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ROLLINS ADAMS EMERSON (1873-1947) HORTICULTURIST, PIONEER PLANT GENETICIST, ADMINISTRATOR, INSPIRING STUDENT ADVISER

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The vigorous and highly productive life of Professor R. A. Emerson spanned 74 years and 7 months. His birth and death took place in New York State, but Nebraska nurtured his early development and schooling. He spent 15 years of his professional career at the University of Nebraska, followed by 33 years at Cornell University.

Rollins Adams Emerson, son of Charles David and Mary C. Adams Emerson (a direct descendant of Henry Adams), was born May 5, 1873 at Pillar Point, New York State on the eastern shore of Lake Ontario. In 1880 his family moved to Nebraska and settled on a farm in Kearney County. Here he grew to manhood, attending the grade and high schools in the district. His parents, who both had unusual ability and character, provided a sound home with emphasis on high moral standards, civic responsibility, and education. A local physician, who was also a naturalist, encouraged Rollins to collect and identify the local flora, and guided his mind toward scientific endeavors.

In 1893 young Emerson enrolled in the College of Agriculture at the University of Nebraska and was fortunate to come under the influence of the great teacher, Charles A. Bessey. Two years later, while still a student, he was appointed Assistant Horticulturist on the Experiment Station staff. In 1896 he presented a talk to the Nebraska Academy of Sciences (of which he was a member) entitled "On the internal temperature of tree trunks." He was interested in this problem because of the possibly injurious effects on trees of high or low temperatures. The talk was based on some tests he had made over a period of three summers to find out how the temperature within trunks (determined by boring holes and inserting thermometers) compared with the temperature at the surface of the bark or in air.

Emerson gave a talk at the annual meeting of the Nebraska State Horticultural Society both in 1896 and 1897. One of these talks was on "The horticultural setting of farm houses."[1/] In it he addressed the farmers in his audience with the plea to beautify the home surroundings. In the following admonishment he showed a remarkable maturity for a 23-year-old student:

1/ Nebraska State Horticultural Society Annual Report, 1897, pages 122-126.

> You began, perhaps many years ago, the most important undertaking of your life, the one in which every true man is sooner or later engaged; you began the making of a home. You worked with a will, and in time you had a home. Then you wished to improve it; you wanted to give your family better advantages; you would do both when you had more money. You worked harder than before. You hurried from morning till night, day after day, year after year, till, in the rush of a busy western life, you seem to have forgotten the real purpose of your work; you have come to believe that all you are here for is to work. You have become so accustomed to your way of doing that it suits you perfectly; and you do not see why others dislike it so. But remember the monotony of your life is broken by variations. Your work takes you to all parts of your farm and of the surrounding country as well. But how about the one whose chief source of pleasure must come from what she sees in one small dooryard?

Emerson then went on to describe the dreary outlook of the farmer's wife:

> Outside the house is the yard, a more or less grassy spot, with a good many weeds and some holes where the hogs have rooted. There are few trees, no shrubs. The house stands bare, without so much as a vine to cover it. Near the door are a few small flower beds, with half their beauty destroyed by being fenced in with laths and pieces of boards to keep them from the hogs. To the left stand two or three small posts, which, together with the corner of the house, form a support for a clothes line. A little farther from the house and to the right, the sunflowers are growing up about an old wagon. some plows, and a broken mowing-machine. Next come the hay stacks, set so as to hide the only view of the tree-lined valley beyond. Sometimes above the stacks can be seen the smoke of the train as it crosses the valley and buries itself in the trees and the cut on the other side. To the right of the stacks is the barn, a heap of broken fence boards near it. And beyond all, the hill--

only the sky beyond that.

Do you wonder that the mother loses heart, and that even inside the house there is less cheer than there was once? Does it seem strange that the boys find more pleasure on the streets of the country town near them than they do at home? I wonder why, when older, they have learned to look down upon farming as something fit only for ignorant, unaspiring men.

After these blunt words Emerson indicated that a few days of work and a small outlay of money spent on tidying up, rearranging, and landscaping the surroundings could remedy this rather stark picture. He stressed a natural, simple landscape rather than a stiff, formal effect.

In 1897 Emerson received his B.Sc. from the University of Nebraska. His first job after graduation was in the Office of Experiment Stations, United States Department of Agriculture, Washington, D.C. He served there for two years (1897-1899) as Assistant Editor of Horticulture for the publication, Experiment Station Record. However, he did not care for the rigidity and formality of this position.

On May 23, 1898 he entered upon what he considered the most important undertaking of a man's life [2/] when he married Harriet Hardin. He must have become acquainted with her during his student years because she was one year behind him in the university.

