

D.C. Smith completed work for the Ph.D. degree in 1934 with a major in plant genetics and a minor in plant pathology. During his graduate work he was a research assistant in oat improvement and in 1932 carried out the oat breeding research.

Smith's thesis problem, "Correlated inheritance in oats of reaction to diseases and other characters," was published (1934) as Technical Bulletin 102. The study was a direct part of the experiment station oat improvement project. As in similar studies the physiological races of stem rust, *Puccinia graminis avenae*, were made available by Stakman and coworkers.

In addition to studies of disease reaction of varieties in Minnesota and other states, Smith briefly reviews a 5-year study by Levine, Stakman, and Stanton carried out at many stations in the United States regarding varietal reaction to stem rust. These writers concluded that Iogold, Hajira, Richland (Minota X White Russian), released hybrids, White Russian, Green Mountain, and Edkin were the most resistant of various varieties grown.

A brief summary was given of reaction in oats to known physiological races of Puccinia graminis avenae:

Variety	Type of reaction to physiological races								
	1	2	3	4	5	6	7	8	9
Group I Rainbow	1	1	1	4	1	4	1	4	X
Group II White Russian	2	2	4	4	2	4	4	2	2
Group III Joannette	1	4	1	1	X	4	4	4	4
Group IV Victory	4	4	4	4	4	4	4	4	4

Reaction classes 1 and 2, with very small to small pustules, condition resistance to races in the field from heading to maturity; reaction class 3 is more resistant than class 4 which denotes complete susceptibility; reaction

X produces two types of rust pustules, largely denoting susceptibility mixed with resistant type pustules.

Smith's plan was to study crosses of Gopher—a very desirable early, stiff strawed, high yielding variety susceptible to all races as listed for Victory. Due to an apparent error in the seed selected to represent Gopher, it seems apparent that a homozygous derivative of a Minnesota White Russian cross was selected and crossed with Rainbow. This mistake gave fruitful results. In the subsequent summary the data will be presented as if the cross had been known to be between a homozygous White Russian derivative X Rainbow, although Smith presented the results as if they were a Gopher X Rainbow cross. The breeding behavior was the same as would be expected for reaction to stem rust if an open-panicled early oat with the stem rust reaction of White Russian had been crossed with Rainbow.

For the F_2 generations and their parents, the field epidemic was produced using Races 2, 3, 5, and 7, and in F_3 Race 1 was used in addition to the other four. In the F_3 studies in 1933, 20 collections of rust uredospores were made from various sources throughout the infection nursery and used to inoculate differential hosts. Race 7 was identified nine times, Race 3 identified three times, Race 2 identified five times, Race 5 identified twice, and Race 1 identified once.

Under greenhouse conditions segregation in F_3 gave class 1 and 2 types of reaction to Races 1, 2, and 5, while segregation to Races 3 and 7 gave 1 and 4 type reactions. The reaction to Races 1, 2, 3, 5, and 7 in F_3 again supported the field data that only a single pair of factors was involved.

Reaction to Race 8 was of greatest interest. F_3 families that bred true for resistance to Races 1, 2, 3, 5, and 7 bred true for susceptibility to Race 8. F_3 families segregating for reaction to Races 1, 2, 3, 5, and 7 also segregated for reaction to Race 8. These results indicated that it was not possible to combine resistance to forms 7 and 8 from a cross of Rainbow X White Russian selection. Smith concluded there was evidence of multiple alleles but does not clearly state, as was done later, that the genes for type 1 resistance in Rainbow to Race 7, for type 2 resistance in White Russian derivative to Race 8, and for susceptibility to both races are the genes concerned in the allelic series.

Correlated data on F_2 plants indicated independent inheritance for stem rust reaction and breaking strength, culm diameter, lemma color, basal hairs and blast, and a slight evidence of correlation between rust reaction and awn strength. There was the same correlation between all combinations of other botanical and agronomic characters studied as would be obtained if they were in the same linkage group.

A preliminary study was made of crown rust reaction for crosses of the resistant variety Victoria with a homozygous selection obtained from

a cross (Minota X White Russian) X Black Mesdag II-22-220 that is smut resistant and carries the White Russian type of stem rust resistance, and with Anthony and Minrus.

In these crosses Victoria was resistant or immune to all physiologic races studied: 1, 2, 3, 4, 6, 7, 17, and 21. The double cross was susceptible. F_1 between crosses of resistant and susceptible parents was either resistant or intermediate. Segregation occurred in F_2 , but the variation of parental reaction cast doubt on accuracy of conclusions.

Twenty-six F_3 progenies, with only small numbers in each, indicated that fully resistant types could be recovered although the limited data preclude careful analysis.

Dr. Smith is the author of numerous bulletins and researches in plant breeding and plant genetics.

L.G. Kulkarni (1934) was the first Indian student to complete work at Minnesota for the Ph.D. degree with a major in plant genetics and a minor in plant pathology. He made a study of "Correlated inheritance with special reference to disease resistance in spring wheat." He used random F_2 plants of a cross between Hope and Liguleless and random F_2 selections of Ceres X Hope and Ceres X Double Cross, III-31-12. Twenty-three rust races were used to produce the field epidemic.

In the Ceres X Hope F_3 material, 45 lines bred true for the high resistance of Hope, 66 segregated, and 29 bred true for semi-resistance. The results were explained by the hypothesis that the resistance of Hope was due to two dominant factors *AABB* and that Ceres carried the genotype *aaBB* for semi-resistance. The segregation for the ligule vs. liguleless character was on a 15:1 basis.

In the Hope X Liguleless cross the F_1 was semi-resistant. In F_2 , 93 plants were classed as resistant, 99 semi-resistant, and 261 susceptible. The segregation for resistance vs. semi-resistance and susceptible gave a ratio of 3:13 with a P value of .30 to .50. This Kulkarni explained by supposing Hope carried a factor for resistance *R* and that Liguleless carried an inhibitor of *R*, or *I*, which in the presence of *R* caused susceptibility. He supposed that another gene for semi-resistance, not inhibited by *I*, was contributed by Hope.

Semi-resistant selections averaged to yield slightly higher than the resistant selections, although the semi-resistant group was not equal to the resistant group in seed plumpness and therefore not as desirable from the standpoint of grain quality.

Kulkarni also tested the homozygosity of 192 pedigreed lines of winter and spring wheat, where H44 and Hope were used as one parent, to physiologic Races 21 and 36. These 192 lines had been classified as

carrying the field stem rust resistance of their H44 or Hope parent. This research was conducted by studying seedling reactions to each of the two races of rust. Of the 192 so-called homozygous lines, 43 were resistant to Race 21 and 60 to Race 36. Other lines varied from 1 or 2 susceptible plants to 113 breeding true for susceptibility to Race 21 and 87 breeding true to susceptibility for Race 36. It is apparent that studies of an individual race had little value as a means of learning field reaction expectations.

W.M. Myers (1937) completed work for the M.S. degree in 1934 and the Ph.D. degree in 1936 with a major in plant genetics and a minor in plant pathology. His Ph.D. thesis was entitled "The nature and interaction of genes conditioning reaction to rust in flax." Myers reviewed previous studies of Henry (1921) (1930). Henry in the 1921 study reported the consistent immunity of Ottawa 770B, Argentine Selection, and Bombay when thoroughly tested to various collections of rust from the United States and Canada and from rust collections of Tammes, Netherlands. In 1930, Henry concluded from studies of crosses that the immunity of Ottawa 770B and Bombay was dependent upon a single dominant factor, while in Argentine Selection, apparently two dominant factors were present, either or both conditioning immunity to rust.

Flor (1935) in studies carried out at North Dakota reported the differentiation of 14 physiologic races of *Melampsora lini* by using seven cultivated varieties. Of 165 varieties of flax tested with Races 1 to 5, 152 showed no specific response to the five races of rust, while 13 gave indications of being rust differentials. The lack of genetic purity of the varieties to rust reaction was one of the striking features.

Myers used a collection of rust obtained from the Winona variety at University Farm and form 4 obtained from Flor.

No standardized classes of rust reaction were available as were for the cereals. It was necessary to set up classes as notes were taken; 11 classes were used to differentiate reaction.

In field studies crosses of Ottawa 770B X Redwing and Ottawa 770B X Pale Blue were grown. Pale Blue previously had been classified as moderately susceptible and Redwing as resistant. In the field studies two classes only were used for F₂ plants of Ottawa 770B X Redwing, i.e., immune and rusted, and for F₃ lines three classes: immune, segregating, and rusted. Immunity of Ottawa 770B in these studies was, as previously noted by Henry, dependent on a single dominant gene.

In the greenhouse studies, 15 varieties were used and studied in their reaction to form 4 and to the collection. Rust reaction classes 8, 9, and 10 were used to denote greatest susceptibility. No reactions in these classes were obtained when form 4 was used in the inoculations.

The parent varieties of crosses studied were placed in five classes for rust reaction:

- (1) Immune, Ottawa 770B, Newland CI 438, and an immune strain of Bolley Golden.
- (2) Near immune, Long X E, CI 416-3, and the near immune strain of Light Mauve.
- (3) Resistant, Bolley Golden, Light Mauve, and CI 712.
- (4) Semi-resistant, Bison, Redwing, and CI 391.
- (5) Susceptible, Pale Blue, CI 149, and Abyssinian Yellow.

Various crosses were studied using for the most part randomly selected F_3 lines between parents belonging to each of the five groups.

The results of all crosses except those involving Long X E, a near immune parent, were explained by assuming factors in two different allelic series where L and M are duplicate factors for immunity to the collection of rust and where there were other allelic factors for both L and M . The l^n and m^n are duplicate factors conditioning near immunity; I^r and m^r duplicate factors for resistance and the genotype $llmm$ conditioned complete susceptibility.

Myers has held many positions with the U.S. Department of Agriculture, chiefly with forage crop research. He became head, Department of Agronomy and Plant Genetics at Minnesota in 1952 and in 1963 was appointed Dean of International Relations.

L.J. Johnson (1932) completed studies for the Ph.D. degree with a joint major in agronomy and plant genetics and a minor in biochemistry. His thesis research was entitled "Correlation studies with strains of flax with particular reference to the quantity and quality of the oil."

An extensive yield trial of 46 varieties and purified crosses was grown in 1929 and 1930 at University Farm, St. Paul. Argentine and domestic types were included, giving a wide range in characters.

The characters studied both years were percentage of oil, dry weight of 1,000 seeds, date of maturity, and number of days from full bloom to maturity. Iodine number, as a measure of quality, was studied only in 1930.

Interannual correlations were studied for the two years. Each character was highly heritable, with r values for percentage of oil, dry weight of 1,000 seeds, date ripe, and days from full bloom to maturity of .86, .95, .51, and .70, respectively.

The interrelations of characters were studied by the use of partial and multiple correlations. Partial correlations make it possible to study the relationship between two variables, when the influence of other variables is removed.

The importance of weight of 1,000 seeds and oil percentage is evident when partial r values were computed holding date ripe constant. Values for 1929 and 1930 were .67 and .70, respectively. For 1930 iodine number and weight of 1,000 seeds, holding percent oil constant gave a negative value of $-.40$. A similar value of $-.45$ was obtained when number of days to maturity was held constant.

Low nonsignificant partial correlations between iodine number and date of maturity, holding constant percent oil and weight of 1,000 seeds, indicates that time of maturity has little relation to iodine number of the seeds.

There were high positive R multiple correlations between percentage oil with seed size, date ripe, and full bloom. The R values for 1929 and 1930 were .72 and .79, respectively. The low multiple correlation for iodine number and the percentage of oil, weight of 1,000 seeds, date ripe, and length of days between full bloom and maturity of approximately .42 indicates that iodine content is not greatly dependent on these other characters.

Johnson has published extensively in breeding and genetics of corn and sweet clover.

S.C. Salmon (1933) completed work for the Ph.D. with a major in agronomy. He is included in the review because his leadership in agronomy has been devoted partially to the broader phases of crop improvement.

His thesis study, "Resistance of varieties of winter wheat and rye to low temperatures in relation to winter hardiness and adaptation," consisted of intensive greenhouse and laboratory studies of differential varieties to determine the physiological basis of hardiness. The literature cited and briefly reviewed is extensive.

It seems worth recording that Minhardi and Minturki winter wheats previously discussed and bred in Minnesota were among the most hardy varieties. Properly hardened material under controlled laboratory conditions reacted in a very comparable manner to actual winter hardiness ratings when grown under field conditions.

Salmon has been an extensive contributor to wheat improvement, statistics, wheat physiology and crop ecology.

H.M. Tysdal (1933) completed work for the Ph.D. degree with a major in agronomy. He, like Salmon, is included in the present review because his later work was largely in the field of crop improvement. His thesis, "Influence of light, temperature, and soil moisture on the hardening process in alfalfa," had the aim of developing methods of testing hardiness under controlled laboratory conditions. The studies were conducted in the plant pathology greenhouses of the Nebraska Agricultural Experiment Station.

Tysdal has published extensively in the fields of plant physiology and plant breeding, particularly relating to alfalfa improvement.

Chapter 6

Staff Research, 1937-52 Inclusive

Some special phases of crop improvement research will receive first attention.

RECOMMENDED VARIETIES

Immer (1942) made a short, but rather complete, summary of the basis for selecting an annual recommended list of farm crop varieties in Minnesota.

Tests of large numbers of strains and varieties of small grains and flax were made in the early test stage in rod-rows at the central and branch stations. Prior to this, the list was decreased by preliminary yield trials at University Farm under the direction of each crop project leader. Final yield trials were made in cooperation with leaders at the branch stations and, when desirable, in other localities.

Larger plots with small grains and flax were grown where the number of varieties and strains does not exceed about 25. After surviving the rod-row trials the final test was made in the larger plots where farmers have a chance to observe new varieties.

New varieties from other breeders were included in some of these trials as they became available.

A uniform yield trial with 25 promising varieties of spring wheat was grown in 17 different localities in eight states. This is an illustration of interregional cooperation. In a similar manner new strains of flax have been grown in 20 locations in 13 states with two tests in Canada.

Extensive studies in disease reaction were carried out on these same strains and varieties in cooperation with and under the leadership of research workers in plant pathology.

For tests of quality, milling and baking, trials of wheat were carried out cooperatively under the leadership of research workers in agricultural

biochemistry. Malting tests of barley were conducted in cooperation with the Regional Malting Laboratory at the University of Wisconsin. The oil percentages and iodine numbers of flax strains were determined in agricultural biochemistry by a representative of the U.S. Department of Agriculture cooperating on the flax improvement program.

Corn hybrids, both single and double crosses, were grown at numerous stations throughout the state, as time of maturity is important in relation to local adaptation of hybrids.

Before recommendations were made, field, laboratory, and quality determinations were made by experiment station investigators in plant genetics and agronomy, plant pathology and botany, and biochemistry. U.S. Department of Agriculture investigators and coordinators, the National Foundation Seed Stock Program, and in some cases Interstate Cooperation each play a part in the collection of research data and increase of seed stocks.

A conference of research workers in these various fields, to which several representatives of the Minnesota Crop Improvement Association are invited, was held annually. This group decided on the basis of available data which varieties, inbred lines of corn, etc., are of sufficient promise to release. This cooperation has developed through the years, and changes of procedure are made as seems desirable.

SEED DISTRIBUTION METHODS

Borgeson, who has been in charge of seed increases at Minnesota for many years, described methods used in seed increases (1949). Approved growers were selected by county seed distribution committees, their chief qualification being a satisfactory seed certification record. These selections of approved growers had to be approved by an experiment station advisory committee which had the responsibility of developing distribution policies.

The approved grower agreed to apply for certification and make the entire crop available to the agricultural experiment station, making it possible to recall all seed of a new variety if for any reason that seemed desirable. If the seed is not recalled, the grower agreed to sell at least 50 percent of the crop to other growers at a price established by the advisory committee.

Without great detail, because it fits into the story at this time, it seems worthwhile to state that policies have been adopted to make it possible for the larger seed companies to take part in these early increases and distributions of new varieties.

This work is self-supporting through the establishment of a seed revolving fund. The profits from seed increases were used to build the Seed Storage and Processing Laboratory; aid also was given by making funds available to help finance the cost of that part of the building housing offices and laboratories

of the Minnesota Crop Improvement Association. The close cooperation among research workers of the Minnesota Agricultural Experiment Station, members of the Minnesota Crop Improvement Association (largely seed growers) and the Crop Quality Council (largely members of industry) is one of the best illustrations of the value of cooperation. Its aim is the development of agricultural policies on a sound business basis with particular reference to the production of food and fiber, not only for the producer but also for the consumer.

Seed increases of and distribution of inbreds and single crosses of corn and of registered seed of the recommended varieties are under the immediate direction of Borgeson. The necessary offices, processing laboratories, and seed storage rooms are located in a so-called seedstocks building. The processing laboratories are equipped with the essential facilities. A rather large seed storage room is equipped with temperature and humidity control which makes it possible to store seed increases so that seed remains viable for many years. This is essential and is used for seed of all farm crops.

Borgeson and Hayes (1941) outlined a method of increasing and maintaining inbred lines of corn. This method was summarized by the writer in Hayes, Immer, and Smith (1955) as follows:

Hand-crossed and selfed seed of all inbred lines needed in the corn program is planted each year in foundation plots at both the southern and central stations. The crop risk is distributed as much as possible by planting at two stations with several dates of planting at each location. Sufficient selfed ears are produced to provide the necessary seed that is needed the following year in the crossing plots where single crosses are produced. The selfed ears are inspected both before and after drying.

The seed is harvested and dried in fine-meshed bags in tray driers. Twenty to 30 individual representative selfed ears of each culture are saved and the balance of the selfed seed bulked to use for producing single crosses. Short "ear-to-row" cultures from 20 to 30 selfed ears of each inbred also are planted in the foundation plot. Hand crosses are made between the individual ear cultures obtaining several crossed ears from each combination of "ear-to-row" cultures as follows: 1 X 2, 2 X 3, 3 X 4, etc., where 1 to 4, etc., represent the "ear-to-row" cultures of each of the inbred lines, respectively. The hand-crossed ears in each culture are examined and desirable crosses are bulked using representative cultures. The crossed bulked seed is used the following year as the parental source of the rather extensive hand selfing program that furnishes the major source of selfed seed for single cross increases. In some cases it is necessary to use hand controlled sib-pollination when self-pollination for any reason in some lines does not prove feasible. The plan then consists of alternately producing selfed and crossed seed for each inbred line.

The major features of the plan may be summarized briefly as follows: When an inbred line seems relatively homozygous, sufficient selfed seed of each inbred is produced each year to plant the necessary single cross plots the following year. The seed planted for the selfing plot is obtained the preceding year from hand-pollinated crosses made by crossing the progeny of "ear-to-row" cultures within the inbred lines produced from selfed ears.

Hayes, Immer, and Smith also discuss briefly the essential features of the International Crop Improvement Association, the National Foundation Seed Stock Program, the Canadian Seed Growers' Association, Interstate Cooperation, and the Minnesota Plan for Certain Crops. Interested readers may consult this and other publications for more detailed information on the production of quality seed stocks.

In recent years it has seemed evident that larger seed companies and growers could more advantageously be looked to for seed production of hybrid corn. The Minnesota Agricultural Experiment Station and some other state experiment stations have developed more liberal policies in relation to release of seed of desirable inbred lines, with the expectation that seed growers themselves were capable of determining how these could be used most desirably in crosses.

SOYBEANS AS A CASH CROP

One of the most remarkable developments in this period from 1936 to 1952 in Minnesota and in other states has been the phenomenal increase of soybeans as a cash crop. This led J.W. Lambert (1949) to discuss the question, "Are soybeans here to stay?" From a few thousand acres in Minnesota in 1936 there was a gradual but rapid increase to over 800,000 acres in 1948. Methods of soybean improvement, as soybeans are a self-pollinated plant, have consisted of introductions, improvement by selection, and hybridization.

Most of the earlier varieties, as with other self-fertilized plants, were produced by plant selection from local and introduced varieties. This has been followed by extensive studies of hybridization. In many cases the crosses and early increases through F_1 have been made at the U.S. Regional Soybean Laboratory, Urbana, Illinois, and breeders in different states have cooperated in tests of promising strains and varieties isolated at individual state stations.

As with other crops, improved varieties adapted to the conditions where they will be grown are a first essential step. In the earlier years the enthusiasm and leadership of such men as R.E. Hodgson, for so many years superintendent of the Waseca Station, played a very important part in soybean studies.

The mechanization of handling the crop, the knowledge that soybeans

could follow corn planting without serious problems, and the establishment of the oil-seed processing industry in Minnesota have been of great importance to the industry. The all-purpose combine has become generally available, and marketing at satisfactory prices has encouraged expansion of the crop. The National Soybean Association also has been responsible for developing sound principles of production, marketing, and utilization of soybeans. Soybean oil is used widely, and soybean meal is of great value for livestock feed. Soybeans also have been used for many other industrial purposes.

In recent years the export trade in soybeans has been an important outlet. In some cases, as in exports to Japan for use as food, this requires special consideration of varietal standards. The Japanese desire a bean with an uncolored hilum or colorless eye. These specifications present new problems that must be solved by the breeder.

In the earlier years diseases were not a serious problem. With more extensive growth, however, the development of disease resistant varieties will without doubt be an essential phase of soybean breeding problems.

TEACHING AND RESEARCH IN CYTOGENETICS

An early appreciation of the importance of facilities for cytogenetics research in relation to plant genetics and breeding was evident from the early 1920s when laboratory facilities and a research microscope were obtained. It was difficult, however, to obtain the necessary leader with sufficient time to carry on research. Powers, when associate professor, made real progress, although he was handicapped by having too many other duties. It was hoped that Myers would be given opportunity to develop cytogenetic phases of research, but it was evident that the necessary financial support was not available.

On returning from China in the spring of 1937 the writer spent a month in Hawaii in relaxation. There he renewed acquaintance with Dr. J.H. Beaumont with whom he cooperated in earlier days in teaching the first course in genetics in Minnesota. At the time of my Honolulu visit Dr. Beaumont was head of the Department of Horticulture, University of Hawaii. Dr. Beaumont arranged for me to visit the president of the University of Hawaii and to my surprise left me with the President shortly after completing my introduction. Like other visits of mine with University Presidents, I expected a few minutes with a busy executive. However, President Crawford seemed in no hurry. He guided our talk and for several minutes we discussed the value of home owned farms and whether such would be feasible for Hawaii. At that time, and also today, I believed in the importance of the home owned farm as a farm business although I now know it usually is necessary to have sufficient land so that it is possible to carry on the business with profit. Later I learned that President Crawford did not believe it could be the usual plan in Hawaii where their two large agricultural industries

were pineapple and sugar production. We had an interesting and enjoyable discussion.

On returning to Minnesota from China in 1937, I had two opportunities to go to the University of Hawaii, the first as Dean of the College of Applied Sciences, and the second as Director of the Hawaiian Agricultural Experiment Station. I decided to take the job offered as director but thought it only fair to see what ideas the Minnesota administration had. Eventually I was asked to meet with President G.S. Ford.

I described the frustrations through the years of attempting to carry out cytogenetic researches and was asked what we needed. My reply was sufficient funds to make the position attractive and continued support so the man in charge would stay at Minnesota because here he had a real opportunity. President Ford said go back home and send in your request for the man. Dr. C.R. Burnham was offered the position to teach graduate courses, direct thesis problems in cytogenetics, and carry on research that he thought most worthwhile. And Dr. Burnham is still at Minnesota. His recent book "Discussion in Cytogenetics," his research papers, and the respect that students have had for him, leads to the conclusion that his appointment was a fortunate one for Minnesota plant genetics research and for Minnesota graduate students.

A COMPREHENSIVE REVIEW

Because of his leadership in breeding wheat for disease resistance Ausemus (1943) was asked to summarize disease resistance studies. He reviewed breeding for disease resistance in wheat, oats, barley, and flax and cited 269 research papers. This 40-page review gives a birdseye view of the great amount of research that was carried out, although in many cases the work of several early investigators was summarized in a single sentence. The review rather clearly portrayed some of the difficulties involved when both the genetics of the organism causing the disease and that of disease reaction on the host plant were emphasized. It was of great value in bringing together brief reviews of the more important studies and the status of the problem at the time. A researcher interested in a particular disease should find the review very helpful.

WEED CONTROL

R.S. Dunham (1951) took part in a conference at Wisconsin and presented a paper on "Differential Responses in Crop Plants to 2,4-D." In this review he summarized numerous researches made in Minnesota and elsewhere.

Particular attention was given to the response of small grains, flax, and corn. It was concluded that there are differences in reaction to 2,4-D among species and among varieties and strains of the same species. Rapidity of

growth during the vegetative phase of plant development at the time of application was an important factor in influencing the results from using 2,4-D or metoxone (MCPA).

Morphological reactions to treatments by herbicides in corn, flax, and small grains were presented in some detail. In many cases these undesirable immediate effects may disappear or be minimized during subsequent growth of the affected plant.

Increase in protein percentage in cereals due to 2,4-D have occurred in barley and wheat, sometimes accompanied by reduction in yield. Marked varietal differences have occurred in extent of oil percentage and iodine number in flax varieties due to herbicide treatment.

INDIVIDUAL STAFF RESEARCHES

In Wheat

Ausemus, Stakman, Hanson, Geddes, and Merritt (1944) collaborated in the production of Newthatch wheat. This variety was produced by crossing Thatcher with Hope, the latter produced by McFadden (1930) in South Dakota from a cross of White Spring Emmer by Marquis.

The Hope variety was known to be resistant to both stem and leaf rust, susceptible to black chaff, and not entirely satisfactory for milling and baking purposes. Thatcher, described previously, was moderately resistant to stem rust, susceptible to leaf rust, and had the record of being widely adapted, of excellent agronomic characters including high yielding ability except where leaf rust was severe, and of excellent milling and baking qualities. It has been grown for many years more extensively in the spring wheat area of North America than any other variety. It was never well adapted to Minnesota, however, because of severe injury from leaf rust. While leaf rust often causes severe reduction in yield, it does not as a rule cause great shriveling of the kernels as results from stem rust.

The backcross method was used in producing Newthatch, backcrossing for three generations to the Thatcher parent and selecting plants that excelled in leaf rust resistance and were free from black chaff. This was followed by pedigree breeding under rust epidemic conditions. Where possible, selection was practiced also for freedom from other diseases including bunt, loose smut, black chaff, scabs, and root rot. Methods used consisted primarily of growing selections in the disease garden, in the F_4 and later generations, after lines were relatively homozygous.