In the spring of 1899 Emerson accepted an appointment at the University of Nebraska as Assistant Professor and Chairman of the Horticulture Department, and Horticulturist in the Experiment Station. He held these positions for 15 years, with a promotion to full professor in 1905. For at least part of this period in Lincoln, Nebraska the Emersons resided at 1205 North 33rd Street, just a few blocks from the campus. Mrs. Emerson, a very pretty, gracious young woman, was busy with the care and activities of a growing family. Eventually there were four children, two boys, Sterling and Eugene, and two girls, Thera and Myra.

2/ See page 2.

setting he would have developed for a rural school, so different from the usual barren grounds.

Results and ideas from this beehive of horticultural activity were published in the annual reports and bulletins of the Nebraska Experiment Station and the Nebraska Horticultural Society. Emerson was a life member of the Horticultural Society, and on several occasions during the early 1900's served as a delegate to meetings in neighboring states.

Through the years in Nebraska Professor Emerson became increasingly absorbed in a different and fundamental type of research, the nature of heredity in plants. He had begun to hybridize kidney or garden beans (*Phaseolus vulgaris*) in 1898 while he was in Washington, D.C., to find out if there were any definite principles controlling heredity in plants. When he returned to Lincoln, Nebraska in 1899 he brought the bean materials with him and continued the experiments.

In the initial stages of his studies on beans Emerson was not aware of the genetic laws established by Gregor Mendel from studies on garden peas over 40 years earlier in Austria. Mendel's paper, entitled "Experiments on plant hybridization", had been published in 1866 in an obscure Austrian periodical[5/] with limited distribution. The significance of the paper was not realized until 1900, when de Vries of Holland, Correns of Germany, and von Tschermak of Austria independently published papers in which they referred to Mendel's work and conclusions. Each was able to confirm by his own experiments Mendel's law of separation of characters in crosses, Correns and von Tschermak using peas, de Vries using a number of different plant species. On May 8, 1900 the English scientist Bateson gave a lecture to the Royal Horticultural Society of London on "Problems of heredity as a subject for horticultural investigation.[6/] He referred to the published reports of de Vries, Correns and von Tschermak concerning the work of Mendel. In 1901 an English translation

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5/ Vert. naturf. Ver. in Brünn, Abhandlunger, IV. 1865.

6/ J. Royal Hort. Soc. London 25:54-61. 1900-01.

From his earliest report, published in 1902, Emerson realized the necessity for growing large numbers of individuals so that statistical methods could be applied to make a quantitative study of variation. By following this approach he was able to demonstrate for a number of bean characters the validity of Mendel's law of segregation of unit characters in predictable proportions. In most of these cases one character was completely dominant over the contrasting character in the F_1 hybrids. However, he did find incomplete dominance for certain types of seed color and for pod stringiness. As an example, in crosses between varieties having stringy versus stringless pods, the pods on the F_1 plants were intermediate between the parents in stringiness, and segregation occurred in the F_2 progenies for stringy, stringless and intermediate conditions.[7/] Emerson found the intermediate group difficult to classify, which made the numerical proportions less reliable than clearcut differences. Adverse weather conditions during the later stages of the study also affected the expression of this character. Thus, he encountered in this early work two factors which have continued to complicate genetic studies ever since, the effects of environment on character expression, and the subjective element in classifying a sample of individuals.

In 1909 Professor Emerson summarized his findings on "Inheritance of color in the seeds of the common bean, *Phaseolus vulgaris*" for the annual report of the Nebraska Experiment Station. He found that the presence of pigment in bean seeds was dominant to its absence, and segregation followed Mendelian expectations. At this time he subscribed to the presence-absence hypothesis which had been proposed by Bateson and Punnet[8/] for all-or-none effects, such as presence or absence of pigment. In other words, pigment was lacking because the factor for it was believed to be missing from the organism. The difference between total pigmentation of the seed and partial pigmentation, where pigment was confined to the hilum or "eye", behaved in crosses as a unit character. However, crosses between races with

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7/ Nebraska Expt. Sta. Ann. Rept. No. 17:33-68. 1904.

8/ Bateson, W. 1909. Mendel's principles of heredity. Cambridge University Press, N. Y.

crosses available to test which, if either, of the hypotheses was correct. However, none of his subsequent publications dealt with this aspect of heredity in beans.

Professor Emerson's interest in corn for studies of heredity began around 1908 when he grew some plants from a cross between a rice popcorn and a sweet corn variety for a teaching demonstration. The segregation of starchy and sugary kernels deviated from the expected ratio based on a single factor pair. This aroused his curiosity and, many years later, he published an explanation for the distorted ratio. [9/]

From 1908 until he left Nebraska in 1914, Emerson accumulated a wide variety of genetic deviants in corn, many of which were used in later studies at Cornell University. Some of the material originated as single, open-pollinated ears displayed, often in a "freak" class, at local agricultural fairs, at the Annual Corn Shows held during the winter in Lincoln, or at a National Corn Exposition held in Omaha in 1909. Others arose when plants from the open-pollinated seeds were self-pollinated or when controlled crosses were made between different types of corn, such as pop by dent or pop by sweet.

Emerson was particularly interested in collecting and experimenting with the different color types in maize. In one of his earliest reports on inheritance in maize[10/] he noted a marked tendency for the colors affecting different parts, such as pericarp and cob, to stay together in inheritance. He reasoned that if the color of each part was due to a distinct gene, the genes were not independently inherited. In "genetic correlation" or "gametic coupling" the dominant characters were present in one parent, absent from the other, and remained together in inheritance. In "spurious allelomorphism" the dominant characters were in separate parents and remained separate. He saw these two conditions as basically the same phenomenon,

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9/ Anat. Rec. 29:136. 1925, and Genetics 19:137-156. 1934.

10/ Nebraska Expt. Sta. Ann. Rpt. 24:58-90. 1911. (Also read at a meeting of the Amer. Soc. Naturalists at Ithaca, N.Y. December 30, 1910.)

though Bateson, one of the discoverers of genetic linkage, considered them to be distinct. At the time Emerson presented his report, the relationship between genetic linkage and chromosomes had not jelled. Yet, he suggested "that if genes were definitely located in chromosomes and that if parental chromosomes separated bodily at the reduction division (as has been suggested by several writers), we should have an 'explanation' not only of perfect genetic correlation and of allelomorphism-spurious or otherwise - but of independent inheritance as well."

While still in Nebraska, Professor Emerson made some initial studies on a red-striped (variegated) pericarp condition which occurred in certain varieties known locally as "calico corn." He described the character by its "incorrigible irregularity." From his work on variegated pericarp, he provided evidence that mutations could arise in somatic cells contrary to the prevailing opinion that they occurred only in germinal tissue,[11/] and that the changes affected only one of the two like [allelomorphic] factors.[12/] In Nebraska Research Bulletin No. 4 published in 1914, Emerson postulated that a genetic factor for variegation, V, was changed to a self-red allelomorph, S, in a somatic cell. The time at which the change occurred would determine the extent of red stripes or sectors and also whether the change would be transmitted. He offered two interpretations for these somatic changes: the V factor might be a temporary, recessive inhibitor of color which, sooner or later, permanently lost its inhibitory power, or there might be merely a dominant factor for self-color, S, which was temporarily inactive but, sooner or later, became active. At that time he could not conceive of the cause or nature of the changes. However, he laid the groundwork for more extensive and highly significant studies in later years.

The kind of genetic research discussed thus far both in beans and corn involved qualitative traits. These are usually governed by one or two genes, with dominance of one allele over another and segregation into predictable ratios of sharply contrasting phenotypes. Professor Emerson realized that many characters, particularly

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11/ Am. Nat. 47:375-377. 1913.

12/ Am. Nat. 47:633-636. 1913.

those involving size and shape, did not fit the qualitative description. In crosses the F_1 hybrids often had intermediate or "blending" characteristics instead of the dominant imprint of one parent. He knew that these quantitative characters would be more difficult to investigate than the qualitative ones, but he had the determination and curiosity to tackle more complex problems. In 1908, by making some crosses between a Missouri dent corn and two dwarf types of popcorn, he initiated a study on quantitative inheritance in corn.

In 1911, Emerson spent a year at Bussey Institution of Harvard University pursuing a graduate program for a D.Sc. which he was awarded in 1913. His advisor was the distinguished geneticist, Professor E. M. East, whose special interest was quantitative inheritance. East, from studies on endosperm color in maize, and a Swedish geneticist, Nilsson-Ehle, from studies on color segregations in wheat and oats, independently proposed what came to be known as the multiple factor hypothesis to explain the inheritance of quantitative characters. They assumed that the continuous variation in segregating progenies was governed by several to many genes which were cumulative in their action. Emerson as early as 1910 was able to apply this theory to some data he had collected on size and other quantitative characters in summer squash, gourds, maize and beans.[13/] In each case he could show that, as expected, the F_2 was more variable than the F_1 as measured by the coefficient of variability.

Emerson and East collaborated in compiling Nebraska Research Bulletin No. 2 on "The inheritance of quantitative characters in maize", which was published in 1913. They discussed in detail the application of the multiple factor hypothesis, which they thought could satisfactorily explain their own studies and all previous similar studies on plants and animals. They presented extensive data for the following characters: ear length, diameter, and row number; weight and breadth of seeds; plant height; number of stalks per plant; number of nodes per stalk; internode

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13/ Am. Nat. 46:739-746. 1910.

length. For each character, the means and coefficients of variability were given for the parents and the F_1, F_2 and F_3 from various crosses. In addition to the material derived from crosses which Emerson had begun in 1908, they also had progenies of crosses between pop and sweet or flint and dent initiated by East in 1906. They concluded: "In general, then, it may be said that the results secured in the experiments with maize were what might well be expected if quantitative differences were due to numerous factors inherited in a strictly Mendelian fashion." Their contribution was a very important milestone in quantitative genetics, largely because the theoretical aspects were strongly supported by adequate data. Modern genetics textbooks still use the experiments and photographs of this bulletin to illustrate the application of the multiple factor hypothesis.