Lines that appeared desirable were bulked and placed in yield trials. Seven lines thus produced, and their parents Hope and Thatcher, were tested for seedling reaction to 20 individual races of stem rust under greenhouse conditions. Hope was resistant to 15 races and susceptible to 5, while

Thatcher was resistant to 7 races, intermediate to 2 races, and susceptible to 11. All of the selections were susceptible to several races. Their reaction to both stem and leaf rust also was determined under field epidemic conditions.

Seven purified selections, selected in F_5 , descending from the same F_2 plant, were so nearly alike that their seed was bulked to produce Newthatch. In yield trials in field plots from 1941-43, Newthatch, on the average, greatly exceeded Thatcher in yield at University Farm and Crookston and gave excellent yields at Morris where Thatcher also yielded well. In these trials Pilot, Regent, Rival, and Renown, which were bred at other stations and had inherited stem rust resistance from Hope or H44, were also tested. Except at Grand Rapids and Duluth, Newthatch gave good yields. Newthatch also proved desirable in milling and baking quality.

Ausemus and Stakman (1944) described Newthatch wheat in Minnesota Farm and Home Science. They reviewed the production of Marquillo from the cross of (Marquis X Iumillo). It carried mature plant resistance but lost favor because of undesirable yellow loaf color. The production of Thatcher which combined the rust resistance of Marquillo under field conditions with Kanred's rust immunity to a group of races, desirable yielding ability, good milling and baking qualities, but susceptibility to leaf rust, was reviewed. When Ceres became susceptible because of the prevalence of Race 36, Thatcher took over. It was grown on about 17 million acres in North America in 1941 and has continued to be grown extensively for many years.

Intensive studies were made during the backcross and segregating generations of crosses of Thatcher X Hope for the purpose of obtaining, as far as possible, resistance to all prevalent races under field conditions.

Ausemus and Stakman (as McCall and Coffey had done in the Foreword of the 1934 Thatcher bulletin) emphasized that "the development of new improved wheats is.....a continuous process."

Perhaps one may learn a lesson from Newthatch. It was never grown very extensively over wide areas in marked contrast to Thatcher. It seems probable that Thatcher and Hope, the parents of Newthatch, differed by many factor pairs. If there were as many as 15 factor pairs and only three generations of back pollinating, only 37 percent of the plants would be, on the average, homozygous for the 15 characters of the recurring or Thatcher parent.

In retrospect several more generations of backcrossing would have been essential. Newthatch did not have the wide adaptability of Thatcher. This is not strange because Hope, while carrying resistance to both stem rust and leaf rust, differs widely in origin from Thatcher and is not particularly desirable in many of its characters. Newthatch lacked many of the characters of Thatcher that made this variety so widely adapted.

Hanson, Ausemus, and Stakman (1950) studied varietal resistance in spring wheats to *Fusarial* head blights. They refer to early studies of crosses of Marquis with Preston and Haynes Blue Stem wheats where lines were isolated by the writer. In studies of these recovered lines Christensen and Stakman found wide differences in resistance to head blight between lines.

Extensive studies of varieties, F_3 lines from random F_2 selections, compared with their parents, have been made under partial environmental control in both nonshaded and shaded plots. Corrections have been made due to time of heading and extent of infection, as there is a rather direct relation between time of heading and infection in artificially induced epidemic plots. The value of these studies in relation to the development of resistant varieties is evident. Although the reaction is conditioned by heredity and the extent of resistance is of great importance, no completely resistant variety has yet been obtained.

Myers and Powers (1938) made further studies of meiotic instability using wheat varieties of great importance in the breeding program for disease resistance. The four more important varieties studied were Marquis, Thatcher, Supreme, and H44. Supreme previously had been shown to be somewhat unstable cytologically, while Marquis had a low percentage of meiotic instability.

Within varieties, selection for high and low meiotic irregularities was continued for several generations with significant positive results. It was apparent, therefore, that meiotic instability was an inherited character.

In these studies Thatcher, as well as Marquis, was low in meiotic instability. Selections within H44 clearly indicated the probability that a more desirable strain of H44 with low instability could be isolated.

In Oats

Hayes, Moore, and Stakman (1939) studied inheritance of characters differentiating *Avena byzantina* and *A. sativa*, stem and crown rust reaction, and smut reaction.

The Bond parent *A. byzantina* was susceptible to stem rust but resistant to prevalent races of crown rust and resistant to smuts. The *A. sativa* parents Anthony, Iogold, Rainbow, and two strains of Double Crosses (Minota X White Russian) X Black Mesdag were resistant to stem rust and the double crosses were resistant to both species of smuts, *Ustilago avenae* and *U. levis*. The Bond and *A. sativa* parents were differentiated by spikelet disarticulation, floret disjunction, and basal hairs, characters used to separate *byzantina* and *sativa*. Bond was of special interest as it excelled in plumpness of seed and kernel size, being less affected by unfavorable environmental conditions than varieties of *sativa* then available.

For studies of stem and crown rust reaction there was good agreement between seedling reaction to individual races in the greenhouse and field reaction to a collection of races from heading to maturity.

For stem rust reaction the segregation agreed well, a 3:1 ratio with resistance dominant. The races used were those to which White Russian is resistant. For crown rust reaction under field conditions the Bond X Rainbow approached a ratio of 3 resistant to 1 susceptible while the other crosses agreed well with the hypothesis of 9 resistant : 7 susceptible. For stem and crown rust the data included both F_2 and F_3 progenies.

In crosses of Bond with Iogold and Anthony the segregation for smut reaction was explained on a single major factor difference with some evidence of minor modifying factors. In the Double Cross X Bond crosses where both parents were resistant, susceptible plants occurred in F_2 . Previous studies of crosses between susceptible *avenae* varieties and Black Mesdag, one of the parents of the Double Crosses, were explained on a two factor pair basis.

Separation of the lower floret of the spikelet vs. normal, and long basal hairs vs. normal each approached a 3:1 segregation. In the Double Cross X Bond, where differences in floret disjunction were found, there was evidence of a single factor difference. For other crosses floret disjunction was more complex in inheritance. Calculated linkage relations for the three factor pairs was:

Spikelet disarticulation and basal hair development	2.7 ± 0.3
Floret disjunction and basal hair development	24.0 ± 0.3
Spikelet disarticulation and floret disjunction	25.7 ± 0.3

Both crown and stem rust reaction seemed independent in inheritance of characters differentiating the *sativa* and *byzantina* species.

It seemed evident that percentage plumpness of grain, a character in which Bond excelled, could be combined with other differential characters.

Hayes (1941) compared 158 purified selections of crosses of Bond X A. *sativa* varieties with their parents grown in rod-row yield trials at the central and branch stations. Data included means for stooling, yield per acre, and weight per bushel. Part of the data were collected by C.C. Tsu as part of his M.S. thesis.

In individually spaced plots in 1938 Bond was about equal in stooling to the average of the other parents. Probably because of the larger number of hybrids, seven of the 158 excelled any of the parent determinations for stooling where only 40 separate determinations were made.

Similar results were obtained in rod-row trials at University Farm and Waseca. Apparently Bond in these trials was equal to *sativa* varieties in stooling capacity. Little or no relation was found between stooling capacity

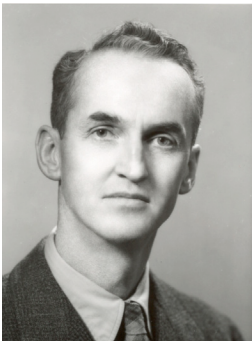
as determined in spaced plots and in rod-row trials where the same varieties were grown in both types of planting. On the average Bond and the Bond crosses were superior to the *sativa* parents in stooling. At University Farm and Waseca 154 selections from crosses where Bond was one of the parents were grown in rod-row trials. An r value of .30 was computed between stooling at the two stations.

For yield the *sativa* parents averaged 58.7 bu, 13 other *sativa* varieties averaged 51.3 bu. Bond yielded 54 bu, and Bond crosses averaged 55.1 bu. Rainbow had the highest yield at Waseca, 75 bushels, and was partially responsible for the high average yield of parent varieties.

Other rod-row trials at University Farm, Waseca, Morris, and Crookston in 1940, where selected hybrids were compared with parents, showed that many hybrids were outstanding in yield.

In weight per bushel Bond and a considerable number of the hybrids were markedly superior to the selected *sativa* parental varieties. It is evident that Bond was an excellent source of parental germ plasm for several agronomic characters already discussed, in ability to withstand lodging and for crown rust and smut resistance.

Several of the Bond crosses were named; Bonda and Mindo were available for seed growers in 1947. Andrew and Zephyr from Bond crosses later were increased and distributed. Yield trials of these four varieties were reported by Hayes (1948) and descriptions are given in the Extension Folder 22 (1948) as prepared by the experiment station staffs. The folder includes varieties recommended by the vote of all crops research workers in agronomy and plant pathology at the central and branch stations.



Matthew B. Moore, Plant Pathologist and Active Cooperator in Oat Breeding Investigations. Moore has been an enthusiastic cooperater and has been responsible in a marked degree for the accomplishments resulting from the oat breeding project.

Moore, Hayes, and Stakman (1945) discussed stem rust reaction of hybrids and varieties of oats in relation to problems of developing varieties adequately resistant to rust. The basis of this discussion was the rust reaction of hybrids and varieties under field conditions in 1943. Selections from hybrids having Rainbow or Iogold as the rust resistant parent and the varieties Tama and Vickland often showed two types of pustules, resistant and susceptible, on the same plant. Hybrids carrying the White Russian type of resistance bred true for resistance and semi-resistance with no large confluent pustules.

Nine collections were made from the sources presumed to carry resistance in the seedling stages (Iogold, Rainbow, Tama, Vickland) to Races 1, 2, 3, 5, and 7 and susceptibility to Races 4, 6, 8, 9,

and 10. Eight collections were made from certain White Russian derivatives (Anthony, Bond X Double Cross A and B) carrying resistance to Races 1, 2, 5, 8, 9, and 10 and susceptibility to Races 3, 4, 6, and 7. Four races only were identified from the White Russian group sources. All were Races 2 and 5 except one that contained 30 percent of pustules of Races 8 and 10. All nine collections from large pustules on the logold group were Races 8 and 10.

Welsh (1937) reported that seedling resistance to Races 1, 4, 5, and 6 could be obtained from a resistant selection from a cross of Hajira X Joanette. Welsh found, however, that this type of resistance broke down, partially at least, at high temperatures. In later work this has been referred to as the Canadian type of resistance.

The discussion emphasizes the importance of a knowledge of the prevalence of races of *Puccinia graminis avenae*, the production of new races that in some cases may be more virulent by hybridization and recombination, as is known to happen for *P. graminis tritici*, and the necessity of continued research and experimentation if one wishes to continually have available adequately resistant varieties.

Kehr, Hayes, Moore, and Stakman (1950) collaborated in a summary "The present status of breeding rust resistant oats at the Minnesota Station." At that time Kehr was a research assistant in oat breeding investigations supported by funds from the Quaker Oats Company.

As already reviewed, the accomplishments of several graduate students majoring in plant genetics with minors in plant pathology have been of special value. These include Garber (1922) who found that the White Russian type of stem rust resistance was dependent upon a single factor pair $R_{WR}r$; Smith (1934) who discovered that the White Russian type of stem rust resistance, R_{WR} to Races 1, 2, 5, 8, 9, and 10 and the Richland-Rainbow-logold type of resistance, R_R , were multiple alleles with the series of alleles R_{WR} , R_R , and r ; Foote (1948) who concluded that the Canadian type of stem rust resistance to all races functioned at moderate temperatures to condition resistance and was independent of inheritance of either the White Russian or logold types of resistance. Foote concluded that the Canadian type R_C was due to a single factor pair. Unfortunately, the Canadian type breaks down at high temperatures, and under these conditions the oat varieties and strains become susceptible.

The writer, Kehr, and others discussed the difficulty of determining strains that combined the Canadian factor with that for either the White Russian resistance or the logold-Rainbow-Richland factor. If the gene for Canadian resistance R_C was epistatic to that for the other types R_{WR} or R_R , there would be no value in such a combination.

Graduate theses also have been of great value in relation to crown rust resistance. Smith (1934) presented a preliminary study of inheritance

of the Victoria type of resistance to crown rust. Although resistant types could be recovered from crosses with ease, it was impossible in this study to determine the factor basis. Extensive studies at Ames, Iowa, in a thesis problem (Litzenberger, 1948) led to the conclusion that the Victoria type of resistance was conditioned by a single factor pair.

Intensive studies of races of crown rust have been made. Hoerner (1919) made an early study. Sources of resistance used in Minnesota were Victoria, resistant to 82 of 88 known races¹; Bond, resistant to 79 Races; and Landhafer, resistant to all known races at that time.

Hayes, Moore, and Stakman (1939) concluded that the Bond type of resistance to crown rust resulted from the dominant condition of two main complementary factors. Similar results with a slightly different interpretation were obtained by Torrie (1939). There was a late epidemic in the rust nurseries in 1939, presumably due to Race 45 to which Bond was susceptible. This led to a condition where resistant plants produced, as a rule, large numbers of small pustules with a small number of large confluent pustules.

Kehr (1949) in his Ph.D. thesis (see Kehr and Hayes, 1950) concluded that Landhafer resistance to crown rust, in crosses with other varieties, was due to a single factor pair that was non-allelic to the Bond factors for resistance. Litzenberger found Landhafer to be moderately resistant to certain crown rust races in the field under heavy epidemics. Bond, however, in the Minnesota studies carries two complementary factors for resistance which appeared to function satisfactorily to races prevalent at the time, except for the case where Race 45 caused some large pustules on Bond and Bond derivatives.

Breeding for stem and crown rust resistance at Minnesota has been a major problem in the cooperative work. References under graduate student studies have been discussed in some detail. These have been essential in the oat breeding program where extensive studies of agronomic characters in yield trials have been made. The four Bond derivatives, Bonda, Mindo, Andrew, and Zephyr, have been described although at present none of these varieties are still on the recommended list.

In connection with the registration of oat varieties, D.D. Morey² (1962), associate agronomist, Georgia Agricultural Experiment Station, describes new varieties AB-110, Radar 1, and Radar 2. Morey described the use as a parent of a selection from Minnesota, 0-200-10 from the cross of (Hajira-Joanette X Bond-Rainbow) X Santa Fe where a few F₃ seeds that carried crown and stem rust resistance were obtained from Minnesota.

¹Letter from Dr. H.C. Murphy, USDA, Bureau of Plant Industry, Soils and Agricultural Engineering, Ames, Iowa, March 25, 1949.]

²Morey, Darrel D. 1962. *Crop Science* 2:531

The Hajira-Joanette resistance was first obtained at the Dominion Rust Laboratory, the Bond resistance in Bond-Rainbow from Minnesota, and Santa Fe and Bond from USDA introductions. Thus, a considerable number of workers was responsible for the Minnesota 0-200-10 F₃ line.

Hayes (1946) in a discussion, "Yield genes, heterosis, and combining ability," emphasized the importance of disease resistance to yield performance, particularly in wheat, with illustrations from Hope, H44, Thatcher, and other varieties. The study also pointed out to the breeder the value of genes for kernel quality and other characters as well as disease reaction, as exemplified by oat varieties Bond and Victoria, which have been used so widely as parents by oat breeders.

In Barley



Dr. J.J. Christensen, active cooperater in many phases of disease resistance problems. Chief of Division of Plant Pathology from 1953 to 1961. Inspirational teacher and research leader.

Immer, Christensen, and Loegering (1943) tested susceptibility of strains of barley to *Fusarium* and *Helminthosporium* kernel blight when grown under muslin tents and in a field nursery.

It was concluded that reaction to *H. sativum* and to *Fusarium* blight was essentially the same. Date of heading was significantly related to degree of infection, especially under tent where selection for resistance would lead to the selection of late heading strains. Some strains or varieties like Peatland were consistently lower in infection than others, and some strains consistently had high infection. There were distinct varietal differences of marked significance.

The researchers used two resistant and two susceptible varieties that had been consistent in their reaction under field conditions to a collection of races of stem rust. Twenty strains that were selected from a cross of the resistant and susceptible parent varieties were included in the study. They used 19 races of *Puccinia graminis tritici* and one of *P. graminis secalis*.

The trials were run individually to each race in the seedling stages in the greenhouse. The varieties and strains resistant or susceptible in the field reacted in the same manner to each of the races in the seedling stages. All varieties were susceptible to race 29 in the seedling stages and also, as far as tested, in the mature plant stage. This collection of Race 29 was obtained from aecia on barberry.

The physiological races were furnished by the Division of Plant Disease Control of the Bureau of Entomology and Plant Quarantine, United States Department of Agriculture, and the Minnesota Department of Plant Pathology.

In Flax

Arny (1949) described an improved variety of flax named Dakold, Registration No. 8, developed through cooperation by the North Dakota, Minnesota, and Montana Experiment Stations and the Division of Cereal Crops and Diseases, U.S. Department of Agriculture. Special attention was given to yield, quality of oil, and disease resistance.

This variety has been immune to races of rust, *Melampsora lini*, prevalent east of the Rocky Mountains and moderately resistant to wilt, *Fusarium lini*, and to pasmo, *Sphaerella linorum*.

The new variety excels in yield, is intermediate in oil percentage of seeds, and produces satisfactory oil quality.

A new variety Minerva, Registration No. 9, produced by cooperation of the Minnesota Station and the USDA was described also. This variety exceeds Dakold in oil percentage of seed, is the equal of Dakold in quality of oil, and has proven to be a little higher in yield. It is about equal in wilt resistance and lower in pasmo infection.

In Sugarbeets

R.W. Henderson, associate geneticist, and H.W. Bockstahler, assistant pathologist, collaborated in a study (1946) of reaction in sugarbeets to "black root" caused by *Aphanomyces cochloides* Drechs, under the leadership of Dr. G.H. Coons, principal pathologist, Division of Sugar Plant Investigations, BPI, USDA. Dr. Coons is recognized as a worldwide leader in sugarbeet research, particularly in relation to disease resistance.

They primarily studied the chronic phase of the disease which affects plants not killed in the acute stages (within a week or two of emergence of seedlings).

Material used consisted of U.S. 216 definitely resistant in the chronic phase, a hybrid S.P. 1-9-00 highly susceptible, and 216 open-pollinated seed progenies of mother beets that survived in heavily infested soil. Duplicate 16-foot progeny rows were grown in heavily infested soil at Waseca, where Hodgson was a supporter of the studies. Twelve inbred lines, one synthetic variety, and a commercial variety were compared in eight randomized blocks of 33-foot single rows at Waseca and in 20-foot single rows at University Farm, St. Paul.

When the 216 progenies were compared with U.S. 216, 70 were superior in top growth, 61 were equal to U.S. 216, and 85 were inferior in post emergence survival; for root development 50 of the 70 superior progenies in top growth were also superior to U.S. 216 in average vigor of roots.

The investigators also compared several susceptible and resistant

inbreds with crosses between inbreds of the types susceptible X susceptible, susceptible X resistant, and resistant X resistant, a mass selected synthetic, and a local commercial variety. The resistant X resistant led in root yield on infested soil at Waseca and were the equal of the commercial variety on uninfested soil at University Farm.

In relation to the chronic phase of the disease there was excellent agreement between reaction to *A. cochloides* of three sugarbeet strains when grown in the greenhouse on steamed inoculated soil plus inoculum and reaction in the field in heavily infested soil.

Further studies of black root resistance (see Gaskill et al., 1948) were made in 1947 to see if manner of reaction to the black root disease was due to differences in biotypes of the pathogen involved. Some of the strains isolated and reported previously were used; plantings were made in Blissfield, Michigan, and Waseca, Minnesota.

Sixty-two strains were grown at each location under severe black root exposure conditions with two replications at each location. The checks, resistant and susceptible, respectively, responded in the same manner at both locations. Although in general there was good agreement between reaction at the two locations, one or two strains reacted differently. The investigators stated that the value of making tests at several localities was of importance. Perhaps I may suggest that differences in reaction due to environmental or ecological differences often cause modifications in disease reaction as well as in agronomical and botanical characters. The probability of biotype differences in the pathogen are very great, even if such differences have not been demonstrated completely.

In Forage Crops

Breeding of grasses in Minnesota was initiated in the spring of 1936. Shultz (1941) and Tsiang (1942) in thesis studies and Myers (1942) reviewed the literature relating to self- and cross-fertility of the grasses.

Hayes and Schmid (1943) studied selection of self-pollinated lines of *Bromus inermis* Leyss., *Festuca elatior* L., and *Dactylis glomerata* L. To insure selfing, vegetable parchment bags 18 by 3 by 2 ½ inches were used to cover the panicles. They were tied to supporting stakes by string inserted in an eyelet at the base of the bags. Progenies of selfed lines and commercial check varieties were grown as individual plants in spaced plots. Previous studies of Shultz and Myers had shown there are inherited differences in seed setting with orchard grass under conditions of self-pollination. Tsiang previously had shown inherited differences in brome grass in reaction to leaf spot.

During each of the 5 years of study (1937 to 1942), sufficient seed per plant was obtained to furnish a basis for selection in self-pollinated lines, providing three times as many plants were handled as were desired to use in

growing individual progenies.

Although there was evidence of reduction in vigor in selfed lines, on the average after 2 years of selfing with all three species, there were a few lines of each crop that were as vigorous as the commercial checks.

Although there were highly significant differences in leaf spot reaction caused primarily by *Selenophoma bromigena* in orchard grass, there were not sufficient plants grown to make it possible to explain the factors involved.

F₁ crosses between S₁ clones were grown for brome and orchard grass in small space-planted plots and compared with the commercial check as 100. With brome the yield of F₁ ranged from 126.5 to 220.9 percent. The highest yield was from a cross of two leaf spot resistant lines. The F₁ crosses of orchard grass yield, on the average, about the same as the commercial check.

Selection in self-pollinated lines of each of the three species would seem to be a desirable method of isolating disease resistant strains and appeared promising as a desirable procedure for other breeding problems with each of the three grasses.

H.L. Thomas (1946) describes briefly in Farm and Home Science the effect of wilt in relation to yield and stand of alfalfa from replicated plots under the direction of R.O. Bridgford, agronomist at Morris. Ladak gave the highest average yield, 1941-44 inclusive, of 4.7 tons per acre. Ranger yielded 4.4 tons, Grimm 4.2 tons, and Northern Common 3.8 tons. Bacterial wilt appeared in 1944. Stands in the spring of 1945 for the four varieties were Ladak 70 percent, Ranger 88 percent, Grimm 30 percent, and Northern Common 40 percent.

In these same studies Hardistan, Crestan, and Cossack were resistant to bacterial wilt while Kansas Common and Kaw were clearly susceptible.

Thomas and Hayes (1947) made a short review of studies with Kentucky bluegrass. This involved the selection and propagation of 261 vigorous plants obtained from 60 sod pieces dug up in old pastures in Minnesota. Small plots were used by originally planting a rectangle containing 7 X 11 pieces, 7 inches apart each way, of each clone.

Thirty of the 281 clones were selected, and from these both open-pollinated seed and seed obtained by isolation under a bag was produced. Seedlings were started in the greenhouse and transplanted into rows for individual plant study for each of two seed sources for these 30 clones. In this comparison there was excellent agreement between seed progenies from the same original plants produced from isolated seed under bag and seed of uncovered heads. This agrees with previous work on parthenogenetic development of seeds.

The mowing plots were harvested as desired, making six or seven cuttings

per year. White clover also was established in a part of the mowing plots. When conditions were similar in different years, there was relatively good agreement in productivity from year to year. For some reason productivity of different strains in 1944 was not correlated with that of other years.

It was concluded that most strains were highly apomictic, that wide differences occurred in clonal line production in mowing trials, and that the protein content of grass alone in mowing tests of six or seven cuttings a year for different clones gave significant differences. The crude protein content ranged from 23.8 to 27.7 percent of the dry matter. Several strains that were more productive than the commercial bluegrass check were selected and established in a new trial.

Thomas, Hayes, and Schmid (1948) summarized results of 10 years of field testing of forage grasses in Minnesota at the central and branch experiment stations. The studies included Kentucky bluegrass, Parkland and commercial brome, timothy, redtop, Fairway crested wheat, meadow fescue, Ladak alfalfa, and mixtures of alfalfa with brome and timothy.

Brome and alfalfa were superior, on the average, in both hay and in clipped plots, although timothy gave excellent yields in many comparisons. Percentage of protein in plots cut for hay were the highest for Ladak alfalfa, 16.1 percent on a dry basis, followed by alfalfa and brome at 15 percent and commercial brome at 14 percent. Timothy was lower at only 10.8 percent. In clipped plots cut to simulate pasture the grass and alfalfa mixtures were equal in protein percentages to alfalfa alone.

A considerable number of introduced grasses and legumes as given in the bulletin were tested rather extensively. None of these were of sufficient promise to warrant presentation of detailed data.

Thomas and McPherron (1949) reported "Tests of brome grass strains in Minnesota." McPherron was agronomist, Soil Conservation Service, with headquarters at Winona. Many of the strains were supplied by M.A. Hein of the Bureau of Plant Industry Forage Crops Investigations, Baltimore, Maryland.

Three-year averages were presented with three replications from hay plots established at seven stations in central and southern Minnesota and at two northern stations, Breckenridge and Crookston. Average yields as hay from the first cutting were given for each of five stations, for three southern stations and for the two northern stations.

Lincoln, Fisher, and Achenbach, well-known southern strains, preformed well and yielded well in nearly all trials. Differences between strains were not great.

The southern strains, particularly in southern Minnesota, were distinctly superior in early growth to other strains. The Martin variety was intermediate

in early growth habit and clearly superior to most strains except the southern varieties.

In seed production trials where only four varieties were grown at six localities for 3 years, Canadian commercial gave an average yield of 194 lbs per acre; followed by Martin at 177 lbs, and Parkland and Fisher with yields of 152 and 122 lbs, respectively.

Kernkamp, Gibler, and Elling (1949) studied damping off, caused by *Rhizoctonia solani*, of alfalfa cuttings. They presented data to show that severe damping off was a result of infection with *Rhizoctonia solani*. This was largely controlled in later experiments in the greenhouse when all essential equipment including flats, soil, and vermiculite was autoclaved prior to making plantings. It also appeared desirable to use partial sterilization with formaldehyde of soil in benches on which flats were placed. They recommend the use of sterile clay saucers under the flats and suggested that the external portions of the cuttings be dipped in dry Phygon immediately preceding planting.