Professor Emerson also made a genetic study of plant height in beans while still in Nebraska, but the information was not published until 1916 (Nebraska Research Bulletin No. 7). He approached this experiment in the same thorough, detailed way as in corn, using crosses between bush beans, which have a determinate habit of growth, and pole beans, which are indeterminate. While growth habit segregated on a single factor basis, with indeterminate habit dominant, Emerson found that considerable variation occurred among races of bush or pole beans and was related to internode number and length. He reasoned that the actual internode length of bush beans was considerably less than potential internode length because the plant axis was terminated early in the growth period. After carefully analyzing segregates from crosses between bush and pole beans, he decided that measuring the first five internodes of bush beans would indicate their potential internode length. Likewise, in pole beans the first 15 internodes would give the most accurate indication of internode length. This character showed a quantitative type of inheritance for crosses within bush bean or pole bean types. Both internode length and number segregated on a quantitative basis in crosses between bush and pole beans. From these facts Emerson postulated one factor with complete dominance for the difference in growth habit between pole and bush beans, and two or more factors, lacking dominance and with less potency, for the difference between tall and short bush or pole beans. He

termed this combination of factors with different dominance effects and unequal potencies a "modified multiple-factor hypothesis." He considered these assumptions to be simpler and more direct than interpreting the data by a single factor for growth habit with modifying factors.

Professor Emerson's achievements and contributions were recognized by his alma mater in 1917, when the University of Nebraska conferred on him an honorary LL.D. degree. Meanwhile, through his publications and attendance at various scientific meetings throughout the country, he became known in other universities. In 1914, he accepted an offer from Cornell University at Ithaca, N.Y. to become Professor and Head of the Department of Plant Breeding, positions which he was to hold until his retirement in 1942.

In the New York Experiment Station Annual Report for 1914, he presented a number of recommendations for developing the Plant Breeding Department, including the following lines of work:

(1) inaugurate clonal selection with fruit and flower crops, including scion selection with apples.

(2) make biochemical-genetic investigations of color inheritance.

(3) bring in nonresident lecturers in various phases of genetics for the benefit of the graduate students.

(4) add a fulltime extension specialist to the staff.

(5) develop a botanic-genetic garden to include native and foreign species, wild and cultivated forms, and some classic genetic materials, such as pea hybrids and variants, to illustrate Mendel's experiments.

As Department Head, Professor Emerson gave his staff almost complete freedom in their positions. He considered the person doing the work to be in the best position to make decisions regarding it. However, he never relinquished the direction of farm operations, and was usually at the farm headquarters 15 minutes ahead of the workmen, who began work at 7 A.M. This reflected his philosophy that both a scientist and a potential scientist (i.e. student) should be familiar with the routine

procedures of a plant breeding experiment. Also, he thought that a scientist should never ask a workman to do something he himself could not do.

In dealing with staff members, students, and others, he had a forthright, genial personality, a sound judgment in evaluating research proposals, and a constructive imagination. Precise in his speech, he would begin a telephone conversation with "R. A. Emerson speaking." He was a man of high principles, who firmly believed in backing what he considered proper and right.

During his first ten years at Cornell University, Professor Emerson was author or coauthor of 14 publications, all except one dealing with maize genetics. One paper was a cooperative effort with his own son, Sterling, then aged 22, who would voluntarily assist during the busy corn-pollinating season. It was a source of pride to his father that Sterling decided on his own to make genetics his life profession.

Three of the papers published during this period dealt with color inheritance. One of these, "The genetic relations of plant colors in maize," (Cornell Memoir 39) is a classic in illustrating the scientific method. Emerson distinguished six main plant color types, purple, dilute purple, sun red, dilute sun red, brown and green. He tested the effect on these color types of various environmental factors, such as sunlight, soil moisture, temperature, and soil fertility, including specific nutrients. He made crosses between purple and green plants, and from the ratios of color types in the F_2 and backcross progenies, he formulated a working hypothesis of three independent genes for plant color. The gene A for anthocyanin pigment proved to be the same one which he had postulated earlier for color in the aleurone layer of the kernel.[14/] The other two genes were B for brown pigment and Pl for purple pigment. Appropriate combinations of the dominant or recessive forms of these genes would give the six plant color types. Emerson tested this theory by observing the behavior of each color type in the F_3 and F_4. He intercrossed them in almost every possible combination, and carried the progenies to the F_2, and in several cases to