In Corn

Hayes (1940) summarized briefly the improvement of B164, an inbred line of corn, by the backcrossing method. The procedure used was to cross B164 with an early inbred C37 that was smut resistant. Smut free plants were backcrossed for two generations to B164 and the resultant material self-pollinated and selected for smut free plants for two succeeding years. Inbreds were selected for about the same maturity as B164. Several of these proved desirable and have been used in the corn breeding program.

Similarly in the double cross Minhybrid 403 (11 X 14) (374 X 375) where 374 and 375 were relatively smut resistant and 11 and 14 were rather susceptible, three backcrosses were used of (11 X 375) 11 and (14 X 374) 14. In these crosses 11 and 14 were inbreds from Minnesota No. 13, and the original origin of 374 and 375 was an inbred received from Holbert.

By following the same procedure as for B164, inbreds were obtained that were decidedly superior in smut resistance and other characters to inbreds 11 and 14.

The extensive breeding studies with corn have been reviewed in "A Professor's Story of Hybrid Corn," Hayes (1963).

FURTHER APPLICATIONS OF COOPERATION IN OTHER COUNTRIES

During 1932 while on leave of absence from Minnesota the writer held the position of Professor of Plant Breeding at Cornell, as previously mentioned in Chapter IV. Shortly after arriving at Cornell, Manuel Elgueta

from Chile called at my office. At that time he was on leave of absence from his position as Director Departamento de Genetica Y Fitotecnia, Departamento de Agricultura, in Chile and had spent six months as a graduate student in California. He wished to spend some time with me as he was greatly interested in all phases of crop improvement. When he learned I was to be in Cornell he decided to spend the second half of his leave at Cornell. He was a frequent visitor, not only in my office, but both he and his wife often visited in our home. Our talks ranged over a wide field but more frequently about crop improvement. I learned of some of his problems in agricultural research. He hoped to arrange for me to visit Chile.

In 1941 I was a member of the Nelson Rockefeller Committee to aid in the development of cultural relations with South America. On going to Chile I was asked to teach at the University of Chile a small group of students and technicians interested in the development of crop research in their country. At least four of this rather small class of 18 later took graduate work in agronomy and plant genetics at Minnesota, and over a dozen continued in agricultural research. Two of the students, Rene Cortazar and Carmen Sanz first met in my class, and later married. Miss Sanz came to the United States and completed a year of study in Dr. Blakeslee's laboratory in cytogenetics at Smith College, while Rene majored in plant genetics at Minnesota. Both earned M.S. degrees, and Cortazar completed work for the Ph.D. in Minnesota in 1962.

In Chile, after nearly completing my visit, Manuel Elgueta, whom I had known at Cornell, and I drew up a report with a plan for nation-wide cooperative crop research.

A summary of the investigations of the Ex-Departamento de Genetica Y Fitotecnia, 1940-1947, was published in Monograph Form in 1950 by the Departamento de Investigaciones Agrícolas, Direccion General de Agricultura by Elgueta and co-workers, many of whom were in the class I taught in 1941. In presenting this volume to me Elgueta wrote on the title page, "With sincere appreciation to Dr. H.K. Hayes whose teachings and inspiration made a great part of this work possible."

Relative to our story of disease resistance are breeding studies reported by Cortazar with wheat in relation to stem rust and leaf rust, and studies by Dora Volosky of physiologic races of rust. Miss Volosky was a student in the class I taught in Chile and completed training in Argentina with Dr. Jose Vallega, who had majored in plant pathology at Minnesota.

On the way home I met several Argentine research workers who later became students in our department. During these foreign contacts I emphasized constantly the value of cooperative research, such as I like to think is admirably exemplified by the Minnesota cooperative disease resistance program.

Chapter 7

Graduate Student Research, 1937-52 Inclusive

INTRODUCTION

The reviews in this chapter have been placed under the following headings: wheat, oats, barley, flax, rye, corn, soybeans, cotton, sugarbeets, onions, tomatoes, and forages taken collectively. Each thesis has been reviewed separately and the major and minor fields of study have been given.

INDIVIDUAL THESIS PROBLEMS

In Wheat

C.L. Pan (1940) majored in plant genetics and minored in plant pathology for the Ph.D. degree. He studied inheritance of mature plant reaction to stem rust and reaction to black chaff in wheat using a rather wide series of parent varieties. Available races of stem rust were used to create an epidemic. The parents included:

1. Marquis X H44, III-31-7 from the Dominion Rust Laboratory, Canada. Resistant to stem rust and black chaff.
2. Pentad X Marquis, III-34-1, also from Dominion Rust Laboratory. Semi-resistant to stem rust and resistant to black chaff.
3. Double Cross, II-21-80, (Marquis X Iumillo) (Marquis X Kanred). Moderately resistant to stem rust and resistant to black chaff.
4. H44 and Hope, produced by McFadden. Resistant to stem rust and susceptible to black chaff.

Parents and crosses were studied in F_2 , and breeding behavior of selected plants was tested in F_3 and F_4 . An artificial epidemic of rust was produced while black chaff developed normally.

Hope and H44 bred true for resistance to stem rust while other parental material, Pentad X Marquis, III-34-1, Double Cross, II-21-80, and Marquis X H44, III-31-7, produced both resistant and semi-resistant plants with a few

classified as susceptible. The Pentad X Marquis variety and the Double Cross selection produced more plants classified as susceptible than other parents. The cause of the variability was not determined. The Double Cross parent and the Pentad X Marquis selection were somewhat less resistant to stem rust than other varieties in the study.

The data obtained from appropriate crosses indicated that a factor for rust resistance in the H44 X Marquis selection is the same or allelic to a factor carried by Hope because only resistant plants were obtained from their crosses.

Pentad X Marquis, III-34-1, and Double Cross, II-21-80, both carried the same pair of complementary recessive genes for stem rust resistance.

When Hope was crossed with the selection of Pentad X Marquis, or Marquis X H44 was crossed with Double Cross, II-21-80, the F_1 was resistant and segregation in F_2 produced a range from resistant to susceptible indicating no close association between genes for resistance from the two sources.

A natural epidemic of black chaff occurred, and both Hope and H44 X Marquis were moderately to severely infected. The few F_1 plants grown of these crosses appeared about as susceptible to black chaff as the susceptible parent. Segregation occurred in F_2 although it was impossible to determine the factor basis.

There was an association in inheritance between resistance to stem rust and susceptibility to black chaff in appropriate crosses, but the association was not complete.

These results indicated that the same gene for stem rust resistance functions in Hope and in the parental selection H44 X Marquis. This was the first proof that Minnesota double crosses which obtained their stem rust resistance from Lumillo durum carry the same two complementary recessive factors for mature plant resistance to stem rust as are present in the vulgare-like wheat selection, Pentad X Marquis, III-34-1.

From 1953 to 1958 Pan was stationed in Egypt with FAO. He led in selecting a variety of rice named Nahda that was resistant to several prevalent diseases and less susceptible to stem borers than varieties being grown at that time. Nahda excelled in yield, milling, and cooking qualities. Following Pan's recommendation the variety was increased and soon occupied approximately 760,000 acres. Under improved cultural practices suggested by Pan, Nahda gave increased yields over varieties previously grown. This work has been referred to as one of the outstanding FAO accomplishments in the field of crop improvement.

J.R. Weir (1944) completed work for the Ph.D. degree with a major in plant genetics and a minor in plant physiology. The thesis work, "A study

of the inheritance of protein content, date of heading, and height in a cross of Prelude X Dicklow spring wheat," was carried out at the University of Alberta.

The Dicklow parent was a low protein spring wheat obtained from Northern California; Prelude was an excellent milling and bread making variety characterized by high protein content. This work was a phase of the study to obtain an early, high quality, soft white spring wheat suitable to the grey soil of the prairie provinces.

Seventy F_2 plants selected at random from Dicklow X Prelude were grown. Composite samples of the same number of seeds from 50 F_3 individually spaced plants were used for nitrogen determinations.

The parent varieties from separate plantings each had a narrow range of variation for protein content. There was a wide range in the means of 70 F_3 lines, although F_3 hybrid lines with protein content similar to that of the parents were not recovered. From F_4 tests and studies of their standard deviations, some lines with low variability in various classes were relatively homozygous and ranges in the means of progenies, where much larger numbers of F_4 lines were grown, nearly covered the total range in protein content of the two parents.

Time of heading and height of plants also were studied. All characters including protein content were complexly inherited and dependent upon multiple factors.

There was a highly significant negative relation in the hybrids between protein content and days to heading and between protein content and height of plant similar to the relationships in the parents. No very important relationships were found when correlations of other characters were studied, although some r values were statistically significant.

Howard R. Peto (1945), with a major in plant genetics and minor in plant physiology, made a study of "The nature of drought resistance in spring wheat."

Previously Peto had found that selection for drought resistance was very difficult during 7 years in the drought area of Western Canada.

The ability of plants to tiller under normal conditions appeared to be associated with ability to yield under drought conditions.

Varietal selection on the basis of resistance to atmospheric conditions in an artificial drought machine where temperature, light, humidity, and air currents were controlled, was not found to be correlated with yield under conditions of both soil and atmospheric drought.

Numerous other studies of chemical and physiologic relationships resulted in no associations of practical value for differentiating varietal

differences in drought reactions.

I.M. Atkins (1945) studied inheritance of characters associated with lodging in a winter wheat cross for his Ph.D. thesis problem with a major in plant genetics and minor in plant pathology.

The cross studied was between Kanred, the hard red winter wheat, and Coppei, a lodging resistant club wheat. Measurements of weight per unit, breaking strength of the culm near the base of the plant, and other morphological characters were studied. As no lodging occurred during the course of the study, he was unable to determine associations between various measurements and lodging as expressed under field conditions.

Correlations between breaking strength of F_3 parent plants and the mean of their F_4 progenies in 1937 and 1942, respectively, were .53 and .62. Weight per unit volume relationships in the same material were definitely lower.

Atkins has published extensively on various aspects of small grain investigations, especially disease resistance.

F.H. Abbasi (1945) studied "Mature plant and physiological resistance to stem rust in crosses of Premier with Kenya" for the Ph.D. degree with a major in plant genetics and a minor in plant pathology. Abbasi held the Sir Currimbhoy Ebrahimbhoy Scholarship of the University of Bombay, India.

Premier was developed at North Dakota from a cross of Ceres X. (Hope X Florence) X Canadian Rust Laboratory No. 625. It is a bearded variety similar to Hope in stem rust resistance. Kenya R.L. 1373 is an introduction from Kenya Colony and was obtained from the Dominion Rust Laboratory. It is awnless, resistant to many races of stem rust in the seedling stages, and susceptible to leaf rust. Ausemus supplied F_2 material, and Abbasi produced seed of F_1 and backcrosses. F_2 crosses of Hope X Kenya also were studied.

The classification of material from both crosses under a field epidemic caused by many races proved to be rather difficult when the breeding behavior of a plant for rust reaction was compared with that of its progeny. Under field conditions the F_1 generation was resistant. Results were explained by the assumption that the parents differed by two factor pairs—a dominant factor for the mature plant resistance from Hope, epistatic to a factor from Kenya for physiologic resistance to many races—and that these two factor pairs were independent in inheritance.

Premier was moderately resistant to leaf rust and Kenya susceptible. Results for leaf rust reaction agreed with a single factor difference.

There was no evidence of association in inheritance of genes conditioning the mature and seedling types of resistance to a collection of races of stem rust.

There was slight, although not very significant, evidence that lines with both mature and physiological resistance tended to yield higher than closely related lines carrying mature plant resistance but lacking the genes for physiological resistance.

Yield, seed plumpness, and test weight were rather significantly correlated in comparable hybrid material.

William Semeniuk's thesis study for the Ph.D. degree with a major in plant genetics and a minor in plant pathology was published (1947) posthumously after he was reported missing in action as a member of the R.C.A.F.

His research, "Chromosome stability in certain rust derivatives from a *T. vulgare* X *T. timopheevi* cross," was a phase of the cooperative wheat investigations at Minnesota.

The anomalies in chromosome behavior included micronuclei in quartets, lagging univalents and bivalents and other types of non-oriented univalent and bivalent chromosomes, and abnormal pollen grains. Data were taken on seed set in individual florets and in the spike.

Correlations were highly significant for the extent of various types of chromosome irregularities and for percentages of pollen abortion. This latter character was considered to be useful to the plant breeder in some cases in the elimination of highly unstable progenies, although some lines with high chromosomal instability had no appreciable abortion of pollen. The frequency of micronuclei in quartets and of microspores was thought to be of value in later use to establish the stability of selected lines.

The original material, obtained from S.L. Macindoe, Australia, consisted of single spikes of F_5 and F_6 selections that had been selected for stem and rust resistance from Pridham's cross of Steinwedel, a soft white common wheat, X *T. timopheevi*. Semeniuk concluded, "It was possible to select lines from Pridham's material which combined high chromosomal stability with *vulgare* characters and resistance to stem and leaf rusts."

G.S. Smith (1947) studied "Inheritance of stem rust reaction, glume tenacity, and head type in Mindum durum X Vernal emmer" for his Ph.D. thesis with a major in plant genetics and a minor in plant pathology.

Mindum was susceptible in both seedling and mature plant stages to the most prevalent stem rust races attacking durum and was resistant to the uncommon Race 147, while Vernal was resistant to Race 17 and susceptible to Race 147.

Seedling reaction to both races was studied, and a single factor pair seemed to explain the reaction. The Sr^V gene from Vernal emmer, however, was allelic to the Sr^m derived from Mindum. Inheritance of stem rust reaction in the field, where Races 17 and 38 were recovered, was governed also by

the factor Sr^V .

There was no relation between the inheritance of glume tenacity, or head shape, and rust reaction.

Smith in later years has been very successful in breeding stem rust resistant varieties of durum wheats that have excellent macaroni qualities and that excel in agronomic characters.

S.Z. Hasanain (1948) completed studies for the Ph.D. degree with a joint major-minor in plant genetics and plant pathology. He studied "Stem rust reaction and other characters in Indian wheat varieties and their crosses.

Before coming to Minnesota he held a 2-year fellowship from the Government of the United Provinces for research in plant breeding at Pusa, and from 1937 to 1945 he was in charge of the Wheat Breeding Station at Simla when he was awarded a fellowship by the British Indian Government for overseas training. He studied in Great Britain for several months.

The investigations at Minnesota were undertaken (1) to study mode of inheritance of rust reaction in crosses between resistant varieties and desirable susceptible Indian varieties known to be adapted to the Indian Peninsula and (2) to study the effects of environmental conditions on the variability of rust reaction in these varieties and their hybrids.

Inoculation with races by hypodermic needle under field conditions using Races 15b and 116, the latter similar to Race 40 of India, showed rather wide variation from the time of inoculation to sporulation. This varied from 8 to 10 days in Pusa 4 and Pusa 120, susceptible in the seedling stages in the greenhouse, to an incubation period of 15 to 18 days for the variety K58 and other resistant varieties.

The variety Gaza-Bobbin in the field was resistant until July 28 when high temperatures lowered its resistance and it became moderately susceptible.

Pusa 4 and P120 were completely susceptible in the field, Gaza-Bobbin moderately susceptible, K58 and K144 moderately resistant, and Khapli highly resistant.

In crosses of Pusa 4 X K58 and Pusa 120 X K144, there was phenotypic dominance of susceptibility over resistance. The hypothesis was used that there are three pairs of factors of equal and cumulative reaction to Race 15b and that four or more dominant factors conditioned resistance to 15b—also that a different set of factors conditioned reaction to Race 40(116).

In crosses of Pusa 4, susceptible, X Kenya Rust Lab. 1374 the Kenya parent was moderately resistant to Race 15b and highly resistant to Race 40. One major factor pair differentiated reaction with susceptibility dominant.

There was no evidence of association between agronomic or botanical characters studied and rust reaction.

M.A. Ayad (1948) studied "Correlated inheritance of reaction to stem rust and other characters in crosses between Egyptian varieties of wheat" with a major in plant genetics and minor in plant pathology.

The purpose of the study, supported by funds from the Egyptian government, were (1) to identify races of stem rust prevalent in Egypt, (2) to study mode of inheritance in crosses of three rust resistant varieties and one susceptible variety, and (3) to study extent causes of variability in rust reaction due to environmental causes.

Racial prevalence studies were attempted by having Egyptian collections sent to Minnesota. Only a few spores germinated in each of 2 years. From this material Race 21 was identified and also a low proportion of Race 38 in one sample. It was suggested that this race may be an admixture of material from greenhouse studies.

The stem rust resistant varieties used as parents in crosses were Hindi Immune, Giza 139, and Cross 951A; the susceptible parent variety was Hindi 62. Reactions to the five races—15b, 17, 19, 21, and 38—were studied using Minnesota races as furnished by plant pathology. The three resistant varieties were found to be highly resistant to all races except 15b; Hindi Immune was susceptible to 15b while Giza 139 and Cross 951A were moderately resistant. Races 17, 21, and 38 were selected to be used in studying crosses. Hindi 62 was completely susceptible to all races.

Greenhouse rust reactions of the four parental varieties were very stable in studying reactions to Races 21 and 38, when the studies were made under controlled differential conditions for light and moisture.

Intercrosses between the three resistant varieties were studied in F_3 for reaction to Races 17, 21, and 38. Only highly resistant reactions were obtained for the parental varieties and the progeny of the crosses.

When the resistant varieties were each crossed with the susceptible variety, Hindi 62, the cross with Hindi Immune was in agreement with the hypothesis that a single factor pair explained reaction to all three Races 17, 21, and 38; with Giza 139 the reaction to Race 38 could be accounted for on the basis of two factors for resistance with resistance dominant; one of these genes conditioned rust resistance also for Races 17 and 21, and the other conditioned resistance only to Race 38.

The inheritance of agronomic and botanical characters was studied. In no case was there a very definite relation between resistance vs. susceptibility and segregation for other characters.

S.L. Macindoe (1949) completed studies for the Ph.D. degree with a major in plant genetics and minor in plant pathology with the writer as adviser. Most of the studies were carried out at University Farm, St. Paul, although preliminary investigations were made in Australia. Macindoe held

a Commonwealth Fund Service Fellowship.

The research consisted of an extensive, detailed study of the reactions of numerous varieties and crosses to an artificially induced epidemic in the field to individual races and a collection of races, reaction in the seedling stages to Race 34, and in a few cases to Race 15b to which Kenya selections and Red Egyptian are resistant.

Varieties susceptible to stem rust in the field in Australia were susceptible when similarly tested in North America. Varieties resistant in Australia were placed in three groups: A, varieties resistant in St. Paul and Winnipeg, including Hope, H44, and Thatcher, possessing mature plant resistance—Red Egyptian S979 with very high physiological resistance was placed in this group; B, varieties resistant in Winnipeg but only moderately resistant or susceptible in St. Paul and possessing high physiological resistance to many races, although high temperatures in the field greatly reduced resistance; and C, varieties resistant in Australia but clearly susceptible both at Winnipeg and St. Paul. It was considered probable that different biotypes of races in Australia and North America were the cause of Group C reactions.

Attempts were made to liberate different groups of races in separate field plots and then study races recovered. There was little or no relation between those released in particular plots and the races recovered from the same plots.

Studies were carried out—under both low (60-62° F) and high (70-80° F) temperatures—of reaction of varieties in the seedling stages to Races 34 and 15b. Some wheat selections remained resistant under all conditions to both races while the resistance of others broke down at high temperatures.

Under Australian conditions physiologic resistance functioned rather satisfactorily, but in North America mature plant resistance of the Hope, H44, and Thatcher types has been most valuable, although it was recognized that each of these varieties carried genes for seedling resistance to certain races.

Macindoe concluded that it was desirable to utilize mature plant resistance but desirable, or necessary, to combine this resistance with factors for as many physiologic races as possible, and where possible to utilize genotypes for physiologic resistance not seriously modified phenotypically by high temperatures.

Results from drought studies in spring and winter wheat crosses were difficult to explain on any biological basis.

C.S. Wu (1950) studied "Inheritance of leaf rust reaction and other characters in a spring wheat cross" for the Ph.D. thesis problem with a major in plant genetics and a minor in plant pathology.

The study was made in a cross between Lee and Mida. The origin of

these varieties has been outlined previously. Lines of Lee and Mida that reacted consistently to four leaf rust races—9, 35, 37, and 52—were used. Studies were made of parents, F_1 , F_2 , backcrosses, and F_3 .

Under field conditions 14 races of leaf rust and 31 of stem rust were used to produce a field epidemic. Mida was susceptible to leaf rust, Lee was resistant. By statistical analyses it was concluded that “the genes which differentiate the percentage of infection were additive in effect and that the higher percentage of infection was partially dominant.” This latter effect seems very small as the percentage of infection in F_1 was 28.2 and that of the average of the parents was 23.2, and backcrosses showed less deviation from the predicted. The extent of partial dominance certainly was of small degree. Two gene pairs seemed to be involved as determined by Power’s method.

Lee, Mida, F_1 , and backcrosses were resistant to stem rust, although of 371 F_2 plants 19 were susceptible. Wu concluded each parent contributed a different gene for resistance that was dominant to susceptibility. The gene from Mida without doubt was obtained from Hope, but there is some question of the source of the gene from Lee. Watson and Stewart (1956) concluded the stem rust resistance of Lee probably came from Gabo, although Gabo is susceptible to Race 11 in the seedling stages and Wu used Race 11 as well as 30 other races to produce the field epidemic. If a single factor from Lee causes field resistance to 31 races, including Race 11, it is not easy to accept Watson and Stewart’s conclusions regarding the source of wide resistance found in Leo.

Data from inheritance of other characters need not be summarized as there appeared to be no association between stem or leaf rust reaction and inheritance of other agronomic character differences.

K.S. Koo and E.R. Ausemus (1951) reported studies of “Inheritance of reaction to stem rust in crosses of Timstein with Thatcher, Newthatch, and Mida.” The studies were used by the senior author for the Ph.D. thesis with a major in plant genetics and minor in plant pathology.

Timstein was selected from a cross of *T. timopheevi* with Steinwedel (*T. vulgare*), made by Pridham of Australia. Several F_5 selections of this cross were brought to Minnesota by Macindoe and later named Timstein. They were immune in Australia to both stem and leaf rusts.

Thatcher has been discussed previously. It carries genes for mature plant resistance to many races and a gene for high resistance to certain stem rust races in the seedling stages. Mature plant resistance to most races of stem rust carried by Thatcher usually has been dependent upon the homozygous recessive condition of two complementary factors.

Newthatch was produced in Minnesota by Ausemus et al. (1944) from a

cross of Hope X Thatcher, backcrossed to Thatcher three times followed by pedigree selection. Seven strains with similar characteristics were combined. This variety carried mature plant stem rust resistance to many races in the field, conditioned in crosses by a single factor pair, therefore probably of the Hope origin; resistance in the seedling stages to many physiological races; and susceptibility to other races. It carries physiological resistance to some races of leaf rust and susceptibility to others.

Mida bred at North Dakota was selected from a cross of Mercury (Ceres X Hope-Florence) by (Ceres X Double Cross). It is resistant to bunt and probably carries the mature plant resistance of Hope dependent upon a single factor pair, and, possibly, two recessive, complementary genes from the Double Cross parent from which Thatcher was selected. Its gene complex for stem rust resistance seems somewhat doubtful. It carries resistance to some races of leaf rust.

The breeding background of these *T. vulgare* varieties was supplied by Ausemus.

The research consisted of a study of seedling reaction to many races and mature plant rust reaction in the field to a collection of races.

For field reaction to a collection of races Thatcher, Newthatch, and Mida were more resistant than Timstein which was susceptible in these studies. When the progenies of random F_2 plants were studied in the field, and when classified by considering F_3 lines as resistant as Thatcher, Newthatch, and Mida, as resistant, and segregating and susceptible lines in a second category, the ratios obtained of resistant to other lines in the three crosses agreed well with a ratio of 1:15 for Timstein X Thatcher and 1:3 for Timstein X Newthatch or Mida.

F_4 lines from F_3 resistant parents of all three crosses were grown under field conditions. Those resistant in F_3 bred true for resistance in F_4 . Those segregating or susceptible in F_3 bred as expected in F_4 from a knowledge of the F_3 genotype.

Seedling reaction was studied where Timstein was resistant to 21 available races and susceptible to Race 15B and the other three parents resistant to certain races and susceptible to others as published.

A single race was selected to use for each of the three crosses to which Timstein was resistant and the other parents, Thatcher, Newthatch, and Mida, respectively, were susceptible; for the Thatcher cross with Timstein, Race 36; for the Newthatch cross, Race 11; and for the Mida cross, Race 17. Progenies of F_4 lines and the parents were tested for seedling reaction. In all three studies seedling reaction was on a single factor basis.

In the Thatcher X Timstein crosses lines resistant to Race 35 were also resistant to 20 other races and probably carried a gene from Timstein

for resistance to all races. As these same lines in the field were moderately resistant to a collection of 32 races including 15b, it seems that genes for mature plant resistance of Thatcher are inherited independently from the gene in Timstein that gave seedling resistance to 20 races. The mature plant resistance of Thatcher may have been responsible, under the conditions, for resistance to 15b as Timstein was susceptible under field conditions.

M. Hashim (1951) studied "Inheritance of leaf rust reaction and other characteristics in crosses of Frontana with Thatcher and Newthatch" with a major in plant genetics and minor in plant pathology.

Frontana, a Brazilian variety, was highly resistant to a collection of leaf rust races in the field and resistant in the seedling stages to 32 races but susceptible to Race 107 of leaf rust. It also was moderately resistant to a collection of stem rust races under field conditions.

Thatcher and Newthatch are moderately resistant to a collection of many races of stem rust but became susceptible to certain races in the field in 1944. Newthatch in the seedling stages is resistant to many races of leaf rust and also susceptible to many races, while Thatcher has consistently been susceptible to leaf rust under natural infection conditions since its introduction.

As in other cases some races that would have been of interest to use in field epidemics were not available. Fourteen available races of leaf rust were used and 41 races of stem rust, not including 15b, for field studies.

Field reactions to leaf rust were studied and the reactions of Thatcher X Frontana, where Frontana was resistant and Thatcher was susceptible, were explained on a single factor basis with resistance dominant to susceptibility. In the cross of Newthatch X Frontana, where Newthatch was susceptible, the results were explained on the basis of duplicate factors with resistance dominant. Resistance was dependent upon the presence of one or both genes that conditioned resistance when in the dominant condition.

By more complete analysis it was concluded that Thatcher carried two closely linked factors—*I*, inhibitor of resistance, and *R* for resistance—Frontana two duplicate factors for resistance, and Newthatch all three factors in a recessive condition.

Reaction to Race 126 was studied in the seedling stages. Results were explained by assuming Thatcher carried a dominant factor for susceptibility and Frontana a dominant factor for resistance with the factor from Thatcher epistatic to that of Frontana leading to a ratio of 13 susceptible to 3 resistant.

Other studies of reaction to individual races of leaf rust were explained satisfactorily by assuming several factor pairs.

For stem rust under field conditions where all three parental varieties were moderately resistant, the crosses of Frontana X Thatcher and Frontana

X Newthatch led to the production of some susceptible plants in F_2 . In studies of seedling reaction to Race 15b of stem rust (to which Frontana is resistant and the other two parents susceptible), rust reaction was explained on the basis of two dominant duplicate factors for susceptibility. Incomplete association was observed by statistical methods for reaction to individual races of leaf rust in the seedling stages and to the collection under field conditions.

Glume color segregation showed association with reaction to both stem and leaf rust under field conditions. In the Frontana X Newthatch cross there was an association in inheritance of stem rust reaction and genes for normal vs. dwarf plants.

G.L. Jones completed work for the Ph.D. degree in September 1952 (see 1956) using as a thesis problem, "Inheritance of mode of reaction to stem rust, particularly 15b, and leaf rust in two crosses of vulgare wheats." He majored in plant genetics and minored in plant pathology.

Race 15b of stem rust was responsible for a severe rust epidemic in 1950.

Frontana was used in the studies because of its resistance to many races of leaf rust. The two other parents were selections from crosses of Mida X Kenya 117A and Kenya 58 X Newthatch. Both selections used were resistant to collections of stem rust in the field and to Race 15b at all temperatures in seedling stages in the greenhouse.

Interest centered on the feasibility of combining resistance to 15b and other races of stem rust with factors from Frontana for resistance to leaf rusts.

Reactions of 171 random F_3 lines were tested in the field using a collection of 24 available races and a composite of Race 15b. Of these, 27 were classed as resistant, 132 segregating, and 12 susceptible. The epidemic was not very satisfactory, however, and the number and nature of genes controlling rust was not determined. Seventeen F_3 lines that were classified as resistant in the field to the collection of races used in producing the epidemic, were tested under greenhouse conditions for reaction to Race 15b. Two lines were resistant in the seedling stages and 15 lines segregated for seedling reaction.

F_2 progenies of both crosses were used in studies of seedling reaction to Race 15b. Reaction could be explained on a single factor pair basis. A random selection of F_4 lines of Frontana X Mida-Kenya were tested for seedling reaction. In each of three tests under different conditions of temperature and light, the numbers of resistant lines from a total of 173 were 30, 33, and 51, respectively. It is apparent that a single factor pair does not explain these results. From the combined result of all three trials

the lines were classified as 27 resistant, 124 segregating, and 22 susceptible. A somewhat complex interaction of three gene pairs was used to explain the combined results where any two pairs in the dominant homozygous condition produced resistance. A similar hypothesis in the seedling stages explained reaction to a collection of forms of 15b.

The other cross, Kenya 58 X Newthatch, gave somewhat similar reactions, although there were some discrepancies.

Both crosses were studied for reaction to individual races of leaf rust 5 and 15 and to a collection of 18 races. Reactions studied independently to each of two races were explained on the basis of seven breeding true to resistance and nine segregating and susceptible. To the collection of races, segregation was on a more complex basis with 30 lines of 173 breeding true to resistance in Frontana X Mida-Kenya and 48 out of 173 breeding true for resistance in Frontana X Kenya-Newthatch.

There seemed to be no difficulty combining leaf and stem rust resistances.

E.H. Hannah (November 1952) studied "Inheritance of reaction to bunt in crosses involving Redman wheat and some of its ancestors" with a major in plant genetics.

Parental varieties used were Redman from a cross of Regent X Canus, Regent selected from a cross of H44 X Reward, and Canus selected from a cross of Kanred X Marquis.

A single collection of bunt, identified as Race 1 of *Tilletia foetida* (Wallr.) Liro, was used for the main study. Certain F_3 lines were increased and tested for reaction to Race 2 of *Tilletia caries* (D.C.) Tul. and the virulent Race T48-7 of *T. foetida*.

The parent varieties had the following reaction to bunt:

Race	Canus	H44	Redman	Regent	Reward
TF 1	Resistant	Resistant	Resistant	Resistant	Susceptible
TC 2	Resistant	--	Resistant	Resistant	Susceptible
TF 48-7	Susceptible	--	Resistant	Resistant	Susceptible

The resistant by resistant cross Regent X Canus segregated some susceptible lines, while the crosses of Redman X Canus and Redman X Regent produced only resistant progeny. It was concluded therefore that Redman received genes conditioning resistance from both the Regent and Canus parentage.

Data from resistant X susceptible crosses indicated that Canus carried a partially recessive major gene and a minor dominant gene conditioning resistance to Race 1 of *T. foetida*. When the major gene was homozygous recessive, the effect of the minor gene was masked. Regent differed from

the susceptible parent by multiple factors, possibly three gene pairs.

The combination of genes in Redman led to greater resistance than that of either parent.

E.G. Heyne (1952) completed work for the Ph.D. degree with a major in plant genetics and minor in plant pathology. His thesis title was "Inheritance of leaf rust, *Puccinia rubigo-vera tritici* (Eriks, and Henn.) Carl. reaction and other characters in crosses among three wheat varieties."

Three parental varieties, Pawnee, Redchief, and Timstein, were used, and the crosses grown were Pawnee X Redchief, Pawnee X Timstein, and Redchief X Timstein. Pawnee and Redchief winter wheat varieties were available in Kansas and Timstein was supplied by Ausemus. Pawnee and Redchief were susceptible to adult stem and leaf rust reaction and Timstein was resistant.

Under field epidemic conditions in crosses of Pawnee X Redchief, all progenies were susceptible to a collection of races.

Crosses of Pawnee X Timstein and Redchief X Timstein were studied in F_3 progeny trials. From the first cross 16 F_3 lines out of 156 and from the second cross 10 F_3 lines out of 198 bred true for resistance. Other individual F_3 lines, however, had variable reactions and ranged from all plants moderately resistant although less so than Timstein, through various types of segregation, to all plants highly susceptible. Susceptible lines were more frequent than resistant lines.

Reactions to several individual races were studied. There was some association, although not very great, between seedling reaction to individual races and mature plant reaction to a collection.

A gene for Pawnee's resistance to Race 9 of leaf rust and another for Timstein's reaction to stem rust were linked with a recombination value of 21.8 ± 7.8 percent.

L.M. Martinez, Ausemus, and Burnham (1953) presented a study of "Inheritance of reaction of leaf rust and of mature plant reaction to stem rust contributed by the Thatcher parent." This study included the greater part of a Ph.D. thesis of the senior author with a major in plant genetics and a minor in plant pathology. It was a continuation of cooperative studies with special reference to disease resistance in wheat.

The parents used were Thatcher, susceptible to most prevalent races of leaf rust and a selection of Premier X Bobin-Gaza-Bobin, Nursery Stock No. II-39-2, resistant in the seedling stages to 33 of the prevalent leaf rust races and susceptible, as far as tested at that time, only to Race 129. Ten F_0 seeds, seeds of 16 F_1 plants, and 109 randomly selected F_2 plants were made available to Martinez from the cooperative wheat project.

Previous extensive studies were reviewed in which segregating generations were compared for reaction to individual races in the seedling stages and to a collection of races in mature plant stages under field conditions. Different collections of races were used by the various investigators, and because the problems of inheritance are so complex in some cases, it is not strange that there is not more complete agreement in various studies. This would be expected when one notes the wide diversity of origin of the sources of resistance.

The studies of Martinez et al. need not be analyzed here in complete detail. By studying reaction to individual races, various important conclusions seem reasonable. However, these require further investigation in some cases to be confident of the accuracy of conclusions.

Studies of reaction of 103 random F_4 bulked lines and their parents were utilized in the research. These 103 lines and their parents were studied for seedling reaction to each of nine races and to a collection of 18 available races. Eight of the 103 F_4 lines were resistant in the seedling stages when studied in relation to the collection. The results of segregation to the collection agreed with a three factor pair hypothesis.

For certain individual races the seedling reaction agreed statistically with segregation on a single factor basis. With other races wide deviation occurred in the expected for a single factor basis, i.e., one resistant, two segregating, and one susceptible.

On the basis of segregation of 1:2:1, the reaction to individual Races 1, 2, 5, 15, 28, and 128a could be explained on a single factor basis.

Previous research workers had not attempted to reconcile deviations from complete agreement when comparing reaction of the same lines to two different races because of possible misinterpretation of an occasional natural cross or other cause. The problem may be considered by taking an example from this study:

Seedling reaction	Seedling Reaction			Total
	Resistant	Segregating	Susceptible	
Race 1		Race 2		
R	20	2		22
Seg	1	55	2	58
S		1	22	23
Total	21	58	24	103

Although the agreement was excellent with this number and with each race to an expectation of 25.75:51.50:25.72, one may note the exceptions. Of 22 lines apparently homozygous for resistance to Race 1, two of these segregated for reaction to Race 2, and 20 gave only resistant reactions. Other similar studies bring out peculiar relationships. Of the 103 F_4 lines, 87 reacted in a similar manner to all six races. Using Immer's (1934) formula for

calculating linkage relations, the hypothesis was set up that the six individual pairs of genes necessary to explain reaction to these six races represent closely linked genes. All calculations made for reaction to these same races were adequately explained if the order of genes in the genetic map was as follows:

Races

1	128a	15	2	28	5
0	0.9	1.9	2.9	3.8	5.6

Further analysis of more complex reactions of the 100 F_4 lines to three other races and to the collection could be explained only by more complex factor action and interaction, although for any race the results agreed well for some hypotheses of two interacting pairs of factors. It was concluded that eight or nine genes were responsible for reaction to the nine races used in seedling studies for reaction to a single race.

It is worthwhile to point out the relationship between these results and those of Flor for flax rust. Flor used the hypothesis that for each gene pair in the host plant for rust reaction, i.e., resistance vs. susceptibility, there was a corresponding gene in the pathogen for avirulence vs. virulence. There was also some evidence that genes, or gene complexes, for similar characters occur together in the chromosome, or are closely linked on the basis of classical genetics.

Martinez et al. studied reaction at seedling (first leaf) and six-leaf stage to a collection of races for the parents and some 314 bulked F_4 lines. Twenty rows of parent II-39-2 were resistant at both stages; six rows of Thatcher susceptible as seedlings gave two resistant and four susceptible at the six-leaf stage. From the 304 F_4 lines (plants) the following results were obtained: of 57 resistant at the seedling stage 53 were resistant at six-leaf stage, three were susceptible, and one mesothetic; of 106 mesothetic (somewhat intermediate) at seedling stage 66 were resistant, 30 were mesothetic, and 10 susceptible at the six-leaf stage; of 141 susceptible at the seedling stage 24 were resistant, eight were mesothetic, and 109 susceptible at the six-leaf stage. These results gave some idea of the difficulties of using seedling reaction in classifying genotypes for rust reaction. Differences in reaction at different growth stages are important.

For stem rust reaction to a collection of 41 races under field conditions Thatcher and II-39-2 in different areas of the nursery were somewhat variable, although Thatcher was distinctly more resistant than II-39-2. About one-fourth of the lines reacted as Thatcher; therefore, the results were explained on the action of one major genetic factor pair with susceptibility

dominant. On this basis II-39-2 must have been homozygous for one of the two complementary factors usually carried by Thatcher, which in a homozygous recessive condition led to “mature plant” resistance of the Thatcher type.

In Oats

W.H. Foote (1948) with a major in plant genetics and a minor in plant pathology, studied “The inheritance of stem rust reaction in oats.” The study was a direct phase of cooperative disease resistance studies in oats between Agronomy and Plant Genetics, Plant Pathology and Botany.

Four parents were used in the study:

Bonda with the White Russian type of stem rust resistance to Races 1, 2, 5, 8, 9, and 10, but susceptible to Race 7;

Bond-Rainbow with the Richland type of resistance to 1, 2, 3, 5, 7, and 12, but susceptible to Race 8;

Canadian selections – Hajira-Joanette, R.L. 811, and Victoria X Hajira-Banner, R.L. 1276 – resistant under moderate temperatures to Races 1 to 12. Both in the field and greenhouse these selections have been highly resistant to stem rust at University Farm for several years. With high temperatures in the greenhouse and low light intensity during winter months, however, these Canadian selections have been rather highly susceptible.

While there were some discrepancies between expected and actual results, it was relatively well established that a resistance factor from Bonda to Races 1, 2, 5, 8, 9, and 10 is independently inherited from a factor carried by the Canadian selections for resistance to all races; and likewise there is a factor for resistance in Bond-Rainbow to Races 1, 2, 3, 5, 7, and 12 that is independent in inheritance from the Canadian factor for resistance to all races.

W.R. Kehr and Hayes (1950) reported studies of inheritance in crosses between Landhafer, *Avena byzantina* L., and two selections of *A. sativa* L. The results were summarized from the Ph.D. thesis problem of the senior writer who completed work for his doctorate with a major in plant genetics and a minor in plant pathology. The thesis was a detailed study of a part of the cooperative disease resistance research of the two departments.

At the time of the study Landhafer, introduced from Germany by the U.S. Department of Agriculture in 1938 and made available to oat breeders by that department, was resistant to all collections of crown rust in the seedling stages.

The *A. sativa* parents were selections from crosses of the Minnesota oat breeding program Mindo X Hajira-Joanette and Bond-Rainbow X Hajira-Joanette which carried the Canadian type of resistance to stem rust that

functions best at moderate to low temperatures and the Bond type of crown rust resistance to many races, but susceptibility to races 33 and 45 to which Landhafer was resistant.

In these crosses two types of gene action were segregating for crown rust reaction: the Landhafer type carrying a gene for resistance to all races studied and simply inherited, and the Bond type with interaction of two complementary factors for resistance to certain races.

To differentiate reaction of Landhafer from that of Bond, reaction was studied to crown rust Races 33 and 45, where Landhafer was resistant and Bond susceptible. Segregation to these two races was on a single factor basis with resistance dominant to susceptibility. Lines resistant to Races 33 and 45, as far as tested, were resistant to other crown rust races.

The Canadian type of stem rust resistance can be differentiated by reaction to Race 6 to which White Russian and Rainbow are susceptible. After first studying reaction to crown rust, the seedling leaf used in the study was removed, and reaction to Race 6 of stem rust was determined. The recovery of lines resistant to Race 6 was more frequent than would be expected on a single factor basis.

In the Landhafer crosses, as in other crosses with *A. byzantina* varieties, inheritance studies of the characters differentiating *byzantina* and *sativa* were made. Results were similar to those previously reported.

The inheritance of the Canadian type of stem rust reaction from Hajira-Joanette, which previously had been combined with the Bond types of resistance to many races of crown rust, was independent in inheritance of crown rust type of reaction from Landhafer. Agronomic studies of the value of these hybrid selections and the extent of their desirability required further research.

R.O. Osler, and Hayes (1953) reported further research, "Inheritance studies in oats with particular reference to the Santa Fe type of crown rust resistance." The paper utilized a part of the Ph.D. thesis of the senior writer, who majored in plant genetics with a minor in plant pathology.

The crosses studied were between Santa Fe X (Bonda X Hajira-Joanette) and Santa Fe X (Hajira-Joanette X Bond-Rainbow). The Santa Fe parent at the time of the study was resistant, as far as tested, to all known races of crown rust, but susceptible to stem rust. The other parents carried genotypes for the Canadian type of stem rust resistance. They were of unknown genotype for the type of stem rust resistance of White Russian origin carried by Bonda and that of Rainbow origin carried by Bond-Rainbow. Both of the parents crossed with Santa Fe carried the Bond genotype for resistance to many races of crown rust to which Bond was resistant.

In the review of literature two previous M.S. theses were briefly

summarized. K. Maung (1950) studied crown rust resistance in the same crosses as reported by Osler and Hayes. Maung studied reactions of F_2 plants and F_3 progenies to physiologic Races 45 and 57 of crown rust to which Bond and its crown rust resistant derivatives were susceptible and to which Santa Fe was resistant. Maung concluded resistance to these two races was dependent upon the complementary action of two dominant factors *C* and *D*, or to the dominant action of *S* alone. He concluded that Santa Fe was homozygous for the *Ss* factor pair, but it was not known whether both complementary factors were carried by Santa Fe, genotypically expressed by *CCDD*, or if it was of the genotype *CCdd* or *ccDD*. If the latter hypothesis was correct, the other parent would have of necessity carried a gene pair *CC* or *DD* in the homozygous condition. Maung also studied stem rust reaction to Races 7 and 8 of the Canadian type and concluded this was conditioned by a single dominant factor.

Another M.S. thesis, by Andrews (1950), was a study of reaction to halo-blight and to races of stem rust 7 and 8, carried by one of the parents. His results indicated that resistance of the Canadian type to a mixture of Races 7 and 8 could be explained on a single factor basis.

In addition to these two studies Finkner (1950) in a Ph.D. thesis at Iowa State College studied the reaction of crown rust resistance to Race 57 and other races to which the Santa Fe parent was resistant and the other parent was susceptible. His conclusion was that possibly the Santa Fe variety was a mixture of genotypes for crown rust resistance, some plants carrying two different dominant factors for resistance, and some only one. On the basis of Osler and Hayes' studies Santa Fe then would have the genotype *SSAabb* or *SSaaBB*.

Without presenting a detailed review of data regarding crown rust reaction, the following summary of the status of crown rust inheritance in these Santa Fe crosses may be made using three genotypic groups. These are summarized in tabular form with three possible genotypic conditions that are in agreement with extensive data of Finkner, Maung, Andrews, and the results presented by Osler and Hayes.

Genotype Group	Bond X Hajira-Joanette and Hajira-Joanette X Bond-Rainbow	Santa Fe
I	<i>ccddSS</i>	CCDDSS
II	<i>CCddss</i>	ccDDSS
III	<i>ccDDss</i>	CCddSS

A method is presented to differentiate reaction of F_3 lines as given by line 31 in the (Bonda X Hajira) X Santa Fe cross and line 81 in the (Hajira-Joanette X Bond-Rainbow) X Santa Fe cross. Santa Fe was known to be resistant to all physiologic races used in the studies, while Bond was resistant to certain races but susceptible to others. By selecting F_3 lines such as 31,

or 81, from Osler and Hayes data that were homozygous for resistance to races to which Bond was resistant and which segregated for resistance and susceptibility to races to which Bond was susceptible, it would be possible to select in the progenies for homozygous resistance factors for crown rust resistance of Santa Fe origin, providing lines could be obtained breeding true for such resistance. This would be possible if factors from Santa Fe for crown rust reaction were not allelic to those from Bond.

It was concluded in a separate phase of the study that the Canadian type of stem rust resistance to both Races 7 and 8 was conditioned by a single factor pair.

Studies were completed that indicated crown and stem rust reactions in the Santa Fe crosses were independent in inheritance of agronomic characters that were segregating including date of heading, number of basal hairs, length of basal hairs, percent of florets awned, strength of awn and plumpness of grain.

In Barley

W.H. Leonard in 1940 completed studies for the Ph.D. degree with a major in plant genetics and a minor in plant pathology. The research, carried out at Colorado, was published in 1942 under the title, "Inheritance of fertility in the lateral spikelets of barley."

Previously Harlan and Hayes concluded fertility in lateral spikelets of *Hordeum intermedium* was due to a factor II hypostatic to the factor pair six-rowed vs. two-rowed, *Vv*.

Leonard studied the inheritance of fertility in the lateral spikelets of Morton classified as *H. intermedium*. He presented evidence for an *intermedium* allelic series of *I*, *Iⁿ*, and *i*, with infertility dominant over fertility. The factor pair for *intermedium* was linked with that for hoods vs. awns (*Kk*) in the IV linkage group.

Another phase of Leonard's (1946) Ph.D. thesis was published under the title, "Inheritance of reduced lateral spikelet appendages in the Nudihaxtoni variety of barley." The normal vs. reduced lateral appendage (*Lr lr*) factor pair differentiates the types worked with, although normal appendages on lateral spikelets occur only in the presence of the six-rowed factor (*vv*). *Lr lr* was found to be linked with *Or or* for green vs. orange seedlings.

Leonard has published extensively in agronomy and related fields.

S.P. Swenson (1940) completed studies in 1936 for the Ph.D. degree majoring in plant genetics. The work was primarily a developmental study of a dwarf barley arising spontaneously in a plot of Himalaya barley grown by L.J. Stadler of Missouri. Dr. F.J. Stevenson at Minnesota started the study of linkage relations of the factor for brachytic (*br*). When Stevenson resigned

in 1930, the studies were continued by Powers and later made available to Swenson for completion.

The gene pair *Brbr* was found to be linked with *Fcfc* for green vs. chlorina seedlings and independent in inheritance of genes for each of six other linkage groups. The calculated crossover value was 30.8 “ 1.8 in F2 and 9.27 “ .90 in F3, considered to be more reliable than F2 data.

Brachytic grew less rapidly than its normal Himalaya counterpart and differed from normal in rate of cell division and cell size.

W.W. Brookins (1940) studied “Linkage of genes differentiating stem rust in barley.” Brookins majored in plant genetics and minored in plant pathology.

In this study a single factor pair for stem rust reaction conditioned resistance vs. susceptibility to single races in the seedling stages and to a wide collection of races in the field.

The gene order of three factors found in the seventh linkage group was as follows:

<i>Fc</i>	9.8	<i>Br</i>	12.6	<i>T</i>
<i>fc</i>		<i>br</i>		<i>t</i>
		16.7		

Fcfc differentiates green vs. chlorina seedlings: *Brbr*, normal vs. brachytic plants; and *Tt* resistance vs. susceptibility.

M.T. Henderson (1945) completed studies for the Ph.D. degree with a major in plant genetics and minor in plant pathology. His thesis problem, “Studies of sources of resistance and inheritance of reaction to leaf rust, *Puccinia anomala* Rostr., in barley,” was a direct phase of the cooperative studies in disease resistance.

Some 246 varieties which were resistant to leaf rust at Madison, Wisconsin, in 1942 under field conditions were tested in the field and also in the seedling stages in the greenhouse. Most of these had a low percentage of rust under field conditions. A primary purpose also was to determine the nature of resistance, physiological or the mature plant type.

Thirty-four varieties with low percentages of rust under field conditions in 1943 were susceptible when tested in the greenhouse. Henderson concluded, “It appears probable that part of these varieties possess mature plant resistance not functional in the seedling stages.” Most leaf rust resistant varieties were susceptible to spot blotch and head blight, although seven leaf resistant varieties had only light infection with *Helminthosporium sativum*. These seem valuable as breeding sources.

Intercrosses were made between nine resistant varieties. All crosses and

their progenies also were resistant, except where CI 3410 was one of the parents. The segregation for seedling reaction in F₂ in crosses where CI 3410 was one parent was on a 15:1 basis, indicating inheritance of leaf rust reaction on the basis of two independently inherited factor pairs.

Crosses between resistant and susceptible parents tested in the seedling stages segregated on the basis of a single factor pair.

The Pa factor for resistance to leaf rust was independent in inheritance of Nn in Linkage Group III, Kk and B1b1 in Linkage Group IV, and Rr and Ss in Linkage Group V.

The Pa₁ factor for resistance to leaf rust was independent of B1b1 in Linkage Group IV and Rr in Linkage Group V.

R.W. Woodward (1946) completed studies for the Ph.D. degree with a major in plant genetics and minor in plant pathology. His thesis study, "The inheritance of fertility in the lateral florets of the four barley groups," was carried out at the Utah Agricultural Experiment Station.

The parental material included two-rowed barleys, *Hordeum distichon*, with rounded glume tips on sterile, lateral florets; deficient barleys, *H. deficiens*, with much reduced, non-fertile laterals with no rachilla or sex organs; intermedium barleys, *H. intermedium*, with either infertile inflated or fertile, undersized lateral florets with no awns or hoods; and *H. vulgare*, barleys with lateral florets fertile containing normal sized grains.

Tester varieties with known genotypes were used. The results of crosses were explained by a suggested allelic series of genes, *v*, *V^d*, *V*, *V^T*, for six-rowed, two-rowed, and deficiens.

Linkage studies with both *Y^d* and *V^T*, in relation to previous linkages of the factor pair *vV*, gave results in verification of the allelic series.

A second allelic series for fertility of the lateral florets consisting of *I^h*, *I*, and *i* was established for high partial fertility, inflated sterile lateral florets, and lateral florets typical of two-rowed barleys, respectively. Lesser fertility in the *I* series was dominant over fertility when associated with two-rowed, *V^dV^d* or *VV* genotypes, i.e., *i* was dominant over *I* and *I^h* while *I* was dominant to *I^h* in the presence of the two-rowed gene pairs *V^dV^d* or *VV*. The *V* gene and *VV* genotype was epistatic to the *I* series.

The degree of fertility in lateral florets of barley also was dependent partially upon environmental conditions as determined from spacing studies. There was some evidence of minor modifying factors affecting fertility of lateral florets.

F. Mariota-Trias (1947) completed work for the M.S. degree with a major in plant genetics. He made a study of the effects of six qualitative character pairs on yield and component characters in the F₂ of a cross between two

varieties of barley where the gametes of one parent carried the genes $V B n K Br Fc$ and the other $v b N k br fc$. The results are reviewed here because they are related to similar studies of Powers (1936) with barley. The original data were taken by Immer, but as far as possible Mariota studied the classifications also consisting of data from F_2 plants and F_3 progeny trials.

No attempt will be made to review statistical methods used. Each of the character pairs was known to be independent in inheritance of the others studied, except that $br-fc$ are linked with about 9.8 percent recombination.

To make the results clear the characters dependent upon the character pairs mentioned are as follows (where the dominant gene and character is given first): Vv , 2-row vs. 6-row; Bb , black vs. white glumes; Nn , covered vs. naked caropysis; Kk , hooded vs. awned; $Brbr$, normal vs. brachytic habit of growth; and $Fcfc$, green vs. chlorina seedlings. The latter two character pairs were classified according to East's (1935) terminology as physiological defectives.