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14/ Cornell Memoir 16:231-289. 1918.

the F_3 and F_4. In every case the results closely agreed with the theoretical expectations. In further studies he found that the B locus consisted of three or four alleles which gave variations in color intensity. The R gene for aleurone color also affected the color of various plant parts, such as anthers and silks. He detected six alleles at the R locus and thought it remarkable that one allelic state could have a dominant effect on one plant part, but a recessive effect on another. (It is now known that the R locus consists of two parts, each with several elements.) Overall, he observed approximately 680 progenies and 48,000 plants in developing his analysis of plant colors. Color photography was not available in 1921, but three artists prepared 11 plates of striking water-color drawings to illustrate the color types and the effects of environmental conditions on them.

Dr. Emerson probed deeper[15/] into the variegated pericarp character which he had begun to investigate in Nebraska. He found different degrees of variegation, depending on the rate of mutation, and some evidence that self-color arising from variegated pericarp by mutation could revert back to the variegated pattern. Additional studies[16/] showed that, in crosses of homozygous variegated races with white (colorless) pericarp races, the heterozygous segregates had a higher frequency of mutations from variegation to self-color than the homozygous segregates. However, the mutability of the variegation gene was influenced in varying degrees by the different white races used in the crosses. Emerson's explanation for these results was that the mutability of the variegation gene was influenced by one or more modifying genes linked with it (and presumably introduced into the crosses with the white races). This interpretation hinted at the concept of controlling elements which was postulated for unstable genetic situations in maize many years later by one of Emerson's students, Barbara McClintock, and which was found to apply to pericarp variegation by Brink and his associates.

15/ Genetics 2:1-35. 1917

16/ Am. Nat. 56:64-79. 1922 and Genetics 14:488-511. 1929.

Another abnormality in maize which intrigued Professor Emerson was the occasional appearance of mosaic seeds having sectors of different aleurone or endosperm characters.[17/] Various hypotheses had been advanced to account for the sectoring, but the most logical explanation to him was nondisjunction of the chromosome bearing the pertinent genes during an endosperm mitotic division. He obtained strong genetic evidence for his theory by finding simultaneous loss of dominant linked marker genes in the abnormal sectors whereas, when the marker genes were on different chromosomes, loss occurred for only one gene at a time. Chromosome aberrations, such as trisomics, were not then available for assigning genes to chromosomes, but he advocated the use of mosaic seeds to determine the linkage relationships of aleurone and endosperm genes.

In all his writings Professor Emerson used a clear, straightforward style. Each paper was organized in a logical sequence with a step-by-step reasoning process. Integrity was evident in conscientious efforts to explain any unexpected results. His philosophy relative to the scientific method was that one should look for various explanations of an observed phenomenon rather than set out to prove or disprove one concept.

Through the spring months of 1924 he and F. D. Richey, USDA corn investigator, made a scientific expedition to Argentina, Bolivia, Chile, and Peru. They collected around 200 samples of maize, some from high altitudes or regions of low temperatures, hoping to get some adaptation to the northern regions or higher altitudes in the United States. They also sought sources of resistance to diseases, insects and drought as well as material for genetic studies.

By the 1920's Professor Emerson's brilliant research and magnetic personality had attracted graduate students of the highest caliber. He was able to impart to them his own zeal and enthusiasm for research. Many of the foremost geneticists who have evolved over the past 30 to 40 years received their training from him. Among them are three natives of Nebraska: E.G. Anderson of Concord, who has made

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17/ Z. Vererbs. 14:241-259. 1915; Am. J. Botany 8:411-424. 1921; Am. Nat. 58: 272-277. 1924.

extensive collection of retired tobacco pipes of various sizes and shapes hung in one corner. He would entertain the student with personal experiences and anecdotes which gave an insight into the history of genetics or indirectly conveyed some sound advice. Time was often forgotten until Mrs. Emerson would phone to ask when he was coming home for lunch.

Dr. Emerson's knowledge on a tremendous variety of topics both in biology and in other areas was extensive. He would visualize the passage of electricity through a wire or explain why daylength increased more rapidly at one end of the day than at the other towards the spring season. He did not hesitate to attend lectures in various courses to keep abreast with the developments in different fields, and would not miss a class period unless he had to be out of town. He also enjoyed poetry, especially the works of Kipling, and would sometimes indulge in this branch of the cultural arts during a smoke break.

During the busy corn-pollinating season he would be in the field at daybreak. One of his colleagues was determined to arrive earlier one morning, but Emerson was suspicious of the plan and went to the field long before dawn. As he heard his colleague coming to the field just before daylight, Emerson lit some matches to look at his pollinating cards which he carried in a small wooden box. Those who were familiar with his ways could visualize him chuckling as he later recounted this incident.