Where large numbers of comparisons are made, as in this study, a few reach the statistically accepted level of a difference by chance alone. The method used to differentiate these was on the basis of their consistency.

The six-rowed genotype vw yielded more than the two-rowed, while awned plants, kk , yielded higher than either KK or Kk hooded plants. Higher number of seeds per head, one of the yield components, was obtained in six-rowed vw than in either VV or Vv genotypes. The awned genotype kk had a higher weight of seed than either of the hooded genotypes, KK or Kk . These relationships seemed to be expected on known morphological or physiological effects of the factor pairs concerned. Powers previously found that the Bb heterozygous plants for awn color yielded more than plants carrying the BB or bb genotypes, but Mariota observed no such differential effect. He concluded that the relationship found by Powers was, therefore, not due to the factor pair for color.

Significant relationships were found between qualitative characters, simply inherited, and quantitative characters, such as yield or seed size, where the first dominant factor sometimes produced the same effect as for the homozygous condition of this dominant factor pair, and other cases where the dominant singly expressed less effect than the doubly dominant or homozygous condition.

For the physiological defective factor pairs $Brbr$ and $Fcfc$ it was found that $Brbr$ seeds were heavier than seeds of $BrBr$ genotypes and that $Fcfc$ likewise produced heavier seeds than $FcFc$ genotypes, indications of heterotic loci. As Powers did not obtain similar results these, like the Bb genotype, may have resulted from linkage of desirable genes for seed weight and the factor pairs concerned, rather than heterotic loci.

As with Power's study the gene pair for covered vs. naked seed, *Nn*, had no effect on the yield components studied, indicating that high yielding naked barleys could be obtained if desired by the breeder.

O.J. Webster (1950) completed studies for the Ph.D. degree with a major in plant genetics and a minor in plant pathology. His study, "The genetics and morphology of rachis internode length in barley," was carried out as a phase of research at the Nebraska station.

Webster summarized linkage relations of factors of rachis length as obtained by previous workers and added four new linkage relations as follows:

- 1) Hulled vs. naked seed and *Lala* Linkage Group III
- 2) Normal vs. *zantha* seedlings and *Lclc* Linkage Group VI
- 3) Rough vs. smooth awns and *Lldd* Linkage Group VI
- 4) Long vs. smooth awns and *Lldd* Linkage Group V

As many as six different factors for rachis length were studied in some crosses.

G.T. Den Hartog and Lambert (1953) studied "The relationships between certain agronomic and malting quality characters of barley." The results presented were a part of the senior writer's thesis for the Ph.D. degree with a major in plant genetics and a minor in plant pathology.

Ten crosses with Mars as a common parent were used in the studies along with 15 lines of advanced F_4 generations. The lines were selected after they were studied for fertility ratios, general fertility, weight uniformity, and average kernel weight where separate studies of data were made for central and lateral florets. This made possible selection for as great variation as possible for the characters being studied. From these F_4 lines progenies with the desired ranges in variability were selected for F_5 studies. From analyses of variance in F_5 it was evident that significant differences were found for the characters studied for both "between lines in crosses" and "between crosses."

Intergeneration correlations between F_4 and F_5 as measured by correlation coefficients for average kernel weight, weight uniformity, general fertility, and fertility ratio were significant at the 1 percent level.

The yield trials at University Farm were made in a "multiple" randomized block with eight replications. Malting quality determinations from seed produced in the yield trials consisted of percent protein, barley diastatic power, and percent barley extract. Appreciation was expressed to the Midwest Barley Improvement Association for aid in obtaining the malting quality determinations.

Simple and partial correlations between the agronomic characters

studied and malting quality determinations were calculated.

There were significant negative relations between factors for quality and yield. Results indicated that it was possible to select lines of good yielding ability that had satisfactory values for malting quality.

C.H. Hsi (1951) studied "The relationship of various agronomic and malting characters of barley as studied in 10 crosses between Mars as a common parent and in two generations." The material consisted of more advanced generations from the same sources as reported by Den Hartog and Lambert (1953). The thesis study was published by Hsi and Lambert (1954). Hsi's major was plant genetics with a minor in plant pathology.

An extensive group of agronomic characters, including yield, were studied under replicated conditions in two separate advanced generations. Measures of quality, protein content, diastatic power, and extract were determined.

It was concluded based on heritability estimates for head density, date of heading, and diastatic power that effective selection for these characters could be made in early segregating generations. For other characters the selection was considered to be effective only on a progeny mean basis. The writer suspects that this is an oversimplification of statement. More definite evidence is needed before accepting the conclusion that selection for such characters as date of heading, size and weight of seed, seed plumpness, and perhaps others will not be found to be very effective in early generations.

The conclusion reached was that there was excellent probability of combining all important agronomic characters and quality characteristics in a single variety.

In Flax

A.H. Moseman (1944) studied "Correlated inheritance of height, seed size, seed yields, and other characters in flax." He majored in plant genetics with a minor in plant pathology.

He used a cross of Bison, a seed flax variety, with Talmune. The latter was selected at the Minnesota Station from a cross of Saginaw, a fiber variety, and Ottawa 770b. It resembled fiber varieties, except for somewhat coarser straw. Like fiber varieties it was low in yielding ability. The studies were carried out in F_1 to F_4 generations compared with the parents.

Height of plant was governed by multiple factors. Correlation coefficients were calculated to relate height of F_2 plants with F_3 progenies, F_3 plants with F_4 progenies, and the mean height of F_3 families with that of F_4 family progenies. Values of r obtained were $+0.34$, $+0.69$, and $+0.60$, respectively. Segregates were obtained in F_4 with height similar to both parents. Somewhat similar relationships were obtained for seed size studies.

The parents differed in iodine number and seed color. In this cross the iodine number difference was dependent on a single factor pair, and this factor pair was linked to a factor pair for seed color with a crossover value of 15.0 ± 2.2 percent. There also was a close association between seed color and seed yield in some cases.

Height of plant and seed yields gave an r value of -0.54 in F_4 families where lines were more closely approaching the homozygous condition.

H.L. Carnahan (1949) with a major in plant genetics and a minor in plant pathology studied "The inheritance of oil content and other characters in flax, and the associations between characters in the cross of Dakota X Minerva."

Dakota, produced from a cross of Renew and Bison, was produced by cooperation of the U.S. Department of Agriculture and the agricultural experiment stations of North Dakota, Minnesota, and Montana. It has brown seeds, medium blue flowers, and desirable agronomic characters.

Minerva, selected from a cross (CI649 X Bison) Bison4 at Minnesota has yellowish seeds and dark blue flowers. Its seed contained 3 or 4 percent more oil than that of Dakota under comparable conditions. Both varieties had good iodine numbers and were on the recommended list of the Minnesota Agricultural Experiment Station.

The extensive data of F_1 to F_3 generations yielded interesting comparisons. Oil content was dependent on a major factor pair with the F_1 intermediate between the parents. It seemed probable that the segregation observed was dependent largely on a physiological association between seed color and oil content. There was some indication of minor modifying factors.

Previous studies had indicated no difference between the parents for iodine number. In 1946, however, the 26 rows each of Dakota, Minerva, and the F_1 had mean iodine values of 178.7, 172.6, and 172.9. It appeared that low iodine number was dominant. In random F_3 lines in 1947 yellow seeded lines had a distinctly higher iodine number than brown seed lines or lines segregating for seed color. A considerable part of the differences in F_3 lines in iodine number appeared to be definitely associated with seed color, although again Carnahan thought there was evidence of minor modifying factors.

The characters—weight per 1,000 seeds, seed yield, plant height, and date of full bloom—segregated on a complex quantitative factor basis.

There were slight significant associations as determined by simple and partial correlation coefficients between various agronomic characters, iodine number, and oil content, but all of such a nature that selection for early maturity, high iodine number, high oil content, high yield, and large seed would be facilitated by the relationships obtained.

K.H. Chu (1950) completed studies for the Ph.D. degree with a major in plant genetics. His thesis title was "Studies of the inheritance of seed size and other characters from F_3 data in a cross between an Indian and a North American variety of flax."

The variety Indian 1193-2, producing large seeds, was brought to America by J.H. Mehta in September 1946. It is of short stature, maturing about the same time as Dakota, and has been susceptible in Minnesota to wilt and rust, although it was rust resistant in India.

Dakota has been a widely grown variety in North America and produces small seeds. It is mid-season in maturity, resistant to many races of rust and to wilt, and produces an oil of high drying qualities.

There was a progressive increase in average seed size from 4.4 grams per 1,000 seeds in Dakota: F_1 X Dakota, 6.8 grams; F_1 , 8.8 grams; F_2 , 7.9 grams, slightly below F_1 ; F_1 X Indian, 9.9 grams; and Indian, 10.3 grams.

Mean seed size in grams was studied to compare the weight of seed of Dakota and Indian and 87 random F_3 lines. The three rows of Dakota that were grown were placed in class 4.1 to 5 grams. Two rows of Indian were placed in class 9.1 to 10 grams and one row in 10.1 to 11.0 grams. The F_3 random families for seed weight were placed as follows: 16 lines in 6.1 to 7.0 grams class, 64 lines in 7.1 to 8.0 grams class, and 7 lines in 8.1 to 9.0 grams class. While segregation occurred, the manner was complex and none of the F_3 lines overlapped the parents. That seed size is inherited in a quantitative manner, and of selection value, was shown by the significant interannual correlation of +.54 between seed size of F_2 plants and their F_3 progeny.

For wilt reaction in the wilt nursery the mean percentage wilt of Dakota was 23.2 for three rows, that of Indian 94.2, while 88 F_3 random lines ranged from as resistant as Dakota, or more so, to nearly as susceptible as Indian with a mean percentage wilt of 32.5—more wilt resistant than the average of the parents.

Rust reactions to a collection of rust were obtained from 80 F_3 lines and the parents. Data agreed with a 1:2:1 segregation, a good fit to expectation based on a single factor difference.

There was no association between rust or wilt reaction and seed size based on a study of F_3 lines.

Studies were made of oil content and iodine numbers of the two parents and 37 F_3 lines covering a range for seed size from 5.0 to 9.0 grams per 1,000 seeds. Simple correlation coefficients were calculated to show relationships if any.

Significant r values were obtained for

Oil content vs. seed size	.67
Oil content vs. iodine number	-.54
Iodine number vs. weight of 1,000 seeds	-.76
Iodine number vs. height of plant	.61

When three variables were included—oil content, weight of 1,000 seeds, and iodine number—significant partial correlations were $r_{12,3} = .48$; $r_{23,1} = -.64$, while there was no sensible partial correlation for $r_{13,2}$.

One F_3 family had a seed weight of 9.0, an oil content of 35.9, and an iodine number of 162. It approached the large seeded Indian parent in oil percentage and had a relatively high iodine number, although not the equal of Dakota.

In Rye

F.S. Warren and Hayes (1950) continued rye breeding by studying polycrosses. The senior author carried on the details of the studies using the data as the basis for his Ph.D. thesis with a major in plant genetics and minor in plant pathology.

Some available lines of Dakold and Imperial had been selfed only for one year, several others for several years, and two lines had been selfed for 16 and 19 years. Selection was made for uniformity of seed color, fertility under self-pollination, plumpness of seed, and plant vigor. Originally 64 colorless seed lines were grown under replication in Polycross Nursery I and 23 green aleurone seed lines were grown in Polycross Nursery II.

The inbred lines in these two nurseries were examined for percentage of pollen sterility and micronuclei in spore quartets as a measure of abnormal chromosome behavior in meiosis. Thirty relatively desirable colorless seed lines and 12 green aleurone lines were grown in yield trials. These lines were classified into five fertility groups: (1) all plants highly self-fertile, (2) nearly all plants highly self-fertile, (3) approximately one-half of plants highly self-fertile, (4) approximately one-fourth of plants highly self-fertile, and (5) all plants of medium to low self-fertility.

Yield trials were made in two groups of the polycrosses. Group 1 was made up of 21 lines, 9 from colorless seed parents and 12 from green seed parents; Group 2 consisted of 21 colorless seed parents. These selected lines contained no very undesirable plants and produced sufficient seed for the yield test. Single row plots were used with six replications; Dakold, Imperial, and Emerald were included in each of the two trials.

Analyses of variance were used to calculate S.E. of a difference for each character studied; the data for each character were placed in classes of + or - 1, 2, 3, or more times this S.E.

Characters studied included fall growth vigor, stooling vigor, date headed, weight per bushel, yield bushels per acre, percent fruitfulness, pollen sterility, and weight of 100 kernels. All r values were calculated for correlation of individual characters. All r values for yield and other characters were positive, except that for pollen sterility, although no single relation was very large and some r values were not statistically significant. A positive multiple correlation of R for yield with other characters was .78, highly significant.

In the polycross yield trials, a considerable proportion yielded more than any of the standard varieties. In relation to the five classes for self-fertility, the group of 11 lines for one-fourth plants highly self-fertile averaged in yield 122.6 percent, using standard varieties as 100; the highly self-fertile group of four lines yielded the lowest at 103.1; the intermediate to low self-fertility group of seven lines averaged 113.9; the nearly all highly self-fertile group of nine lines averaged 111.3; and the group of half self-fertile averaged 117.5.

Several groups of lines based on yield in polycrosses and similarity of seed color were set up for the production of synthetic varieties. One low yielding group of lines was selected to be used in producing a low yielding synthetic.

E.D. Putt (1954) completed work for the Ph.D. degree in 1950 with a major in plant genetics and a minor in plant pathology. His thesis was entitled "Cytogenetic studies of sterility in rye."

Cytological aberrations were frequent in the selfed lines. Certain of these were investigated in detail. From the standpoint of breeding it was of interest to note, "From limited investigations it appears possible to produce a line uniform for low pollen abortion and high seed set which will be useful in further studies of pollen abortion in relation to seed set in rye."

In Corn

C.W. Doxtator (1937) completed "Studies of quality in canning corn" for his Ph.D. thesis when an instructor in Plant Genetics at the University. He had a major in plant genetics and a split minor in biochemistry and plant pathology. For several years Doxtator was in direct charge of corn breeding studies at the Waseca Station.

He used nine inbred lines of Golden Bantam sweet corn that had been self-pollinated for four generations, three lines selfed for a somewhat longer time, and the parent variety.

Two replications of single rows of the inbreds and three replications of crosses were studied for each of 2 years, 1929 and 1930. All possible single crosses between the 12 inbreds were made and included in the study. Yield data and puncture tests to determine tenderness of pericarp were studied.

There were highly significant differences among crosses for tenderness as determined by puncture tests made in each of the 2 years.

Interannual correlations for puncture tests of crosses was +0.41, and for yield in these 2 years the r value was +0.25. The r value for average puncture test of each inbred parental line and its F_1 crosses was +0.25.

The inbreds were placed in three groups on the basis of their puncture test values for the 2 years, Group 1 low, Group 2 medium, and Group 3 high. There was an important and significant relation between puncture test values of crosses in relation to the grouping of the parents. Thus Group 1 X Group 1 had an average puncture test value in six crosses of 323 grams; Group 2 X Group 2, 353 grams; and Group 3 X Group 3, 382 grams. When puncture test values and yield were correlated, holding constant date silked and percentage husk, the calculated r value of -0.36 was significant at the 1 percent point.

To determine the relation between the value of making more puncture tests within an ear and increasing ears tested, a formula of Immer's was used, and 96 ears of Golden Bantam Sweet were studied. Comparing the same number of individual kernel puncture tests and using 40 punctures per replicate, it was concluded that eight ears per plot with five tests per ear would be most desirable.

S.K. Wu completed work for the Ph.D. in 1938 majoring in plant genetics. His thesis research was a phase of corn breeding investigations of the department. The origin of inbred lines and their combining ability have been given by Hayes and Johnson (1939) and Johnson and Hayes (1940). There were available improved inbred lines that had been selected from crosses of desirable Minnesota inbreds with several different Corn Belt inbreds resistant to lodging. The inbreds used by Wu in studies of combining ability made it possible to select three types of crosses.

Group A inbreds were selected from a cross of both parents in common, i.e., inbred 49, Minnesota No. 13 X 9-29, Osterland's Yellow Dent where seven inbreds selected from the cross were available. Any single crosses between these lines would have two parents in common.

Group B selected from crosses of one parent in common.

Group C selected from crosses of no parents in common.

Over 20 single crosses for each of the three groups were tested in replicated yield trials for 2 years. Average yields were Group A, 48.3 ± 0.66 bu; Group B, 46.9 ± 0.68 ; and Group C, 49.2 ± 0.65 . The same three comparable check varieties were grown separately with each group and on the average they yielded: Group A, 52.2; Group B, 46.1; and Group C, 46.8. A larger number of single crosses in Group C excelled in yield, and the highest yield was obtained in Group C.

The results were interpreted on the basis that genetic diversity of origin was of importance in relation to yielding ability.

K.W. Wang (1939) studied "Some phases of heterosis in corn" for his Ph.D. thesis with a major in plant genetics.

The studies included growth rate during plant development, effect of foreign pollen on seed-part weights, and detailed morphological studies of the shoot apex.

The material consisted of four inbreds and their F_1 crosses. These inbreds previously were tested for combining ability in inbred-variety crosses and proved to be good combiners. They were not closely related genetically. Their six possible F_1 crosses differed widely as compared in 1938 with yields in bushels of 68.2, 65.3, 59.1, 58.7, 57.6, and 47.0, respectively.

A review of the experimental results is unnecessary. Germ and endosperm size in kernels of inbreds and F_1 crosses varied widely. Germ weight and endosperm weight were increased, with some exceptions, when cross- and self-fertilization were compared. In five cases out of six the hybrid grew slightly faster in the early post-embryonic stages and much faster than the parents after 35 days.

No consistent relations were found between size of the shoot apex in the embryo and heterosis of the produced plant, and no consistent correlation between the extent of heterosis and cell number, cell size, and cell arrangement in the shoot apex.

In three F_1 crosses out of six there was a positive correlation between nuclear size and degree of heterosis in the hybrids.

There was a definite relation between rate of growth, total dry weight, and the cytonuclear ratio; the larger the nucleus as compared with the meristematic cell, the greater the development of heterosis. The cytonuclear ratio of the inbreds, however, was not greatly different from that of the hybrids.

R.P. Murphy (1942) completed studies for the Ph.D. degree with a major in plant genetics and a minor in plant pathology. One of his thesis studies was with grasses, the other with corn. In one study he used two sources of the forage type and the Fairway type of crested wheat grass and studied the desirability of using selection in self-pollinated lines. In the forage type one plant out of 33 had a definite aneuploid chromosome number and the others had a somatic number of 28. Plants of the Fairway type had a somatic count of 14.

Both types were highly unfruitful when self-pollinated under bag. Some space-isolated plants set more seed than when isolated by covering with a bag; one forage type plant that set seed under a bag gave normal seed setting when space isolated. The selfed progeny, however, set little seed

when the bag cover was used. The forage type plants grown in the nursery were severely injured by root rot which greatly limited the studies.

Because of the partial failure of the studies with crested wheat grass, Johnson and the writer made the material from a study of convergent improvement available to Murphy (1942) who used it for another thesis research. The four Rustler white inbreds were the parents used in two single crosses of Minhybrids 401 and 402. With each of the single crosses convergent improvement had been carried out for two and three backcross generations. After 2 years of selection in selfed lines the more desirable inbred lines were crossed to both the recurrent and nonrecurrent parent.

In crosses to the recurrent parent most lines were superior in yield to the recurrent parent. There were four groups of these lines. There was no consistent difference in the yields regardless of whether two, three, or four generations of backcrossing had been carried out before selecting in selfed lines.

The recovered lines also were crossed to the nonrecurrent parent and in this case the yields were compared with the appropriate original single cross. These comparisons may be of greater interest and will be summarized in greater detail.

Recovered Lines	Number	Cross	Av. Yield Bu.	Yield Original Single
C16	9	C16R X C20	48.6 ± 2.0	52.0 ± 1.8
C20	11	C20R X C16	46.1 ± 2.5	50.0 ± 1.7
C15	16	C15R X C19	56.4 ± 2.8	58.1 ± 1.8
C19	15	C19R X C15	55.8 ± 2.8	57.3 ± 2.3

R = recovered lines

There was no relationship, on the average, between the yields of lines in crosses with the nonrecurrent parent and their yield when crossed with the recurrent parent.

Two to four lines that yielded the most in crosses to the nonrecurrent parent were selected. These lines in general showed a marked improvement over the original inbreds in vigor, plant type, ear type, and yield. Selection during backcrossing and selfing was made for resistance to smut. In comparison with the original lines there was, on the average, marked improvement in smut resistance. Then combinations were made to compare yields of each of two single cross combinations, i.e., (C16 X C20) and (C16R X C20R); (C15 X C19) and (C15R X C19R).

For the C16 X C20 group of eight single crosses, one single cross of (C16R X C20R) was placed in the same class for yield as the original cross, one in a class of +2 times the calculated S.E. of a difference or 1.94 bu per acre, and the other six in classes -1 to -3 less than the original cross.

For C15 X C19 there were nine single crosses of recovered lines of (C15R X C19R). Using classes from 0 to minus or plus 1 to 4, there were

four single crosses placed in -1 , one single cross each in classes 0 , $+1$, and $+2$, and two single crosses in class $+4$. Mean yield of $C15 \times C19$ was 58.9 ± 1.4 bu and that of the eight single crosses of recovered $15 \times$ recovered 19 was 56.0 . For $C16 \times C20$ the yield of the original cross was 64.8 ± 1.4 bu and that of nine crosses of recovered $16 \times$ recovered 20 was 66.1 bu.

Murphy concluded that it was possible to improve inbreds by convergent improvement and produce some single crosses between inbreds that were significantly better than the original cross. He concluded that the initial test of recovered lines could best be carried out by studying their combining ability in crosses with the nonrecurrent parent.

Murphy has produced several new varieties of forage crops, including Saratoga smooth bromegrass, Essex timothy, and Cayuga and Saranac alfalfa.

E.F. Frolik (1948) completed work for the Ph.D. degree with a major in plant genetics and minor in botany. His thesis was an intensive cytogenetic study of "Chromosome segregation in maize translocations from X-rayed material and in crosses producing rings of six chromosomes." The research carried out under the guidance of Burnham was a phase of Burnham's research relating to "An 'Oenothera' or multiple translocation method of establishing homozygous lines."

These researches are so indirectly related to the studies presented that no attempt will be made to summarize the results.

E.L. Pinnell majored in plant genetics with a minor in plant pathology for the M.S. and Ph.D. degrees. He studied the variability of characters of double crosses in corn as related to the method of combining the four inbred parents and used the study in a thesis for the M.S. degree (1943).

The four inbred parents of different origin were selected to represent differences. Two were early in maturity, the other two later in maturity; two had short ears with low ear row number; two were of low leaf area and the other two were of high leaf area; and two were tall and two short.

The problems may be illustrated if a consideration of one character pair difference is used. The plan was to compare variability of the double crosses illustrated for time of maturity where E = an early maturity inbred and L = late maturity. The question asked was whether $(E \times E) (L \times L)$ was more uniform in maturity than $(E \times L) (E \times L)$. Similar studies were made for ear length, height of plant, and ear-row number.

It was not possible in these studies, after careful analysis, to predict the relative variability of the double crosses based on character means either of inbreds or of single crosses.

Pinnell (1949) completed studies of "Genetic and environmental factors affecting corn seed germination at low temperatures" as his Ph.D. thesis

problem. This was a continuation of the study started by the writer and associates in 1939 as one phase of cooperative investigations at Minnesota.

Only a brief summary of results will be made. Prior to the detailed study under controlled laboratory conditions, tests were made for several years in wet soil at low temperatures in the field. In general, double crosses germinated best followed by single crosses and inbreds in that order.

Wide differences between inbreds were found, and these differences appeared heritable in crosses.

The genetic nature of these differences appeared complex. The maternal parent's germinating ability was of great importance in determining stands both in single and double crosses. There was little or no relation between the performance of an inbred and its performance as a male parent in crosses.

Pinnell concluded, "Adequate evaluation of an inbred line for cold test performance can be made only through replication of seed source in time and space."

L.C. Saboe (1943) completed work for the Ph.D. degree with a major in plant genetics and a minor in plant pathology. He used chromosomal translocations to study the inheritance and linkage relations in two crosses in corn that segregated for resistance vs. susceptibility to smut. With the resistant inbred from Minnesota No. 13 significant associations were observed with interchanges 3-7b, 5-7d, 6-9a, and 8-10a. In crosses with a resistant inbred from Rustler there were significant associations with interchanges 1-4a, 3-5c, and 5-8a.

G.S. Murty (1948) completed work for the Ph.D. degree using the thesis problem, "A comparison of combining ability in corn of parental inbreds with inbreds recovered from backcrosses." He majored in plant genetics with a minor in biostatistics.

Prior to his Minnesota studies, Murty had over 10 years experience in India in plant genetics and breeding studies, including wheat and barley, and in investigations regarding vernalization. In August 1946 he was deputed by the Government of India for higher studies in the United States.

His study was a phase of Minnesota corn breeding research. The material consisted of three inbreds used in Minhybrid 603, at that time recommended for the south central zone in Minnesota. The three inbreds A334, A344, and A357 were parent in Minhybrid 603(A322 X A334) (A357 X A344). The origin of these inbreds is as follows:

A334, selected from Golden King

A344, selected from Inbred Iowa 53, which it closely resembles

A357, selected from a cross of inbred 6-29—Silver King X H, an inbred from Holbert out of Reid's Yellow Dent.

Three floury inbreds, 389, 387, and 384, were used as sources of the floury factor. Inbreds 387 and 389 were isolated from Price of Plains and 384 from Zina Blue.

The floury factor was incorporated into A334, A344, and A357 from the crosses A334 X 389, A344 X 387, and A357 X 384.

One illustration of the method used will be given. In 1942, A344 was crossed with 387 and a backcross made to A344 using the plants of A344 X 387 as the female. Floury seeds vs. flinty segregated in a 1:1 ratio, and the floury seeds were selected to plant in 1943. About 50 desirable plants were backcrossed to A344 using A344 as the male.

In 1944 ear cultures were grown of these backcrosses and early maturing desirable plants selected and backcrossed again to A344. Thus, three backcrosses were made. Self progenies were continued for two more generations, selection being made for floury kernels, desirable plants, and freedom from stalk and ear rots. During these last 2 years corneous seed types also were selected in the same manner.