He was usually away from home until dark on these busy days, taking enough food for lunch at midday and a snack at the end of the afternoon. Often he was accompanied by his dog, an Airedale in earlier days and a German Shepherd in later years. Dr. Beadle recalled the lunch hours in the plant breeding garden (several acres in a hollow on the campus) during his graduate student days:[19/] "Lunches in the garden house during these periods of intense activity were events of great influence on students. It was on such occasions that the unprinted lore of corn genetics was transmitted and Emerson became best known to those who worked with him."

19/ Genetics 35:1-3. 1950.

While Professor Emerson did not count hours when there was a job to be done, he believed in a time for relaxation. And whatever he did, work or recreation, he liked challenges. He was a fishing and hunting enthusiast. Every year in the deer season he went to the same area in the Adirondacks with a group of hunters. He enjoyed the camp life, cooking, card-playing, and swapping of spicy tales. Other pastimes included brisk walks, bowling, golf, and watching a good football game. One Saturday morning a graduate assistant, M. J. Murray, and his wife were helping Dr. Emerson to harvest corn in the plant breeding garden. He seemed to be going at an unusually fast pace, but the Murrays did not know the reason for the rush until they finished about 11:30 A.M. He said to them: "You've just got time to get some warmer clothes and a sandwich, then meet me at the north gate for the Cornell-Dartmouth football game." He was keenly interested in athletics and was faculty representative on the Athletic Council for a year in the 1920's.

Because of his experience as an administrator and his vital interest in graduate students, Professor Emerson was appointed Dean of the Graduate School at Cornell University from 1925 through 1931. During this time he instituted the title of Resident Doctor for those who had recently obtained a Ph.D. and were awaiting a job. Other administrative appointments were faculty representative on the Board of Trustees for Cornell University (1925-1928) and a member of the National Research Council (1925-1926).

Through the remarkable research activity of Dr. Emerson and his students, more was becoming known about the genetics of corn than of any other organism except the fruit fly, Drosophila. In 1928, an informal conference of 15 maize geneticists was held in Emerson's hotel room during the Christmas meetings of the American Association for the Advancement of Science in New York. The concept of the Maize Genetics Cooperation took shape in attempts to coordinate studies in different places. The Department of Plant Breeding at Cornell University was the logical center for the cooperative effort. The first News Letter, distributed in mimeographed form in 1929, consisted of a letter and a compilation of all the published linkage data in maize,

as well as unpublished records of Emerson and his group. From then on, the exchange of ideas, unpublished data, and lists of genetic stocks through the medium of the News Letters became, with few exceptions, an annual event.

When the Sixth International Congress of Genetics was held at Cornell University in 1932, the maize geneticists asked the Department of Plant Breeding to act as a clearing-house for the information obtained by the numerous workers in different places, to serve as custodian of seed stocks, and to clarify the use of genetic symbols. Two years later, through Emerson's efforts, a grant for this program was made by the Rockefeller Foundation, which continued to provide financial support for almost twenty years.

By 1936, 31 workers in the United States and 10 workers in eight foreign countries were actively engaged in the Maize Genetics Coöperation. Stocks involving newly discovered genes or useful combinations of genes were sent to Cornell University to be maintained and distributed upon request. As the years went on, an extremely valuable collection of genetic and chromosomal stocks was accumulated. In News Letter 18, distributed in 1944, Professor Emerson in a "swan song" indicated that he wished to be relieved of responsibility for this highly successful cooperative program. He wrote:

> I have been connected more or less intimately with Maize Genetic Coöperation from its beginning. Some years I have had to devote considerable time to it and other years almost none. On the whole I feel that I have probably done less than I should and certainly less than I am credited with having done. I am now an 'emeritus' and rather enjoy it. I am anxious to complete (before my number comes up) certain maize genetic problems that have been underway for a long time and which will require yet further years of work. I am willing to admit no more than that I am not growing younger as the years go by.

After Dr. Emerson's death in 1947, the collection of genetic stocks remained at Cornell University until 1953. However, the responsibility for maintaining them

passed from one staff member to another, and the continuity of one person's vital interest was lacking. In 1953, when Rockefeller Foundation support terminated, the stocks were transferred to the University of Illinois under the direction of Dr. M. M. Rhoades, a former student of Emerson. Three years later, the News Letter activities also were moved to Illinois. Thus, the long association of the Maize Genetics Coöperation with Cornell University came to an end.

We must turn back now to the 1930's when Professor Emerson was at the zenith of his professional achievements. His students were assuming positions of leadership and responsibility in numerous high-ranking institutions around the world. In a talk on "The present status of maize genetics" given at the Sixth International Congress of Genetics in 1932, he cited from noteworthy publications by eight of his students or former students. By this time the association in maize between the ten linkage groups and the ten pairs of chromosomes had been established. Mainly through the use of trisomics, each of the linkage groups had been assigned to a specific chromosome.

Largely because of Professor Emerson's prestige, the Genetics Congress was held at Cornell University. As chairman of the local committee, he carried out diverse responsibilities efficiently and economically. An outstanding collection of living genetic materials was grown in the plant breeding gardens under the guidance of Rhoades and Emerson, who began planning for it over a year in advance. Emerson did not neglect the recreational interests of the visitors and arranged with the local Country Club to have all the golfers from the Congress as his guests, so that the fee was greatly reduced. Mrs. Emerson was chairman of the committee to arrange entertainment for the women and children. During the congress Emerson was elected American representative on the permanent international committee. Seven years later, he was a delegate to the Genetics Congress held in Edinburgh.

Despite his diverse administrative commitments Professor Emerson continued to be remarkably active in research. Through many years he carried on a laborious study involving the inheritance of number of kernel rows on maize ears, a

quantitative character. This involved a tremendous amount of self-pollination to get different lines stabilized for row number, before crossing them in various combinations to determine the kind of segregation. He tackled other studies of a difficult nature, such as determining the linkage relationships of a recessive zygotic lethal gene (zl) and a differential fertilization gene (Ga). He and Beadle were interested in the genetic and cytological results of hybridizing maize with one of its wild relatives, teosinte.

In 1935, Cornell Memoir 180 entitled "A summary of linkage studies in maize" was compiled by Emerson, G. W. Beadle and A. C. Fraser. All the known genes (over 300) in maize were catalogued alphabetically, with appropriate symbols, descriptions, and chromosomal locations when known. Emerson was cited for 41 of these genes, which was indicative of the many genetic studies on mutant types which he had made through the years. Another section presented extensive linkage data (published and unpublished) for each chromosome, much of it collected by Emerson or his students. This publication has been a most valuable handbook to maize geneticists and plant breeders.

It was also in 1935 that Professor Emerson, along with other specialists, went to Yucatan at the invitation of the Carnegie Institution. Their mission was to collect information on the probable kinds of food crops grown and used by the Mayan peoples. Dr. Emerson was particularly concerned with the role of maize in this ancient civilization.

During this phase of his life, he frequently gave short talks by radio at noon hour to the farmers of New York State. With his broad background of knowledge and practical viewpoints, he had a precise, effective way of presenting the gist of a topic. While he probably enjoyed these informal discussions more than formal talks, he could be a dynamic speaker addressing a learned symposium in Bailey Hall auditorium on the Cornell campus.

Dr. Emerson usually spent a month to six weeks of late winter in Florida pollinating a corn planting. With the family grown to adulthood, Mrs. Emerson could

accompany him, and they enjoyed the trip down and back as well as the orange groves and other sights of the state.

By now grandchildren were on the scene and Dr. Emerson was a devoted grandfather. When they were with him he would spend considerable time doing things to amuse them. Their play did not bother him, but he could be firm in saying "No" if they were doing something which required discipline.

Through the years Professor Emerson kept his interest in horticulture and in practical applications of genetic principles. He had a longstanding project on breeding beans for high yields, quality and disease resistance. By cooperating with the Department of Plant Pathology, he obtained selections which were resistant to the major bean diseases. He did have some problem in maintaining quality because the disease resistance was introduced from diverse sources. However, he sought to combine these two desirable traits by crossing the disease-resistant lines with a high quality variety. Dr. M. J. Murray recalled that one summer when he helped to grow the selections from this cross, they spent considerable time picking samples, cooking them and sampling for flavor and texture. Emerson continued the breeding work on beans after his retirement until the end of his life.

For a few years (1938-1942) Dr. Emerson was associated with a project on breeding muskmelons for resistance to fusarium wilt. He was very active in two celery breeding projects at different periods of his later life. In the earlier project (1934-1941), he crossed self-blanching types with sources of quality and fusarium resistance. Following conventional procedures, he produced a strain released as Cornell 19. It combined high quality and fusarium resistance, and the first commercial plantings received a premium price on the New York market. He confided to Murray that the development of Cornell 19 celery was as thrilling to him as any of his genetic work. After his retirement he participated in a celery project to incorporate into commercial types resistance to early blight. Some Turkish varieties had resistance but were dark-green, hollow-petioled, and strongly flavored. Cornell 19 was used in crosses with the Turkish varieties. Dr. Emerson

put the plants to be crossed under cages of cheesecloth and, to make the crosses, introduced houseflies which had been reared for this purpose. (At this time I was a graduate student in the department, and cooperated with him in culturing houseflies, which I needed for my thesis research on buckwheat. Needless to say, we did not gain any friends by increasing houseflies, particularly when a few escaped.) By selecting in the F_2 and later generations for solid petioles and resistance to early blight, and backcrossing to edible types, some promising strains were developed. In both the muskmelon and celery breeding projects, he used the team approach, working with members of the Departments of Plant Pathology and Vegetable Crops.