Similar backcrosses and selections were followed for A357 and A334.

The recovered lines and their parent inbreds of each of the crosses were topcrossed with Golden King. Some of the recovered lines were still segregating for corneous vs. floury seeds. These had been topcrossed with Golden King. In this case a comparison was made between topcrosses of the same ears separated into two groups, flinty and floury kernels.

Although the yield trials were planted in three locations only those carried on at the Waseca branch station and at University Farm were used in the study because unfavorable growing conditions were encountered in the third location in Meeker County.

The data will not be given in detail. While differences were very small when the progenies of corneous and floury seeds from the same ear were compared in topcross yield trials, the yields of progenies from floury seeds of crosses were significantly less statistically than for progenies from the corneous seeds of the same ears.

Recovered floury lines compared favorably with their dent parents in combining ability when topcrossed with Golden King. In two groups of backcrosses some recovered lines were superior to their recurring dent parents in combining ability.

O.M. Reece (1949) completed studies for the Ph.D. degree with a major in plant genetics and a minor in plant pathology.

Available material consisted of seed of each of four inbreds, A95, A344, A347, and Os420; of two F_1 crosses (A95 X A344) and (A347 X Os420); and of 50 random F_2 selfed ears of (A95 X A344) and 35 of (A347 X Os420).

The material relating to the cross (A95 X A344) was grown at University Farm and that relating to (A347 X Os420) was grown at Waseca in single row plots of 33 hills each thinned to a stand of one plant per hill with three replications. Studies were made in each of 2 years.

Artificial inoculations of individual plants were made with *Diplodia zae* and *Giberella zae* using the toothpick method and making inoculations at definite, comparable internodes. General infection studies were made using a mixture of seven pathogens causing stalk rot. In addition to the toothpick method the general infection plot was sprayed with a small stream of the mixture, and the field used for the general infection study was isolated from other studies by about $\frac{1}{4}$ mile.

There were highly significant differences between cultures in all disease reaction studies, and the type of inheritance was quantitative in nature. Reaction to *D. zae* infection and *G. zae* was significantly correlated in many of the comparisons.

A notable correlation was found between percent lodging and infection percentage as observed in the general infection plot for each of the 2 years.

K.T. Payne and Hayes (1949) presented "A comparison of combining ability in F_2 and F_3 lines of corn" in relation to studies of early testing—adapted from the Ph.D. thesis research of Payne, who majored in plant genetics with a minor in plant pathology.

The research will not be presented in detail. It was concluded, "In these studies there was some doubt of the practical value of early testing for combining ability as a means of selecting desirable sources of F_3 lines." However, early testing in F_3 was believed to be useful as a method of isolating desirable germ plasm, with which the inbred lines of desirable double crosses may be improved.

R.T. Johnson (1950), with a major in plant genetics and minor in plant pathology, continued the study reported by Payne and Hayes. His thesis title was, "Combining ability in *Zea mays* as related to generations of testing, selection of testers, and characters of the inbred lines." Lines tested in F_2 and F_3 by Payne and Hayes were used for combining ability studies in F_4 . Comparisons were made of the performance of inbreds and their yield trials in crosses, and specific and general combining ability were compared.

Comparisons were made of combining ability of F_3 and F_4 generations. Although highly significant correlations were obtained, it was concluded that most of the associations were due to a relatively small number of low combining inbreds.

When single cross testers of high desirability were used to determine combining ability of F_4 lines, it was concluded that these masked the influence of yield of F_4 lines of different combining ability.

Improved lines produced by the methods of study were used for each of four inbred parents of Minnesota 608. Predicted performance of these lines in double crosses by using the yield of single crosses resulted in several doubles superior to Minnesota 608.

L.S. Wortman (1950) completed his Ph.D. studies with a major in plant genetics and a minor in plant pathology using the thesis, "The inheritance of cold-test reaction in *Zea mays*."

The problem was a continuation of division investigations, of which Pinnell's 1949 study had been the most intensive previous research.

Four inbreds that differed in cold-test germination were used, and seed of these and of certain F₁ crosses was furnished to Wortman. The inbreds were as follows:

Inbred	Origin	Rating for Stand Performance
A21	Golden Gate	High
A34	Rustler	High
A357	6-29 X H	Low
W253	15-28 X 9-29	Low

The available crosses of which seed was furnished were A34 X W253, W253 X A34, A21 X W253, and A253 X A21. Wortman subsequently made the crosses A21 X A357 and A21 X W253. It seems worth recording that the parental inbreds used in the crosses were of diverse origin.

For the three combinations (A21 X A357), (A21 X W253), and (A344 X W253) and their reciprocals, backcrosses were made to both parents using the parent inbreds and reciprocal F₁ crosses both as males and females. Thus for each single cross combination, as (A21) P₁ X W253(P₂), seed was available or produced for P₁ and P₂, P₂ X P₁, P₁ X P₂, P₁(P₁ X P₂) P₁(P₂ X P₁), (P₁ X P₂)P₁, (P₂ X P₁)P₁, P₂(P₁ X P₂), P₂(P₂ X P₁), (P₁ X P₂)P₂, (P₂ X P₁) P₂.



Dr. L.S. Wortman, formerly Associate Director, International Rice Research Institute, Los Banos, Philippine Islands. At present, Director Pineapple Research Institute, Honolulu, Hawaii.

Details will not be given relating to the cold-test studies. Seedling material of parents and test crosses were planted and placed in a warm chamber, 78E to 79E F., for 36 to 48 hours. The flats then were transferred to a controlled cold chamber at a temperature of 47E F. and exposed to low test conditions for 72 to 96 hours, then to the warm chamber for 72 hours before readings were made to rate individual seedlings for performance.

Field soil and sterilized soil were used. Replications varied in different trials in relation to degree of accuracy desired.

The genotype affected cold-test performance as shown by (1) the superiority of F₁ crosses over inbred parents, (2) superiority of backcrosses to the

high parent over backcrosses to the low parent, and (3) transmission of genes for inheritance of cold-test reaction through the male.

Significant differences in cold-test performance were found between reciprocal single crosses, between reciprocal single crosses used as a female in backcrosses, between reciprocal backcross populations when used as a female in crosses with a variety, and between reciprocal F_2 populations. These differences were attributed to cytoplasmic inheritance.

Differences were found between inbreds when used as males in crosses with low-performing females.

The strong maternal effect of the female on cold-test performance was considered due to two main causes: (a) genetically determined maternal inheritance which behave as a mature plant character showing delayed segregation and (b) cytoplasmic inheritance.

M.C. Vacchani (1950) studied the relationship of chromosome knobs with certain agronomic and morphologic characters of corn inbreds for his Ph.D. thesis problem using standard inbred lines, many of which have been used in double-crosses. These included both smut resistant and smut susceptible. The material included inbreds of very diverse origin, most of which have been used in the corn breeding program at Minnesota. Knob positions were located as the distance from the centromere to the knob in relation to total arm length and the particular chromosome concerned. Within the chromosome map there were wide differences in knob number and chromosome concerned.

Within the 20 inbreds, almost all in the low knob group, no definite relationship was shown between knob numbers and morphologic and agronomic characters. However, among 72 tests of association between the presence of a knob and plant characters, two were significant. These are of doubtful significance as several such associations might be expected to occur by chance.

M.A. Ibrahim (1954) completed studies in 1950 for the Ph.D. degree with a major in plant genetics. His thesis problem was "Association tests between chromosomal interchanges in maize and resistance to the European corn borer."

The original cross was between Ar11, resistant to early leaf feeding of the corn borer, and A344 susceptible. F_1 's and backcrosses indicated phenotypic dominance of borer resistance over susceptibility.

Twenty-four chromosomal interchanges were used to determine which chromosomes carried the genetic factors that normally differentiate the resistance of A411 from the susceptibility of inbred A344 under manual infestation. All chromosomes except the short arms of 1 and 5 were tested by at least one susceptible or intermediate interchange, although there was some

question of the adequacy of the test with the long arm of chromosome 7.

“Conclusive evidence was found for association between corn borer reactions and interchanges 3-7c, 3-9c (wf 9), 3-9h (wf 9), and 4-9f (wf 9).” (Wf 9) in parenthesis means in Wf9 background after three to six backcrosses to the well-known inbred line of Wf9. Evidence was fairly conclusive for associations of borer reaction with interchanges 5-9a and less so for 1-9a and 3-5a.

These results led Ibrahim to conclude that the resistance of A411 was due to one gene in the long arm of chromosome 3 and one in the long arm of chromosome 4. Fairly conclusive evidence was found for a gene in the long arm of chromosome 5.

Two resistant interchange lines were found to carry factors for resistance that were different from those carried by inbred A411.

O.C. Zoebisch (1950) completed work for the Ph.D. degree with a major in plant genetics. His study was entitled “The inheritance of some quantitative characters in *Zea mays*.” Important agronomic characters, including yield, were studied in the F_1 , F_2 , and backcross generations of crosses between inbred parental lines that differed rather widely in many agronomic characters.

While wide segregations occurred for most characters, the statistical methods of analysis led to no new knowledge that was not generally available regarding the mode of inheritance of differential quantitative characters.

R. Singh and A.A. Fleming (1951) studied inheritance in corn for reaction to the European corn borer as Ph.D. thesis problems with majors in plant genetics and minors in plant pathology. Singh held a scholarship from the government of Bihar, India. Fleming was a teaching assistant in agronomy at Minnesota. Their research was part of the cooperative program of the Agronomy and Plant Genetics Division and Entomology and Economic Zoology. The latter department furnished the egg masses used for manual infestation.

These theses furnished the basis for a technical bulletin by Fleming, Singh, Hayes, and Pinnell, “Inheritance in maize of reaction to the European corn borer and its relationship to certain agronomic characters” (1958).

Using the method of Powers et al. (1950), based partially on the work of Mather, it was concluded that a few major genes differentiated reaction to leaf feeding and overall damage in each of the crosses studied. Only two genes seemed to be responsible for differences in early leaf feeding. There seemed to be no significant relation between reaction to the borer and agronomic characters of corn including rind hardness, tillering, and flinty vs. floury endosperm.

Extensive studies were made between crosses of inbreds classified as

R and S for reaction to leaf feeding. Resistance was dominant or partially dominant to susceptibility. Selection for resistance or tolerance in segregating progenies was highly effective.

J.N. Warner (1952) with a major in plant genetics and minor in statistics completed work for the Ph.D. degree in 1950. He presented a method of using variances of three segregating populations, the F_2 , and the summed backcrosses to each parent to estimate heritability and presented results of heritability estimates with various characters of corn. For illustrative purposes he used two inbred lines, two backcrosses, and the F_1 and F_2 generations.

In Sugarbeets

J.O. Culbertson (1942) completed studies for the Ph.D. degree in 1941 majoring in plant genetics with a minor in plant pathology. His study was entitled "Inheritance of factors influencing sucrose percentage in *Beta vulgaris*."

Correlation between sucrose percentage of mother beets from segregating populations and the means of inbred progenies were highly significant.

Crosses were made between inbred lines differing in percentage of sucrose content. The average sucrose percentage of F_1 and F_2 generations was approximately equal to the mean of the parents. Culbertson wrote, "It appeared that relatively homozygous lines of desirable sucrose content could be obtained comparatively easily. The ability to store sucrose content was found to be inherited in a quantitative manner and to be dependent upon the interaction of several genetic factors."

In Tomatoes

L.M. Humphrey (1934) completed work for the Ph.D. degree in 1933 with a major in plant genetics and a minor in botany, using a study of "The meiotic divisions of haploid, diploid, and tetraploid tomatoes with special reference to the prophase." The study has no direct relation to this review.

The diploid and tetraploid produced by doubling were both homozygous. The chromosome behavior was regular. In the tetraploid four stand pairing occurred at synapsis, and at diplotene the chromosomes appeared as tetrasomes. At diakinesis and metaphase the chromosomes became separated into disomes.

In Potatoes

W.A. Riedl (1948) completed work for the Ph.D. degree with a major in plant genetics and a minor in plant pathology. His thesis problem was "The inheritance of tuber-set in *Solanum tuberosum* L."

Tuber-set was determined by counting number of tubers over 1 inch in

diameter per hill. Several hill plots with hills separated by 18 inches were used in the studies under replicated and randomized conditions. Generalized standard errors were calculated according to methods commonly practiced and used to determine the significance of differences.

Several years' trials of large numbers of potato varieties and seedlings were tested in replicated trials, and lines were selected that had proven to be different in tuber set. The four lines selected were Katahdin and Bliss Triumph which excelled in tuber set, and two seedling lines No. 29 and No. 471 which were distinctly lower in tuber set when extensive comparisons were made.

Although Katahdin as a clone was significantly superior in tuber set to the two seedling varieties, it did not transmit this characteristic in a marked degree to its sexual progeny. Bliss Triumph, however, produced sexual progeny superior, on the average, in tuber set to sexual progeny of Katahdin, and markedly superior to sexual progeny of the two seedlings No. 29 and No. 471.

When individual plants were selected in S_1 and sexual progenies for each of the parent lines placed in different classes for tuber set, there was a positive relation between S_1 plants for tuber set and the mean of their S_2 progenies.

In Onions

A.C. Ferguson completed work in 1951 for the Ph.D. degree with a major in plant genetics. His thesis was entitled, "A study of the relationship between characters in inbred lines of onions and their crosses." The W. Atlee Burpee Co. generously supplied material.

Statistically significant differences were obtained for nine inbred lines of onions, six male sterile lines, 31 crosses, and five commercial varieties in three types of replicated trials (including in each the five commercial varieties) for each of nine characters including yield.

Hybrid yield was correlated with seven of the characters of inbred parents, each calculated separately, ranging from .36 to .61 two r values being significant at the 1 percent point and five at the 5 percent point. The R value obtained was .70. The more important relationships were for yield, days to mature, and height of inbreds and their F_1 cross yields. Maximum yield was obtained from certain male-sterile inbred crosses, and this yield was significantly better than that of the best commercial variety.

Late by last crosses yielded more than E X L or E X E.

In Cotton

T.R. Richmond (1948, 1949) completed studies for the Ph.D. degree with a major in plant genetics. His thesis study was "The genetics of certain

factors responsible for lint quality in American upland cotton.” He had many years experience in Texas cotton investigations prior to completing studies at Minnesota.

The thesis has no direct relation to the problem of breeding for disease resistance. Methods given to calculate lint index are complex and have not been reviewed. Four strains were used as parents: Lintless (LS) glabrous seed, usually no lint fibers; High Smooth (HS) glabrous seed, approximate lint index = 3.5; Misdell (MS) covered seed, approximate lint index = 5.0; and Half and Half (H & H) covered seed, approximate lint index = 7.5.

Three types of crosses were studied:

1. Glabrous X Covered: H & H X LS, MS X LS, H & H X HS, MS X HS
2. Glabrous X Glabrous: HS X LS
3. Covered X Covered: H & H X MS

Two genetic systems controlling lint quality were identified:

(1) A single gene manifesting itself in three phases—(a) Lintless Phase, where no lint is produced when homozygous for glabrous seed coat; (b) a Linting Phase in which quantity of lint found in the range of cultivated American upland varieties is produced when the gene is homozygous for covered seed coat; and (c) an Intermediate Phase in which the gene in a heterozygous condition leads to an intermediate amount of lint.

(2) A complex of minor modifying factors, each with a minor effect, which together greatly modify lint production, are epistatic to the major gene in the glabrous-lintless phase, and have a very important effect on lint production when acting in the presence of the linting phase.

In Soybeans

T.R. Mehta (1948) studied “Correlation of yield and certain quantitative characters in soybeans” for his thesis research for the Ph.D. with a major in plant genetics.

Mehta had a background of over 10 years of experience in breeding various crops including rice, oil seeds, millets, and pulse crops.

Data were collected using 64 varieties, most of which represented advanced hybrid generations of different crosses. These relatively homozygous varieties were grown at University Farm and at the Waseca Station.

Single rod rows were used for each plot. Records on characters other than yield were taken on a thinned 2½-foot length of row from each plot in order to give an even stand. Characters measured were number of seeds per plant, number of pods per plant, number of nodes per plant, number of pods per node, number of seeds per pod, size of seed, height of plants, height of first pod from the ground, and days to flowering. Seed yields were

recorded for the complete row.

A triple lattice design was used, and the data for University Farm and Waseca were averaged. For each character studied there were highly significant variances as expressed by the 64 varieties.

High positive simple correlations were found between yield and number of seeds per plant, number of pods per plant, and number of pods per node.

High positive simple correlations were found between the following character pairs: number of seeds per plant and number of pods per plant, number of pods per plant and number of nodes per plant, height of plant and number of nodes per plant, height of plant and number of pods per node, number of seeds per plant and number of pods per node, number of pods per plant and number of pods per node.

Size of seed was not significantly correlated with yield and showed significant negative correlation with number of seeds per plant, number of pods per plant, number of pods per node, number of seeds per pod, and number of nodes per plant. Therefore, it seemed difficult to breed a variety of large seed that also excelled in these other characters.

A multiple R value of +.91 between yield and other characters studied was obtained.

A partial r value between yield and any one of the components—nodes per plant, pods per node, seeds per pod, and size of seed—when the others were held constant was high in every case with a multiple R of +.89 for yield and the four characters. When, however, relationships between any two components were studied and the others were held constant, the partial correlation was negative in every case, indicating they are somewhat incompatible.

It was concluded that the more important components of yield of seed are number of pods per plant, number of pods per node, and height of plant. The latter is of importance only insofar as it insures the selection of higher number of pods.

In Sunflowers

W.A. Russell (1952) completed work for the Ph.D. degree with a major in plant genetics and minor in plant pathology. His thesis was “A study of the interrelationships of seed yields, oil content, and other agronomic characters with sunflower inbred lines and their top crosses.”

Ten or 11 characters of 54 inbred lines and seven in their topcrosses were studied. All differences between inbreds and between crosses were statistically significant under the conditions of the experiment. In 1949 there was a significant relationship between some of the characters of inbred lines and their topcrosses, although there was no correlation between the yield of

inbreds as tested and that of their topcrosses. In 1950 somewhat different results were obtained.

Multiple R values were obtained for both years between inbred characters and topcross yields. The R value in 1949 of +0.47 was not significant, while that in 1950 of +0.68 was significant.

There was a highly significant negative r value for percent of self-fertility of inbred lines and the degree of hybridization under open pollination.

There was a positive relation between percent of oil in seeds of inbreds and that of their topcrosses. Other interrelations were studied but were as expected where characters expressing vigor of inbred lines are correlated with percent of oil in seeds.

In Forages

T.M. Stevenson (1937) completed work for the Ph.D. with a major in plant genetics and a minor in plant pathology. His thesis title, "Sweet clover studies on habit of growth, seed pigmentation, and permeability of the seed coat," gives a rather satisfactory idea of the nature of the research when one notes from the review that studies of inheritance were carried out.

Inheritance of mottling of the seed coat in *M. alba* was studied in F_2 and F_3 of crosses. When F_2 classifications were checked by breeding studies in F_3 , it was found that mottled seed coat was dominant and that a single pair of factors determined seed coat color segregation.

The inheritance of plant type was studied in crosses of dwarf branching, called Alpha, X common biennial white sweet clover. The common was dominant to dwarf with segregation on a single factor difference.

Seed coat color and plant habit were not associated in inheritance.

The pigment in the seed coat was located in the lower part of the Malphigian cells and was shown to have all the properties of anthocyanins.

Examination of seeds from 10,982 plants of common sweet clover grown in 1931 showed 99.3 percent of the seeds incapable of germination due to impermeability of seed coats. Selection for two successive generations within selfed plants that had the highest percentage of permeable seeds resulted in marked increases in the proportion of permeable seeds produced, while selection for higher percentages of impermeable seeds also resulted in progress in that direction.

Treatment with sulfuric acid increased permeability in lines that produced a good proportion of permeable seed by rendering hard seeds permeable, but such treatment had little or no effect on highly impermeable lines.

H.K. Shultz majored in plant genetics with a minor in plant pathology, obtaining the Ph.D. in 1940. His thesis title was "A study of methods of breeding orchard grass, *Dactylis glomerata*, L." The only phase of particular

importance in relation to disease resistance was information regarding rust reaction. Eight collections or introductions contained both resistant and susceptible plants. A few first-year inbred lines bred true for rust resistance. There was a negative correlation between yield and rust reaction on the average.

W.J. White (1940) completed work for the Ph.D. degree with a major in plant genetics and a minor in plant pathology. He studied "Intergeneric crosses between *Triticum* and *Agropyron*." The study was initiated and turned over to White by T.M. Stevenson.

The primary object was to develop a large seeded perennial forage grass using as parental material *Hynaldia villosa*, 12 species of *Triticum*, and 10 species of *Agropyron*. All species of wheat except *T. monococcum* were successfully crossed with *A. elongatum* but failed to set seed in crosses with seven wheat species and were slightly successful with *A. trichophorum*, more successful with *A. glaucum*, but not as compatible with the latter as with *A. elongatum*.

There was no seed produced from F₁ crosses with *A. glaucum* or with backcrosses. Therefore, the studies were confirmed primarily to crosses with *A. elongatum*. F₁ crosses set little seed, but backcrosses were more successful. With tetraploid wheats as one parent very little seed set either in F₁ or in backcrosses. With hexaploid wheats, however, F₁ crosses with *elongatum* backcrossed to wheats led to a sufficient percentage of seed set to use in further research.

One of the interesting results in F₁ and in backcrosses to spring wheat parents was the small percentage (2 to 7) of plants of winter wheat type, while in backcrosses to winter wheat from 90 to 100 percent were of winter habit of growth.

The survival percentage was 100 in one test winter when F₁ hybrids between Minhardi X *A. elongatum* were studied and rather high in similar F₁ crosses when spring wheat hexaploid varieties were crossed with *elongatum*. The survival was low from plants produced from the first backcrosses of F₁ to spring wheat parents. Some F₃ families, however, survived well.

The maximum fertility of F₁ crosses of *A. elongatum* with hexaploid wheats was highest, 29 percent, in crosses with Marquis; but it was higher in F₂, reaching 47.5 percent from crosses with Hope.

A. elongatum had an average seed weight per 1,000 kernels of only 6.89 grams. The primary purpose of *A. elongatum* hybridization studies was to obtain larger seed size in a perennial grass. Therefore, plants of F₁ and F₄ generation crosses were compared with hexaploid wheats for seed weight. In F₁ to F₄ generations small percentages of plants in the lower classes of seed weight were obtained as compared to the spring wheat parents. When

backcrossed one, two, or three generations, the percentages of plants with seeds in seed weight classes in the lower range for spring wheat increased.

Other characters of the hybrids relating to forage quality, in comparison with *A. elongatum* and *A. glaucum*, were studied in considerable detail. It is of interest to note that *A. elongatum* has been reported to be highly resistant to rust, smut, and mildew. Ergot was the only disease observed in the F_1 hybrids with *A. glaucum* and with *A. elongatum*. Some plants in later generations of *A. elongatum* backcrosses to spring wheat were susceptible to stem rust.

The *A. elongatum* crosses were not very desirable in forage quality.

R.E. Stitt completed work for the Ph.D. in 1941. His thesis was entitled "Inheritance studies of the tannin content of perennial Lespedeza."

The material used was from 83 different seed lots representing introductions from Asia. From plants grown from these origins 1,937 plants were selected which varied in growth habit, number, and size of shoots. These plants were harvested, dried, and analyzed for tannin content by a short colorimetric method. Six plants covering a wide range were selected.

From the second and later growth of these six plants, cuttings were made and used for a replicated planting in the field.

Five additional seed sources from U.S. Department of Agriculture were used to make further studies.

The six clones were studied at Statesville, North Carolina, for inherent differences in tannin content and various important agronomic characters. Although these six clones were highly significantly different in all characters studied, none were low enough in tannin content to be satisfactory for farm use.

Tannin content of individual plants of the five strains gave a wide variation.

E.H. Rinke (1945) completed studies for the Ph.D. degree in 1943 majoring in plant genetics with a minor in plant pathology. Rinke's thesis problem was "Inheritance of coumarin in sweet clover." The material was from department studies. Work at University Farm was with an Alpha or dwarf type where selection was being made primarily for resistance to mosaic and stem canker. As the Alpha selections were low in seed setting ability, they were crossed with Waseca lines of standard growth habit and good seed setting ability. The inheritance studies were a comparison of coumarin content and habit of growth in parental selfed progenies of the dwarf and standard parents and their F_1 , F_2 , and F_3 generation crosses.

The Alpha selfed parent and Common Biennial White were each selfed 4 years when tested for coumarin and were grown in comparison with F_1

and F_2 generations. Alpha was distinctly lower in content than the Common Biennial White. The F_1 was intermediate, and F_2 , where over 400 plants were tested, covered the entire range of both parents, although less than 50 plants were grown and tested for the parents.

Although the F_2 curve of variability was high, it was unimodal. Approximately 77 percent of F_2 plants were in the range of the selfed line low coumarin parent. F_3 lines tested in several localities varied considerably under different growing conditions. Rinke concluded one major factor was responsible for coumarin content in this material. He also found common habit of growth to be dominant to dwarf and no relation between coumarin content and growth habit.

Y.S. Tsiang (1944), with a major in plant genetics and a minor in plant physiology, completed work for the Ph.D. in 1943 using material of bromegrass that was a phase of the grass improvement program of the department. This consisted of 36 strains from an old pasture in Martin County selected from seed progenies of which selfed seed was available, and 32 clonal lines of Parkland obtained from Dominion Experimental Farms, Ottawa, Canada.

Artificial epidemics were made in the Disease Garden using collections of *Selenophoma bromigena*, the organism responsible for leaf spot.

Selfed lines of both types of brome were grown in small replicated individual plant plots in comparison with commercial seed progenies grown as checks. Sufficient seed was available for eight selfed progenies of Parkland and 20 from the creeping strain from Martin County. Plants from the check varieties ranged from resistant to susceptible. In the selfed lines of Parkland and the creeping variety the leaf spot reaction ranged from resistant to susceptible, and some lines from each seemed to breed true for much greater resistance than the commercial checks. There were highly significant r values for leaf spot reaction of clones and their selfed progenies of +.63 and +.66 for Parkland and creeping types, respectively.

In general there were positive relations between the characters of parental clones and 1-year selfed progenies of both Parkland and creeping brome, although most of the calculated r values were rather low. For plant height, however, the r values were large enough to have predictive value.

Extremely hot dry weather during the latter part of July 1941 made it possible to classify clonal lines and selfed progenies for heat and drought resistance. Rather high consistent relations were found between reaction to heat and drought conditions and important plant characters in Parkland such as degree of leafiness and leaf spot resistance.

Significant differences were found for beta-carotene content, and in creeping brome a significant r value was obtained of +0.76 for beta carotene

content for parental clonal lines and their selfed progenies.

Tsiang was a member of the Department for several years and was in direct charge of corn breeding studies at Waseca. On returning to China for a few years he trained personnel in corn breeding and a little later went to Taiwan where he was Executive Secretary of the Joint Commission of Rural Reconstruction and recently has been appointed as one of 5 commissioners. He has carried on corn breeding in Taiwan as a weekend project and a recent hybrid of two Ohio inbreds, as one single cross parent, with two Taiwan inbreds as the other parent, has given over 70 percent increase in yield over native corn and matures several weeks earlier. In 1962 he was the recipient of an Eisenhower Award and spent 8 months in the United States. During this stay he received a citation as an outstanding alumnus from the University of Minnesota. He was one of several to give an invitation address at the American Society of Agronomy Conference in August 1962.

C.F. Cheng completed studies for the Ph.D. degree in 1946 with a major in plant genetics and a minor in botany.

The seed setting studies were made of material from the grass breeding program of the Agronomy and Plant Genetics Division consisting of 29 clones of creeping brome grass, *Bromus inermis* Leyss., 34 clones of crested wheatgrass, *Agropyron crestatum* (L.) Beauv. and 24 clones of meadow foxtail, *Alopecurus pratensis* L.

Twenty-seven of the 29 clones of brome were from S_2 and 2 were open-pollinated; in crested wheatgrass, forage type, one clone was selected in S_2 , six were of S_1 origin and 5 were open-pollinated, and there were 22 open-pollinated clones of Fairway; and in meadow foxtail 10 clones were of S_1 origin and 24 were open-pollinated selections.

Isolation to insure self-pollination was by bag as described previously by Hayes and Schmid and by space isolation in the small grain nurseries and in addition open-top cheesecloth cages considerably higher than the plants were used to surround the isolated clones.

There was a wide range of variability in seed setting of open-pollinated plants in all three species. In creeping brome there was a highly significant relation between seed setting under open-pollinated and where there was space isolation in pairs of clones. With meadow foxtail there was a consistent important relation between seed setting of clones under self-pollination and open-pollination.

With brome and crested wheat there was a significant negative correlation between the percentage of pollen abortion and seed production. In meadow foxtail, where there seemed to be relatively good seed setting under self-pollination, there was no relation between seed setting and pollen abortion. In brome grass the percentage of aborted pollen was definitely and

closely correlated with the frequency of quartets showing micronuclei, but there was no such definite relation in meadow foxtail.

H.H. Kramer (1947) completed studies for the Ph.D. degree in 1946 with a major in plant genetics and a minor in plant physiology. The more valuable results of the study were published under the title "Morphologic and agronomic variation in *Poa pratensis* L. in relation to chromosome numbers." The study was a phase of the department's grass improvement investigations started in 1936.

Material furnished consisted of clones selected from increases of sod pieces collected in 1937 from many origins in Minnesota and clones of four seed lots from Ottawa, Canada: Ottawa No. 3, Aberystwyth 993, Danish 939, and Svalof 177. Individual clonal selections were made from these four seed lots grown at Waseca.

Purposes were to determine heritable differences in important characters, the interrelationship between character differences, and the relationship between variation in chromosome numbers and the characters studied.

Numerous agronomic plant characters including yield were studied in individual plants and in established clonal sod plots. There was little relationship between types of response in these two kinds of trials. Wide variation was found in mildew susceptibility in clones of both indigenous and introduced material. Positive relationships were found between mildew susceptibility and chromosome numbers with an r value of .48 and between chromosome numbers and spreading rate in mowing plots of $r = .41$.

Chromosome numbers of 35 clones of indigenous origin varied from 50 to 68, about as widely for 13 clones of Danish 939 and Svalof 177. Four clones of Ottawa No. 3 were placed in class 49 to 52, and five clones of Aberystwyth 993 ranged in numbers from class 69 to 72 to class 85 to 88. In general it was concluded that chromosome numbers in Kentucky bluegrass may vary over a wide range with no appreciable effect on morphological characters or agronomic behavior.

J.L. Bolton (1948) completed as his thesis problem, "A study of combining ability of alfalfa in relation to certain methods of selection," with a major in plant genetics and a minor in botany.

Percentage of natural cross-pollination of plants varied from 11 to 100 percent but was generally 90 percent or higher. Self- and cross-fertility ratings of 100 plants gave wide ranges averaging 1.58 seeds per flower when selfed and 5.54 seeds when crossed. There was a slight positive significant correlation of $C.29$ between self- and cross-fertility of individual plants. First, second, and third generation inbred lines, under open-pollination conditions ranged from 0 to 60 pounds per acre of seed; one third generation line

exceeded 60 pounds per acre.

Closely related plants when crossed gave little heterosis, and reciprocal crosses were similar in their progenies.

Combining ability studies of a group of open-pollinated plants were made to test the desirability of using one, two, or four high or low combiners as tester plants in lieu of studying all combinations within a group. The results indicated such tester plants may be useful where the combining abilities of large numbers of plants are to be tested.

Alfalfa breeding methods used at Dominion Forage Crops Laboratory, Saskatoon, consisted of selections for fertility from field populations of disease-resistant stock, and the discard of self-tripping lines. Bolton studied self progenies and the lines used subsequently to observe undesirable recessive genes. To determine combining ability, selected lines were grown in polycross nurseries, and yield trials from polycrosses were made. Lines selected were used to study crosses of all possible combinations.

Bolton suggested the following method of producing commercial hybrid alfalfa. Based to a considerable extent on research results the suggestion was made to use non self-tripping, self-fertile plants to avoid the necessity of a large amount of vegetative propagation.

If four lines were used as parents, A, B, C, D, the cross of A X B or C X D could be made by first growing space isolated $\frac{1}{4}$ acre seed plots of each of four lines, with an estimated production in each case of 50 pounds. Two isolated crossing plots, A X B and C X D, of 100 acres could be grown if seeded at 1 pound per acre to produce single cross seed with an estimated yield of 50 pounds per acre. From this a crossing plot (A X B) X (C X D) of 10,000 acres seeded at 1 pound per acre could be grown to produce double cross commercial seed. With an estimated yield of 200 pounds per acre it would be possible to seed 200,000 acres annually. On a 5-year rotation the above procedure would produce seed sufficient to maintain 1 million acres of double cross alfalfa.

L.J. Elling (1950) completed studies for the Ph.D. degree with a major in plant genetics and a minor in plant pathology. The thesis title was "Evaluation of selected alfalfa clones."

In a previous study with alfalfa 175 clones were selected from several varieties in wilt-injured plots that had been in alfalfa for several years at the Morris Station. From this group nine clones were selected as follows:

Clone 19, Grim	wilt susceptible
Clone 30, Ladak	wilt resistant
Clones 53, 70, Ranger	wilt resistant
Clone 81, Cossack	wilt resistant

Clone 125, Hardistan	wilt resistant
Clone 137, Northern Common	wilt resistant
Clone 162, Crestan	wilt resistant
Clone 168, Crestan	wilt susceptible

These clones had been studied for self- and cross-fertility. All were among the more desirable from previous visual examination except clone 70, selected because of high self-fertility, and clone 168, highly self-sterile but cross-fertile. These two clones, however, were nearly as desirable in most characters as the others. These clones were selected for the most part from different origins.

In addition to these clones selected at Minnesota, S-42-119 was obtained from Bolton at Saskatoon. S-42-119 had been found desirable in combining ability for both seed and forage production. C53 was obtained from Nebraska, recommended by Tysdal as one of the more promising clones studied at that station.

All possible intercrosses were made in the greenhouse between the 11 different clones. Each clone also was pollinated with an admixture of pollen of the 10 other clones, and this was considered polycross seed.

Some 105 single crosses, 32 samples of polycross seed and six commercial varieties used as checks—144 entries in all—were seeded in a triple lattice design with three replications at Rosemount and on the Glen Bergen Farm, Lake of the Woods County, Minnesota. All of the 11 clones were sampled three times to obtain polycross seed except clone C53, for which only two samples were available.

Clones were studied for pollen normality. Four clones with less than 75 percent normal pollen gave progenies in their crosses with low seed set, and Elling concluded such clones should be discarded without further testing.

No clones gave crosses for forage yield superior to the varieties Ladak and Ranger at Rosemount, and none equaled Ladak in forage yield at Williams.

There was relatively good agreement between the mean forage yield of the average of 10 single crosses of individual clones and the average of three polycross trials, although variability of tests from plot to plot and field to field was very high. Clone 53 and clone 70 were considered to be of promise for further use.

T.H. Rogers (1950) completed work for the Ph.D. degree with a major in plant genetics and a minor in plant physiology. His thesis study was entitled "Methods of breeding crimson clover" and work was carried out at Auburn, Alabama.

He made studies of the probable causes, importance, and development of hard seeds. The hard seed character was shown to be based on inheritance.

Three generations of selfing led to the isolation of pure breeding lines. Although, on the average, there was a marked reduction of vigor, the self-pollinated lines were sufficiently vigorous to be used in breeding.

D.H. Heinricks (1951) completed work for the Ph.D. degree majoring in plant genetics. He studied "Methods of breeding intermediate wheat-grass, *Agropyron intermedium* (Host.) Beauv."

Extensive seed setting studies were made under bag both in the greenhouse and field and under open-pollinated conditions in the nursery. There were wide statistical differences between clones in seed setting, and some clones were highly self-sterile.

A rather extensive comparison was made between polycross progenies and open-pollinated progenies as a means of evaluating clones for combining ability. General combining ability was considered to be more accurately evaluated from polycross progenies than from open-pollinated.

W.P. Kneebone (1951) completed work for the Ph.D. degree with a major in plant genetics and a minor in plant pathology. His thesis problem was "Factors related to forage quality and to seed production among eight clones of *Bromus inermis* Leyss. and their polycross progenies."

The studies of the eight clones and their polycross progenies were made in spaced individual plant plots. Significant differences were obtained in protein content, leaf percentage, coarseness of stem, percentage dry matter and seed production.

Although reaction to leaf spots indicated that artificial epidemics could be induced, a satisfactory evaluation for leaf spot reaction was not obtained.

M.W. Pedersen completed studies for the Ph.D. degree in 1951 with the thesis title "Nectar production in alfalfa clones as related to bee visitation and seed production including a study of techniques for measuring nectar." He had a major in plant genetics and minor in plant pathology (see Pedersen, 1953). The studies were conducted at Logan, Utah, from 1946 to 1951 inclusive.

An important correlation was found between deviations in honey bee visitations and nectar production of clonal lines.

Seed yields per plant were significantly different after corrections were made for number of bee visitations, indicating a good possibility of improvement by breeding.

Nectar production from polycross trials was correlated with maternal clonal nectar production with an r value of .83.

J.R. Cowan (1952) completed work for the Ph.D. degree with a

major in plant genetics and minor in plant pathology. His thesis study was entitled "Some plant breeding studies with tall fescue (*Festuca arundinaceae* Shhreb.)." The work was conducted in Oregon.

Two-year studies were made in individual plant nurseries on mode of reproduction, methods of measuring self-sterility, hot water emasculation, seed and forage yield, and the effects of selfing.

Although tall fescue during 3 years' study proved to be highly self-sterile, a few highly self-fertile plants were obtained.

From intercrosses of 10 highly self-sterile clones seed set was obtained in every case. This indicated that self-incompatibility might be one cause of self-sterility.

Tall fescue can be propagated readily vegetatively and as high as 200 clones produced from a 2-year-old plant.

Wide differences were obtained between plants and between varieties in seed and forage production.

The hot-water method of emasculation was successful.

Continued selfing led to reduced vigor.

In Crop Agronomy

S.C. Chang completed work for the Ph.D. degree with a major in agronomy. Chang (1943) studied length of dormancy in relation to after-harvest sprouting of cereal crops.

In 1938 he harvested one large bundle and six small bundles from all varieties in the 1/40 acre trials of spring and winter wheat, oats, and barley. These he left in the field to be exposed to weather. After a period of 2 weeks, 10 heads were taken at 10-day intervals from each small bundle and threshed to determine sprouting percentage. As the rainfall was light this year the bundles were sprayed with water on August 15, 19, and 24. On the basis of differences in sprouting four or five varieties were selected.

Similar procedures were carried out from these varieties in 1939 and the bundles sprayed several times at appropriate 7-day intervals. After sprouting was determined, samples were harvested on the day each variety was mature. A germination test was carried out in an electrically controlled germinator at about 30E C. Germination counts were made on the 3rd, 6th and 10th day of the test, and these tests were made in duplicate for each variety.

Marked varietal differences were obtained in resistance to after-harvest sprouting and in the dormancy period in spring and winter wheat. Less consistent differences were obtained in the oat and barley trials.

Change concluded that "differences in sprouting resistance are in most

cases due to differences in dormancy period, and in some cases they may be due to differences in rapidity of germination." Presence of awns, possession of hulls, and epidermal characters of the glume were thought to play a role in resistance to after-kernel sprouting.

He suggested that similar trials may be of value under conditions where after-kernel sprouting is a problem.

Chang (1943) also studied causes for varietal differences in shattering in wheat.

He determined that length of lemma, width of grain, average length of rachis internode, weight per 1,000 kernels and number of grains per head in relation to shattering gave a multiple R value of .62 which indicates their importance in relation to shattering. The amount of strengthening tissue in the glumes seemed to be related to shattering.

R.K. Tandon (1949) majored in agronomy. Remarkable advances had been made in the control of weeds in flax by the use of selective herbicides. As a phase of development in the problem of weed control by selective herbicides Tandon studied "The response of flax to rates and formulations of 2,4-dichlorophenoxyacetic acid."

Seven varieties of flax were grown under replication and the effect of various treatments with 2,4-D at practical rates of application were studied by using statistical methods. Viability of seed in treated plots remained unaffected.

There was a distinct varietal response; resistant varieties were not affected in yield, but significant lowering of yield occurred in the less tolerant varieties.

While some varieties also were affected in oil content and iodine number, other varieties were highly tolerant to treatment.

At practical rates of application of the herbicide there was no appreciable effect of practical significance on maturity and height of plant.

R.G. Robinson (1949) carried out two researches for the Ph.D. thesis with a major in agronomy. He studied (1) the effects of flax stands on yields of flax and extent of weeds and (2) annual weeds, their viable seed population in the soil, and their effect on yields of small grains. The Central Fiber Corporation of Pisgah Forest, North Carolina, provided financial assistance for the latter study.

Lowering of stand experimentally caused reduction in yield and increase in weed infestation. Greatly decreased stands showed enormous increases in weed population.

In the latter study plots were selected from four locations previously used for flax rotation and tillage studies. A soil sampler was used, capable of

removing comparable plugs of soil, where 154 plugs equaled the volume of 1 square foot of soil at a depth of 6 inches.

Robinson studied two types of samples for weed content, one consisting of 154 plugs and the other of 4 plugs, replication of plugs being made in each study.

Germination tests were made in the greenhouse and weed seedlings identified and counted. Each of the large samples of 154 plugs was washed through a set of sieves to reduce volume and retain weed seeds.

Viable weed seeds per square foot agreed rather well in the two types of samples and varied from a low count of 88 in the small sample method to 98 in the large sample method. The higher count was 4,002 per square foot in the small sample method and 3,068 in the large sample method. In general there was excellent agreement between replicates.

Studies of the effect of weeds on flax were carried out in some cases by seeding various rates of *Setaria viridis* with flax.

Yields of flax were significantly decreased by increasing weed populations. Contrary to expectation, soil moisture tended to be lower on weed free plots than on plots with weeds.

This and similar studies have a direct relation to crop improvement.

H.R. Arakeri and R.S. Dunham (1950) presented a study of environmental factors in relation to pre-emergence treatment of corn with 2,4-D and soybeans with TCA. The study was used as a thesis problem for the Ph.D. degree by the senior writer with a major in agronomy.

“Good control of both grass and broadleaf weeds was obtained with 24 ounces of 2,4-D acid in butyl ester form without injuring the corn crop providing the pH or organic matter of the soil was high or that no rain fell between planting and emergence of the crop on soil of low pH and low organic matter.”

With 6.79 inches of rainfall plus 0.5 inch of added water, 2,4-D at 64 ounces per acre persisted in Waukegan silt loam less than 2 months.

TCA, however, as a pre-emergence treatment for soybeans caused injury to the crop and gave unsatisfactory results.

L.E. Everson and Dunham authored Minnesota Technical Bulletin 197 (1951) containing a summary of research of the effect of 2,4-D on certain weed and crop seeds. The detailed research presentation was used for a Ph.D. thesis with a major in agronomy and minor in botany by the senior author.

No attempt here will be made to summarize the results. The reference is included as Everson has been rather closely connected with crop improvement at Iowa State University Seed Laboratory.

Chapter 8

Concluding Discussions

This story of teaching and research at the University of Minnesota covers a period of nearly 50 years, including the time that has elapsed since my official retirement on July 1, 1952. Since retirement I have had informal contacts with staff and graduate students in the Department of Agronomy and Plant Genetics at Minnesota, 2 years' experience as a member of the Cornell Group at the College of Agriculture and the Central Experiment Station at the University of the Philippines, and seven short assignments of a month or less at land grant institutions. Leading seminars at these institutions with special attention to disease resistance and other plant genetics problems and related phases of plant sciences, I emphasized cooperation in teaching and research as developed at Minnesota.

I have been impressed, in these contacts, with the enthusiasm of many staff members dedicated to furthering knowledge in biological and agricultural sciences, and the application of this knowledge to the improvement of living conditions and the welfare of people engaged primarily in agriculture. At nearly all institutions there have been numerous foreign students, and their dedication to their chosen fields has been an inspiration. These are the main reasons why, in spite of many undesirable interrelations reported vividly in the daily press, it seems the chances are very good for eventual cooperation between the emerging nations of the world and older nations and the eventual evolution of the "One World Idea," where there is opportunity for all.

SOME DIRECT RESULTS OF MINNESOTA RESEARCH

The experiments carried out in cooperative research at Minnesota and other stations with particular relation to breeding crops for resistance to plant diseases have made it possible to arrive at valuable conclusions. Many of these have been emphasized in previous reports or by the writers of special researches. Therefore, they will be only briefly summarized

It is as important to know the genetic nature of the disease organism

as to obtain similar genetic knowledge of the host plant. For pathogenic diseases, crop resistance is due to the interaction of factors carried both in the parasite and in the host plant.

Thus, for reaction to stem rust of cereals where physiologic races are present and where new races develop both by mutation and by recombination of genes during certain stages in the life history of the parasite, it is necessary continuously to study the available races and, as far as possible, classify these by their reaction on a series of differential hosts. By this means the plant pathologist and plant breeder can learn when races that have new parasitic capabilities first appear. With wheat stem rust, for example, Race 15b, discovered in 1939, several years before it became of epidemic proportions, had the capability of attacking Thatcher, Hope, and their derivatives in the mature plant and seedling stages. New sources of resistance were sought, found, and incorporated into desirable varieties soon after 15b became of epidemic proportions.

It was also valuable to learn that both Hope and H44 carried the same factor pair for stem rust resistance and that the mature plant resistance of Thatcher, Minnesota Double-Cross derivatives, and the vulgare wheat developed in Canada from a cross of Pentad durum by Marquis resulted from the interaction of the same two recessive factors in the homozygous recessive condition. Several graduate student studies aided greatly in reaching these conclusions. It was important to know that these two genotypic conditions for stem rust resistance, the one transformed to bread wheats from dicoccum crosses and the other from durum crosses, were independent in inheritance.

Mature plant resistance of Hope, H44, or the Thatcher type furnished a basis for resistance from heading to maturity to most physiologic races and the basis for the type of resistance of greatest practical value for many years. Each of these varieties and their derivatives also carried physiologic resistance to some races. Resistance to Race 15b was found to be independently inherited from either the Hope or Thatcher type of mature plant resistance.

Continued study, therefore, of the disease organism and genes for resistance in the wheat hosts has been necessary. Although there have been cases where wheat varieties formerly resistant have become susceptible, stem rust of spring wheat in North America has been controlled in a rather satisfactory manner.

With oat stem rust, oat crown rust, and wheat leaf rust, new races have through the years appeared and caused new breeding problems. By continued cooperative effort, however, these diseases for many years have been kept under control by breeding, even though there were serious losses for a time when new races first became prevalent.

Two types of stem rust resistance in oats have been known for many years. These are the White Russian and the Richland-Iogold-Rainbow

genotypes. The latter, called Rainbow for convenience, conditions resistance to stem rust Races 1, 2, 3, 5, 7, and 12 while the White Russian type conditions resistance to Races 1, 2, 5, 8, 9, and 10. Smith (1934) first concluded that these genotypes were each controlled by a single dominant factor and that R_{WR} for White Russian was allelic to R_R for Rainbow.

In carrying out studies where the parents differed in their reaction, one parent being of White Russian genotype $R_{WR}R_{WR}$ and the other of Rainbow genotype R_RR_R for stem rust reaction, we had completed the recovery of the White Russian type of resistance in a homozygous condition for Race 8. Matthew B. Moore, my plant pathology coworker, suggested we study these recovered hybrids for reaction to Race 7. This seemed unnecessary, but I agreed we would make an intensive study and to my surprise, and gratification, some lines homozygous for resistance to Race 8 segregated for reaction to Race 7. Another generation was grown which led to lines resistant to Races 8 and 7 as well as to the combined races, to which White Russian and Rainbow together were resistant. It is not known yet how this came about; either the genes R_{WR} and R_R are closely linked or the two genes were incorporated into hybrid lines in some other way. Further study is being made.

With barley leaf rust tests at Madison, Wisconsin, and by Henderson, there was evidence of two types of resistance, physiological and mature plant. For the mature plant type the varieties studied were resistant to a collection of rust races from heading to maturity in the field but susceptible as seedlings. Resistance was dominant, and reaction was based on a single factor pair. Other varieties were resistant to a collection of races both as seedlings and under field conditions. The physiological type of resistance was dependent upon two multiple factors, either alone or together in the dominant condition leading to resistance.

For stem rust reaction on barley, resistance to many collections of races both in the seedling and mature plant stages was simply inherited with resistance dominant to susceptibility. There was complete correlation of seedling and mature plant reaction, and barley stem rust was, therefore, easy to control.

For smut reaction in corn it has been learned that numerous sources of genotypic resistance are available and that genes in various chromosomes lead to resistance to smut. It is rather easy to select inbred lines from various sources with moderate resistance to smut. In general, lines resistant to smut in one locality have proved resistant in other localities even though studies under controlled conditions have shown that physiological races occur. With reaction to smut in corn, it seems that a type of mature plant resistance is conditioned under normal environmental conditions.

RUST DISEASES ARE PERENNIAL PROBLEMS*

The story of breeding for stem rust resistance in wheat, oats, and barley serves to emphasize that diseases are perennial enemies. A discussion of this problem was presented by M.F. Kernkamp at the annual crop improvement day of the Minnesota Crop Improvement Association in 1963.

Early in the season of 1962 there was only a small amount of rust inoculums in the South. However, conditions were favorable for a northward spread of rust earlier than usual, and rust spores appeared in May in Nebraska and South Dakota. In the northern part of the winter wheat area the crop was late maturing and growth was lush, leading to a favorable season for rust development.

One may note that studies were conducted each year to determine the rust races present in the wheat area. For example, in 1962 from 470 collections from the field, Race 56 that destroyed Ceres in 1935 was responsible for 56 percent of the isolates from these collections; Race 15b that attacked, when originally discovered, most of the wheats carrying mature plant resistance from heading to maturity, accounted for 21 percent of the isolates, while Races 17 and 11 together accounted for 20 percent, and Race 38 for 2 percent. Other races in very small numbers were identified.

Winter wheat is grown extensively in Colorado, Kansas, and Nebraska, as well as in other states. It has been reliably estimated that in 1962 losses from rust were approximately 50 million bushels, with a value of over \$100,000,000. This loss could have been controlled by breeding if the winter wheat had carried hereditary factors for resistance to Race 56.

In spring wheat, however, Selkirk, the most extensively grown variety, was highly resistant in 1962, and the durum grown widely in North Dakota also were resistant to rust attacks. These durums have been produced largely by G.N. Smith and coworkers in North Dakota.

The breeding work in relation to resistance to rust is carried out by cooperative effort including federal and state agencies and, in recent years, by international cooperation. In our region the State Crop Improvement Associations, the Crop Quality Council, and the Midwest Barley Improvement League, other interested semi-public agencies, and business leaders in specialized industries have each played an important part in stem rust control and similar problems.

Kernkamp also provided information on disease resistance problems relating to oat stem rust.

Races of rust seem to come and go in rather direct relation to the resistance and susceptibility of the oat varieties grown and their prevalence. Thus in 1962 there were 187 isolates identified in the Cooperative Rust

*Prepared with aid and approval of M.F. Kernkamp, head, Department of Plant Pathology.

Laboratory at St. Paul. Race 6 of oat stem rust comprised 66 percent of these isolates; Race 7A, 14 percent; Race 7, 8 percent; Race 2, 7 percent; and other races, 5 percent.

Race 6, the predominant race in 1962 also was the most prevalent in 1961. It seems apparent that Race 6 has increased rapidly in recent years because the White Russian type of resistance produces a resistant type of reaction to the attacks of Race 7 and other races, and the Rainbow type of resistance controls attacks to Race 8 and other races, while the White Russian and Rainbow types are both susceptible to Race 6. The well known commercial varieties Andrew, Ajax, Bonda, Cherokee, Clinton, and Mo-0-205 with either the White Russian or Rainbow types of resistance also are known to be susceptible to Race 6.

The Canadian type of stem rust resistance of oats has in the past conditioned resistance at low temperatures to all prevalent races, but in some seasons and locations this resistance has broken down at high temperatures. Prior to 1962, Race 6 produced a homogeneous type of reaction on varieties such as Garry, Burnett, and Rodney, which carry genotypes for the Canadian type of resistance. In 1962 most isolates of Race 6 produced mixed reactions on seedlings with both resistant and susceptible pustules on the same leaves, and single spore isolations also gave mixed infection types when used in further inoculation studies. Whether mixed reactions also would be obtained under field conditions is unknown.