Early in 1942 Professor Emerson lost his wife after almost 44 years of marriage. Mrs. Emerson had been in ill health for some years prior to her death. He was very devoted to her and would shorten his work hours during her illnesses. After her death, Emerson continued to live unpretentiously in the distinctive house on Dryden Road with a grapevine covering most of the upper walls. Sometimes he took in a student, with the proviso that the student care for his own room and help to keep the house in good condition. Most of the time Emerson did his own housework, and he became interested in cooking. He liked to experiment with different proportions of flour types in pancake batter and sometimes would bake a pie that was "almost edible" in his words.

On October 1, 1942 Emerson became professor of plant breeding, emeritus. This transition freed him from the administrative responsibilities he had shouldered for most of his life. His active, searching mind could now concentrate on unfinished research. He divided his attention between practical breeding in beans and celery on the one hand, and the basic study on inheritance of kernel row number in maize on the other. He continued to maintain a devoted and often participating interest in the Maize Genetics Coöperation.

In June, 1947 Professor Emerson returned to Lincoln, Nebraska for the fiftieth anniversary of his college class. Later that year he became ill, and died December 8, 1947 at Ithaca, N. Y. Eulogies appeared in newspapers, including the New York

Times, and in scientific publications. Several years later, an R. A. Emerson Memorial was established in the Department of Plant Breeding. It was in the form of a glass exhibit case displaying his photograph and changing exhibits of his work. In 1968 Plant Breeding moved to a new building, which was dedicated as Emerson Hall.

Professor Emerson had started a manuscript based on the extensive data he had collected on kernel row number over many years. But, as he had phrased it, his number came up before he could finish the paper. Fortunately, a quantitative geneticist, Dr. H. H. Smith, who was then in the Department of Plant Breeding, completed the writing, including some interpretations, and it was published in 1950 as Cornell Memoir 296, "Inheritance of number of kernel rows in maize." Emerson had originally selected this character for intensive study because it was only slightly affected by environmental differences in contrast to most quantitative traits. He used 12-rowed, 10-rowed and 8-rowed inbred lines. After self-pollination for many generations in most cases, tests indicated that the 22 lines were practically homozygous for the genes concerned with row number. However, deviations occurred within inbred lines, suggesting non-genetic variability. Crosses among inbreds having the same row number gave F_1 progenies with more rows, on the average, than the mid-parent value. These results were interpreted as either hybrid vigor or genetic differences among lines. Emerson demonstrated that there were a number of different genotypes for row number among the 12-rowed lines. He was able to accumulate genes for higher row number by selection from multiple crosses involving up to seven 12-rowed lines. In some cases the mode was raised to 22 kernel rows. The F_1 from crosses between 8- and 12-rowed lines tended to have fewer rows than the mid-parent value. This indicated that dominant genes for decreasing row number predominated in the 8-rowed types, whereas both plus and minus dominant modifiers had accumulated in the 12-rowed types. The general conclusion from the study was that many genes controlled the inheritance of row number in maize, but their effects were small compared to the non-heritable fluctuations. However, the various 12-rowed genotypes were believed to differ by relatively few genes.

It is fitting to end the biography of Rollins Adams Emerson with this paper,

because it typifies his philosophy in several ways. He would have wanted to be active to the end, even if it meant leaving unfinished work. He had been intrigued by the nature of quantitative inheritance for most of his professional life. He knew that it would not be an easy task to obtain a precise genetic explanation, but he thrived on the problems which demanded physical activity and stretched the intellect. This final study also recalls for many a mental image of Professor Emerson in the busy summers among his corn plants, pollinating bags draped over his belt, curved pipe in his mouth, and constant activity in his thoughts.

Acknowledgments

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American Academy of Arts and Letters

American Association for the Advancement of Science (Fellow)

American Association of University Professors

American Breeders' Association

American Genetic Association

American philosophical Society

American Pomological Society

American Society of Agronomy

American Society of Horticultural Science (charter member)

American Society of Naturalists (vice president 1915, president 1923)

Botanical Society of America

Genetics Society of America (president 1933; member of editorial board of the periodical "Genetics" from 1916 until his death)

National Academy of Sciences

Nebraska Academy of Sciences

Nebraska Corn Improvers' Association

Nebraska State Horticultural Society (life member)

Society for the Promotion of Agricultural Science

Gamma Alpha

Phi Beta Kappa

Phi Kappa Phi

Sigma Xi