The problem of controlling oat stem rust by breeding requires continuous research. Thus Race 7A, which in 1962 comprised 14 percent of the isolates in the central part of United States, can attack Rodney and similar varieties at both low and high temperatures. Here it is necessary to use genotypes of the White Russian type of inheritance that are resistant to Race 7.

Kernkamp mentions Race 6A, identified five times near barberry bushes in New York, which can attack virtually all commercial varieties carrying genotypes for resistance. This includes the White Russian and Rainbow genotypes for resistance and also varieties carrying the Canadian type of resistance. It is generally appreciated by workers that some races of rust, evolving by hybridization or mutation, are short lived and lack ability to reproduce and spread rapidly. This is a research problem investigators face for each new race. Whether Race 6A will ever become prevalent will require further study.

Race 4A also is mentioned by Kernkamp. As yet it has not been identified in the central United States, but so far as known all commercial varieties are susceptible to this new form. Two possible sources of resistance could offer a solution. One of these is resistance that already may be available somewhere, and a search is under way throughout the world to find resistance to Race 4A that may have occurred naturally in oat collections.

If not found present, in a study of all available crop material, "it is possible to produce the desirable phenotype by searching for mutants among segregating progenies of mutagen treated varieties. Some phenotype changes can be produced quite easily with this method of mutation breeding. For example, one may refer to Wallace in Florida who has found that certain combinations of mutagen treatments will produce mutation frequencies at a single locus in oats as high as 1 percent on a per plant progeny basis."*

These brief summaries emphasize that breeding for disease resistance is a constant struggle between the development of new races of the disease organism by so-called natural evolutionary processes and the control of these new sources of disease as they occur by usual methods available to the breeder.

SOME SPECIAL AGRONOMIC AND PLANT GENETIC PHASES

Results of various studies related to cereal crop improvement seem worth emphasis. Numerous studies of staff and graduate students have proven conclusively that there is, in general, a definite, consistent, and significant relation between yielding ability and plumpness of seed of individual plants, lines, and varieties. Plumpness of seed is highly heritable from generation to generation and of important visual selection value, and rather easy to study by observation alone.

Another phase of seed size plumpness may be illustrated from oat breeding experiments in connection with disease resistance studies. In the early period weight per bushel in oats was greatly influenced by environmental conditions. These variations seemed dependent not only on disease reactions but on other environmental reactions. In recent years, as illustrated by the Bond variety and hybrids of Bond parentage, weight per bushel has been stabilized above 32 pounds to a marked degree. Weight per bushel and seed size were highly heritable in segregating generations of hybrids where Bond was one parent. Progress may be made by simple visual selection when such a component of grain yield is available to a breeder.

Investigations of forage crop improvement were undertaken. Extensive comparisons were made of newly introduced species and varieties of grasses and legumes with brome, timothy, alfalfa, and the clovers that make up the larger part of grass forages for our region. No newly introduced varieties from foreign countries that were grown in the trials proved of outstanding value.

Extensive cooperative investigations are now under way to improve the more desirable species or strains of brome grass, alfalfa, and clovers. Myers (1953) emphasized the importance of grassland research with particular

*We appreciate receiving the above statement by letter through the kindness of Dr. A. T. Wallace.

reference to studies under way at the Rosemount Field Station. These studies are conducted cooperatively, as well as individually, by many departments at the University.

Myers was selected as the new department head when I retired in 1952. His many experiences in different phases of research, with widely different crop species, was so evident that it seemed this selection was a fortunate one for the department.

Minnesota farmers, according to Myers, are turning more and more to grassland farming, so important in the production of livestock and essential to the maintenance of soil fertility. Myers wrote, "We must adopt a cropping system that permits maximum and sustained production."

For the grower of cash crops, corn, small grains, flax, and soybeans, crop rotation with grass and legumes in the rotation aids in soil conservation. Proper and extensive use of grasslands in the rotation helps make profitable use of acres not needed for cash crops.

Probably the most notable Minnesota accomplishment in grass improvement since 1952 has been the development of the Park variety of Kentucky bluegrass. This new variety was described in *Minnesota Farm and Home Science* by Thomas (1959).

The material used to produce Park consisted of a mixture of 15 selected clonal lines of Minnesota origin. In 1937, H.K. Shultz and the writer had collected divots from 60 old pastures in Minnesota. These were broken down into 281 vigorous individual plants. Comparative trials of progeny from open-pollinated seed and seed saved under a bag for 30 clones indicated that the material was highly apomictic and would breed true from practical standpoints by seed reproduction.

The 15 clones used in a mixture that produced the Park variety were selected after extensive tests under mowing conditions with and without a mixture of white clover. The 15 strain mixture included three strains from Wadena County, one from Lake of the Woods, three from Todd, two from Blue Earth, one from Waseca, two from Mower, and three from Redwood. The variety has been tested in more recent years by cooperators at other state experiment stations; rather extensive comparisons have been made between Park, Marion, and commercial sources of seed of Kentucky bluegrass.

Park has excelled in seedling vigor and quickly forms a dense sod. (The strains used to produce Park were selected on this basis.) Park also excelled in tests for resistance to rust and *Helminthosporium* (the latter from the thesis of George Bean in plant pathology) but is susceptible to mildew.

This new variety has led to the development of a rather extensive certified seed industry by the seed growers cooperative at Roseau in northern

Minnesota. Thomas has estimated production of approximately 1 million pounds of certified and registered seed produced in Minnesota for each of the 2 years 1962 and 1963.

DISTRIBUTION OF SEED OF RECOMMENDED VARIETIES

One of the most important phases of plant breeding researches is to produce improved varieties that meet with the approval of the grower, processor and consumer. It is evident that a large part of the researches in plant breeding, however, consists of basic studies in plant breeding and allied fields such as physiology, pathology, entomology and other researches relating to the production of crops of high quality for food, feed or fiber.

A number of graduate students, listed in this report, have utilized their graduate training by continuing as active plant breeders in the employ of seed companies and a number are now operating their own seed businesses.

The discussions previously in this report, relating to different phases of plant breeding, have not adequately presented information regarding the production of different classes of seed. The present methods used in Minnesota for the production of breeders, foundation, registered and certified seed will be outlined.

THE RELEASE AND RECOMMENDATION PROCEDURES FOR FIELD CROP VARIETIES

This is an important and necessary step in the development of the program relative to an increase and distribution of recommended varieties. It seems desirable to emphasize the succession of steps in making seed of high quality available to the grower and consumer. This recognizes the leadership of the Agricultural Experiment Station Director.

Essential steps outline the part played by the Crop Variety Review Committee as appointed by the Station Director and of project workers on specific crops.

The nature and work of this committee is here outlined.

Policies regarding release, naming and recommendation of field crop varieties in Minnesota are the responsibility of the Director of the Agricultural Experiment Station. The Crop Variety Review Committee and project workers on specific crops are responsible for:

- (1) Recommending release of new varieties, hybrids, inbreds, clones, and special genetic stocks.
- (2) Recommending seed increases of new varieties, hybrids, inbreds and clones developed by the Minnesota Agricultural Experiment Station in preparation for expected release.
- (3) Approving names of new varieties, hybrids, inbreds or clones developed by the Experiment Station.

- (4) Annually revising the list of recommended varieties.
- (5) Suggesting policies relating to items 1 through 4 (above) to the Director of the Experiment Station.

Membership of the Crop Variety Review Committee consists of:

- (1) One representative of the Experiment Station administration.
- (2) Head of the Department of Agronomy and Plant Genetics.
- (3) One plant breeder.
- (4) One extension agronomist.
- (5) Head of the Department of Plant Pathology.
- (6) One plant pathologist.
- (7) One branch station agronomist.
- (8) Project leader, Foundation Seed Program.
- (9) Manager, Minnesota Crop Improvement Association.

Project leaders are responsible for:

- (1) Making proposals for seed increase, release and naming of new varieties.
- (2) Making proposals for the list of recommended varieties.
- (3) Preparing data summaries in support of items 1 and 2.

An understanding of the various phases of pure seed production can be adequately covered by direct quotation from the plans as organized. The following therefore is quoted directly from the procedures as agreed upon.

The general plans are outlined as agreed upon by interested persons including Experiment Station personnel, project leaders, and the Minnesota Crop Improvement Association representatives.

Other procedures to accomplish the objectives desired may be summarized as follows:

I. Variety Recommendations:

A. Decisions requiring action by the committee:

1. Placing varieties on the 'recommended' list.
2. Placing varieties on the 'other variety' list.

Action by the committee is not required to place a variety on the 'not adequately tested' list. It is expected that, when sufficient data are available, a variety will be placed in 1 or 2 above. Varieties should be dropped from the 'other variety' category when there is no longer interest in them. This is the responsibility of the project leaders.

B. Time for preparing materials for committee action:

Actions to place varieties on the 'recommended' or 'other varieties' list will be taken only at a November meeting of the Crop Variety Review Committee. Data from the project leaders should be supplied to the

committee secretary by the first Thursday in November. Decisions reached in the November meeting will be included in Miscellaneous Report 24 for the following year.

II. Releasing and naming of new varieties:

Decisions on releasing and naming of new varieties are to be made, insofar as possible, at the November meeting to permit incorporation of the information in the new Miscellaneous Report 24. Meetings can be arranged at other times if complete data are not available in November.

Approval for release and naming of a Minnesota-developed variety automatically implies recommendation; unless specifically designated otherwise.

III. Seed increases of new selections and introduced varieties:

A. Seed increases of new selections developed in Minnesota programs:

Actions by the committee on seed increases of promising selections is needed when the breeding project desires participation of the Seedstocks Project. Normally, participation by the Seedstocks Project is available when a variety is being increased with intent to release. The Seedstocks Project may also participate in increase for further testing if the breeding project does not have resources for the increase (for example, increase of forage varieties with contract growers in Minnesota or elsewhere).

When a request is made for increase, the amount to be increased should be specified. If more than one year is required for increase, additional performance data is to be reviewed by the committee annually. Permission to increase Minnesota-developed selections does not imply consent to release.

B. Seed increases of varieties developed outside of Minnesota:

Decisions on seed increases of varieties from other states are not the responsibility of the Crop Variety Review Committee.

These decisions are made by the project leaders, Head of the Department of Agronomy and Plant Genetics, the Extension agronomists directly concerned with the crop, the Seedstocks Project leader and a representative of the Minnesota Crop Improvement Association.”

The essential information regarding various phases of these procedures also seems essential if a complete picture is obtained of these procedures.

IV. Preparation and presentation of project recommendations and data:

Prior to making proposals on release or recommendation of varieties, project leaders should consult with appropriate extension and branch station personnel.

Project recommendations, including appropriate data, should be

submitted for all crops appearing in Miscellaneous Report 24; whether or not changes are recommended. The present status of the variety or selection (e.g., seed availability, present classification in Miscellaneous Report 24) and the area of intended use of the variety should be indicated. Recommendation should be accompanied by:

1. Descriptions of varieties on which action is requested but which were not included in the previous year's Miscellaneous Report 24.

2. Data to support recommendations. These should be presented in summary form, with data from various locations and years combined. Data for individual locations and years should be presented in addition to the summaries, if necessary, to bring out specific points. All available data, including that obtained in regional trials, should be included in the summaries. Care should be taken to include appropriate variety comparisons.

Experimental numbers used for designation of unnamed lines should be consistent from one table to another and from year to year. Only one number should be used for a line.

Fifty copies of project proposals and supporting data must be submitted to the committee secretary so they can be distributed to interested staff members in Agronomy and Plant Genetics, Plant Pathology, and Branch Station Agronomists and Superintendents. Personnel receiving this information may respond directly to the committee or to the project leader.

Project leaders in Agronomy and Plant Genetics and Plant Pathology and the extension agronomist most directly concerned with the crop under consideration should meet with the committee while their crop is being considered. Other interested personnel may be invited at the discretion of the project leader. All of those designated above are encouraged to participate in discussion of proposals.

V. Actions by the Committee:

Each committee member has one vote. In addition, project workers on the crop under consideration will collectively have one vote.

VI. Distribution of supplementary varietal data and report of actions by the Crop Variety Review Committee:

Actions taken by the committee and supplementary variety information will be distributed following the November committee meeting. Examples of supplementary information are: (1) Detailed descriptions of newly-released varieties not included in the previous year's Miscellaneous Report 24 and not submitted to the committee for action. (2) Data summaries of cooperative variety trials. These summaries are to be in addition to that supplied in support of project proposals covered in I (B) above. The summaries are intended to keep cooperators and interested research and extension personnel informed about significant variety trial results.

Fifty copies of such supplementary information should be submitted by the project leaders to the Agronomy Department Head by December 1.”

After presentation of the various steps leading to the development of recommended varieties and the steps in their production it seems worthwhile to also outline the memorandum of understanding agreed upon by the Minnesota Crop Improvement Association and the Minnesota Agricultural Experiment Station in respect to the production and distribution of Foundation Seed. An agreement was drawn up and signed by each of three administrative leaders, consisting of the President, Minnesota Crop Improvement Association, The Agricultural Experiment Station Director, and the Assistant Vice President of Business Administration of the University of Minnesota.

The participants in this agreement recognize mutual interest in and responsibility for providing farmers with high quality seed for the production of improved crop varieties. The Minnesota Agricultural Experiment Station (hereafter referred to as the Station) agrees (a) that this mutual interest and responsibility can best be served by designating the Minnesota Crop Improvement Association (hereafter referred to as the Association) as the foundation seed production and distribution agency for the State of Minnesota, and (b) to designate the Association as such an agency. The Association agrees to assume responsibility for the production and distribution of foundation seed as a service to certified seed growers of the state. Policies governing these activities will be determined by the Board of Directors of the Association in consultation with the Station. The manager of the Association will be responsible for operations to provide these services, and the Association will employ appropriate personnel to assist him.

The foundation seed to be grown for increase in this program will be of recognized varieties and hybrids developed by an Experiment Station, by the U.S. Department of Agriculture, or by qualified commercial breeders and the varieties or hybrids will meet the standards for certification as set forth in the current issue of the Seed Certification Standards of the Association.

For the purposes of this Memorandum definitions of seed classes as set forth in the current Seed Certification Standards of the Minnesota Crop Improvement Association shall apply.

The participants of this Memorandum will meet as needed to plan seed production and distribution. These meetings will be held at the call of the director of the Station upon the recommendation of the manager of the Association.

This agreement shall continue in force until terminated in writing by either or both parties at least 90 days prior to January 1 of the year in which the change is to occur.

To assist in accomplishing the seed increase task the Station agrees to:

1. Provide technical assistance and advice to the Association in the production of breeders seed of Minnesota releases and planting stocks for production of foundation seed of other releases.
2. Cooperate with the Association in the selection of producers for this program.
3. Make available to the Association the equipment and facilities of the

Foundation Seedstocks Building at no cost. These facilities are to be operated under the same general guidelines as the Minnesota Crop Improvement Building.

To assist in accomplishing the seed increase task the Association agrees to:

1. Produce in cooperation with Station personnel, breeders seed and planting stock for the production of foundation seed, including purifying (head rowing, etc.), seed lots as necessary, testing sterility of corn inbreds and single crosses, and other operations required in producing quality planting stocks.
2. Select capable and qualified producers with suitable facilities for producing and distributing foundation seed.
3. Produce and distribute foundation seed as a service to the members of the Minnesota Crop Improvement Association and as a non-profit, non-commercial activity and to maintain records of income and expense separate from those for seed certification. These records will be made available to the director of the Station, or his designee, upon request.
4. In consideration of the services rendered by personnel of the Department of Agronomy and Plant Genetics and other Station personnel and the use of the facilities of the Foundation Seedstocks Building, to allot to the Department of Agronomy and Plant Genetics funds in the Foundation Seed Budget considered by the Association to exceed the needs for operation of the project, plus a reasonable reserve. These funds are to be used in general support of the Department's program related to crop improvement.
5. Maintain facilities made available by the Experiment Station and share them with Station personnel in the discharge of activities for which the facilities were designed. The Association will be responsible for all alterations and improvements and such changes will be made in accordance with University policy.
6. Perform miscellaneous services currently performed by the Cooperative Seed Production and Distribution Project of the Station including: furnishing at reasonable cost seed of crop varieties to departments of the Institute of Agriculture and for County Demonstration Trials and without charge to personnel of the Department of Agronomy and Plant Genetics for their own research needs and for shipment to cooperators at other experiment Stations."

The agreement was executed by the signatures of the President, Minnesota Crop Improvement Association, the Director, Minnesota Agricultural Experiment Station, and the Assistant Vice President for Business Administration, University of Minnesota.

THE IMPORTANCE OF EDUCATION

Addresses by A.H. Moseman, formerly director for agriculture of the Rockefeller Foundation, and now on leave, have a direct bearing on the story of cooperation. At Oregon State University Charter Day, October 24, 1962, Moseman discussed "Agriculture in the Space Age."

He mentioned an FAO inquiry relating to crop improvement training for students from the Near East countries in Mexico rather than at land grant institutions in the United States; commenting that U.S. institutions no longer are furnishing the inspiration and information needed as a basis for

such training. Moseman referred to a Rockefeller Foundation trainee at a land grant institution who returned home because, “he did not come to the United States to learn how to operate an IBM machine.”

My own experience in emerging nations leads me to conclude that the basis of crop improvement training is to learn the value of applying Mendelian principles of heredity of plant breeding in all of their essential features. This requires basic knowledge of genetics. It is essential that foreign students obtain information that will lead to the production, increase, and distribution of improved varieties and methods essential to the maintenance of high quality pure seeds. Methods developed by land grant institutions have emphasized how these essential overall features of crop improvement have been carried out in our country.

Moseman referred to the value of good teachers. He recalled the inspiration received from his early teacher, the late F.D. Keim, who taught the beginning course in genetics at Nebraska and inspired undergraduate students in crop and soil sciences. Moseman also referred to Stakman as an illustration of a land grant institution professor who has been an inspiration to many foreign graduate students. He said Stakman could step from a plane at any major airport of the world and be enthusiastically greeted by a former student.

These references lead me to emphasize that my own enthusiasm and belief in the value of applying genetic principles to crop improvement rest very largely on the basis of graduate student contacts with E.M. East at the Bussey Institution of Applied Biology, Harvard University, and to associations as an assistant and co-worker with East at the Connecticut Agricultural Experiment Station.

The late R.A. Gortner, for many years chief of the Division of Agricultural Biochemistry at the University of Minnesota, was an inspirational leader in teaching and research. I have long remembered a statement of his to a graduating class at the Minnesota Agricultural College: “I do not advise anyone to specialize in biochemistry unless to him it seems to be the most interesting occupation in the world.” Although Gortner believed and practiced the principle that graduate training should supply sound occupational needs, he did not fail to emphasize the importance of intensive interest in and knowledge of the newer unexplored fields of biochemistry, agriculture, and biology.

In another address to experiment station workers at the University of Nebraska, January 4, 1963, Moseman spoke on “New Dimensions for Agricultural Science.” The address has direct bearing on this review. His presentation emphasized the successful Rockefeller Foundation projects such as hybrid corn improvement in Mexico and Colombia, and wheat improvement in Mexico.

Rockefeller Foundation research leaders were trained primarily at land grant institutions in the United States.

The success of the Rockefeller Foundation program is well known and somewhat similar to accomplishments of the foreign Point 4 program of the United States Government: land grant university contracts to aid foreign countries supported largely by AID, such activities as JCRR in Taiwan supported by a bilateral agreement of Nationalist China and U.S., and similar activities of FAO in many countries of the world.

Reference has been made to the New International Rice Research Institute at Los Banos, Philippine Islands, supported largely by Ford and Rockefeller Foundations and staffed by leaders in special fields from many different countries. The former associate director and the geneticist at this institution received their graduate training and Ph.D. degrees in plant genetics at the University of Minnesota. Their training here emphasized the importance of cooperation in research, basic principles related to their specialized fields, and an appreciation that continued research is fundamental to improvement in knowledge and practice.

The working together of teaching and research as exemplified by Land Grant Institutions, the State and Federal Agricultural Experiment Stations, and the important researches of graduate students at these Land Grant Institutions, seem to the writer to be one of the major reasons for the prosperity and leadership that our country so well deserves.

Much has been learned about cooperative endeavors here at Minnesota and at other similar land grant institutions in relation to inspiring others in less developed countries to cooperative research. While guidance should be given to the graduate student in his individual research, it is essential that the student develop the research as seems to him most desirable. The adviser can help in some cases to avoid pitfalls.

In agricultural foreign aid each group of foreign workers must be given free hand to develop their own research. Methods that work in the United States do not necessarily fit the needs of a foreign country, although general basic principles have much the same application in both countries.

I am reminded of a newspaper photograph of a 6-foot 2-inch adviser from the U.S. showing Koreans, "how, by helping plant rice seedlings," and I chuckle derisively. He stands in the muddy paddy with seedlings in his hand. I am confident many native Koreans can plant rice seedlings faster and better than the foreign adviser. Thus, it is not always the know-how that Americans can give. First one must learn the problems, practices, principles, and how best to apply improved methodologies in the foreign country. Perhaps our know-how will consist in teaching coordination, cooperation, etc., based on the country's needs, but not necessarily based on exactly how we do it.

In another newspaper I saw pictures of the Rice Research Institute at Los Banos. The laboratories pictured lead to the conclusion that there will be ample opportunity to carry out the basic research needed to increase rice productivity. The essential laboratories for all phases of plant research are, or will be, available, and the staff seems excellently trained. But the same paper, under a picture of a test for rice quality, stated that the research of this new institution already had led to a three-fold increase in yield in the Philippines. This latter statement fails to appreciate that even with all of today's improvements in technical know-how, a three-fold increase in yield in a country requires basic research in many fields, intensive cooperation between research and extension leaders and farmers, and the application of these basic techniques by the grower, processor, and marketing agency for the benefit of the consumer. These essential studies and their application require continued research, often a considerable period of years to fully obtain the practical applications.

The present occupations of former students indicate rather clearly that the graduate students for the most part have continued in the broad field of plant breeding, although often with different crop plants than used in thesis studies. Numerous former students have taken administrative positions, and often very capable research workers no longer find a great deal of time available for research.

THE DEVELOPMENT OF COOPERATION IN TAIWAN AND THE PHILIPPINES

After retirement in 1952, I spent 2 years in the Philippines with a Cornell group at the College of Agriculture, University of the Philippines.

In 1953, at the request of the Joint Commission of Rural Reconstruction, I was given permission to spend 3 weeks in Taiwan to take part in a school for technicians interested in the crop improvement program. Before my affiliation with the school, Mrs. Hayes and I went by train to southern Taiwan and spent a week traveling the length of the Island by automobile visiting agricultural research institutions. Y.S. Tsiang was our guide. Later during my work at the Crop Improvement School, he and Dr. Ma translated lectures from English to Chinese as I gave them. These lectures, largely adapted from previous plant breeding texts, were mimeographed, bound, and distributed (Hayes, 1953) by the Joint Commission for Rural Reconstruction under the title "Methods of Plant Breeding."

I was impressed in Taiwan by the work of the Joint Commission of Rural Reconstruction and other agencies in cooperative endeavors in crop improvement as well as other fields. Cooperation as taught by H.H. Love of Cornell and others, seemed to have played a small part at least in the admirable accomplishments in rural reconstruction in Taiwan.

A brief reference to work in the Philippines during 1952-54 will round out my experiences in developing cooperative research in foreign nations. The Cornell University contract was similar to other university contracts and part of what now is the AID program. S.S. Atwood, formerly head of the Department of Plant Breeding, and later University Provost, suggested that he thought it desirable to give particular attention to the development of cooperative research between the central experiment station of the college and agricultural research bureaus of the central government, relating particularly to rice and corn research.

Without discussing difficulties I may say that I soon found this did not meet with the approval of MSA leaders in the Philippines, and even today I do not know why. At first Dean L.B. Uichanco at the college was rather skeptical. However, D.C. Umali, my coworker at Los Banos, was an enthusiastic supporter. It is sufficient here to say that with Dr. Umali's strong support we succeeded in getting this cooperation underway. Although the central experiment station had no direct funds for station research in 1952, today over a million pesos have been appropriated annually for the station phases of cooperative research. Greatly increased facilities have been made available also to bureaus of plant industry and extension, Department of Agriculture and Natural Resources, Philippine Government.

The following was presented to me as it appeared in the Manila Sunday Times on June 27, 1954:

HAYES LAUDED FOR WORK IN RICE, CORN PROGRESS

Dr. H.K. Hayes was hailed as the man who inspired and guided the cooperative research pattern for the improvement of rice and corn in the Philippines, and as such he holds a unique position in the history of the agricultural research development of the country. This was the gist of appreciation by his coworkers who entertained him at a special luncheon at the college of agriculture, Tuesday noon.

Almost unbelievable progress has been made in this cooperative effort. The college and experiment station at Los Banos have received support from the Ford and Rockefeller Foundations and seem destined to become leaders in research and teaching of tropical agriculture in the Far East. Cooperation requires more than administrative planning, and the ultimate success is dependent in a large degree on the researchers themselves. It will be interesting to watch developments in the Philippines.

MORE RECENT DEVELOPMENTS AT MINNESOTA

Dr. Myers continued as Department head from 1952 until he resigned in 1964. Myers' wide knowledge of crop research led to rather extensive support for the plant breeder and for related fields of research. During his leadership, and because of wide contacts with others both on the research and administrative levels, added support was given for research in agronomy

and plant genetics. During this period, Ernest Rinke was closely associated with W.M. Myers and functioned as acting head of the Department for a year in 1959 and again for a year 1963-64. Rinke was very active in the Department for twenty-four years and resigned in 1964 to accept a position of research coordinator with Northrup King and Company.

One may round out this story of "The development of plant breeding at Minnesota" by referring to the present department head.

Dr. Herbert W. Johnson accepted headship in the Department on July 16, 1964. It seems probable that Dr. Johnson's work under both Moseman and Myers at Beltsville made him somewhat familiar with the Minnesota story. It seems desirable to state that plant breeding training at Minnesota as obtained by taking a Ph.D. in this field should give the student adequate training for plant breeding teaching and research in both developed and undeveloped countries. Newer methods of research will without doubt include training of such a nature that new methodologies will be recognized. The present staff in the Department of Agronomy and Plant Genetics at the University of Minnesota are dedicated to providing this kind of training and are uniquely qualified to do so.

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