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**Albert Edward Longley, 1893-1984 – Botanist, cytologist, geneticist.**

--Coe, EH and Kass, LB

Albert E. Longley, Ph.D. was a botanist, cytologist, maize cooperator, and early contributor to the *Maize Genetics Cooperation Newsletter*. His graduate training at Harvard University (A.M. Harvard 1922, Ph.D. 1923), in the Plant Morphology Laboratory of eminent botanist E.C. Jeffrey prepared him for his life-time career with the United States Department of Agriculture. Here we present a brief overview of his life and his scientific contributions.

Albert E. Longley was born March 12, 1893 in Paradise, Nova Scotia (N.S.), Canada. He attended Provincial Normal College, Truro, N.S. (1912, first rank diploma), and taught in Nova Scotia and in Western Alberta before attending Acadia University, Wolfville, N.S., where he earned the B.Sc. in Botany with Honors (1920, Assistant 1917-1920). The Great War [WWI, 1914-1918] suspended his scholarly endeavors at Acadia with military service, first with the Canadian Overseas Expeditionary Forces (Aldershot, N.S), then as a cadet trainee in the Canadian Royal Air Force beginning in August of 1918, and ending with the Armistice (Longley's personal journal). Raised on the family farm, he retained constant interest in its progress over his lifetime.

At Harvard University in the Plant Morphology Laboratory of E.C. Jeffrey, Longley, C.W.T. Penland, a fellow graduate student, and Jeffrey co-authored a "Special Article" in a May issue of *Science* (Jeffrey et al. 1922; see Table I for the complete list of Longley's publications) titled Polyploidy, polyspory, and hybridism in the angiosperms. Soon after, both students were awarded master's degrees (*Quinquennial Catalogue*, Harvard, 1930). On April 15, 1922, graduate student Longley had announced intentions of marriage to [Phoebe] Mae Palmer, a telephone supervisor, from Middleton, N.S. (*Cambridge Chronicle*, 1922). They were married April 17, 1922, in Cambridge, Massachusetts. Longley continued on for a Ph.D. (1923), completing a dissertation on *Cytological Studies in the Genera Rubus and Crataegus*, published in *American Naturalist* (Longley 1923). While a Harvard graduate student, Longley was also a botany teaching fellow (Austin Teaching Fellow, 1920-1923) and an assistant/instructor of botany at Radcliffe College (1923). Their daughter, Mary Olga, was born in Arlington, Virginia, July 10, 1927.

In September 1923 Longley was appointed Assistant Cytologist to do research in the Office of Biophysical Investigations, Bureau of Plant Industry, United States Department of Agriculture in Washington, D.C. He immediately published work he had completed for his Ph.D. or had begun at Harvard on economic fruit crops (raspberries and hawthorn). His first USDA publication (Longley and Darrow 1924) was a cytological study in raspberries, continuing work he began in 1921 while at Harvard. Longley (1924c) then began studies on the cytology of chromosomes in

corn (*Zea mays* L.), including materials of G.N. Collins and J.H. Kempton. This would be his major focus for years to come. He also began an important study of the cytology of strawberry (Longley 1926a), which was described the following year in the genetics textbook by Babcock and Clausen (1927, p. 430). Strawberry plants were grown at Glenn Dale, Maryland, by George M. Darrow, pomologist, of the Office of Horticultural investigations, and information about their chromosome numbers was obtained with Longley's collaboration, beginning in 1923 (Darrow 1966, pp. 86-88). Research materials were also grown in the Arlington Experiment Farm in Rosslyn, Virginia (later absorbed by the Pentagon) near Hoover airport, and at other locations suitable for sample collections, coast to coast.

Longley's Cytological and morphological studies were on diverse species that included maize and its relatives from 1924 through 1965 (Longley 1924c, 1925b, 1927b, 1934, 1935, 1937a and b, 1938, 1939, 1941a and b, 1943, 1945, 1948, 1949, 1950a and b, 1952a and b, 1954, 1955a and b, 1956a and b, 1957, 1958a, 1961a and b, Collins and Longley 1935, Randolph, Longley and CH Li 1948, Teas et al. 1949, Anderson et al. 1949, Anderson and Longley 1951, 1952, 1956, 1957, and 1960, Anderson, Kramer and Longley 1954, 1955a and b, Prywer, Longley and Anderson 1954, Longley, Beckett and Coe 1964, Longley and Kato 1965). Other crops and horticultural varieties of interest were raspberry (Longley 1923, 1924a, 1927a, Longley and Darrow 1924; citrus (Longley 1925c, 1926b); strawberry (Longley 1926a, 1927a); blueberry (Longley 1927c); iris (Longley 1928); potato (Longley and Clark 1930); wheat and rye and relatives (Longley and Sando 1930); sorghum (Longley 1932); blackberry (Darrow and Longley 1933); cotton (Longley 1933); oats (Longley and Stanton 1939); rice (Jones and Longley 1941); and *Camellia* (Longley 1958b and c, Tourjé and Longley 1959, Longley and Tourjé 1959, 1960a and b). The wide range of characterizations in these species defined chromosome numbers (most for the first time) and structural variations, ploidy, differences among related species, and stability of chromosomes in meiosis.

Of course, Longley's work on cytology of maize is most relevant to students of maize genetics. And we will concentrate on summarizing those contributions in this report. Maize cytogeneticist Marcus Rhoades, who worked with the USDA for a time in the late 1930s, recalled:

Longley was a cytologist, an indefatigable worker who spent long hours peering down the tube of his microscope. Some idea of his industry is gained from the fact that the knurls on the knob of the fine adjustment focus of the Zeiss he used for many years were completely worn away (Rhoades, 1984).

Rhoades had been editor of the *Maize Genetics Cooperation News Letter* (1932-1935) after completing the Ph.D. with Emerson at Cornell (Murphy and Kass 2007, 2011; Kass et al. 2019). During this time, Longley joined the long list of maize cooperators receiving and contributing published and unpublished data to Emerson's cooperative enterprise to clarify the linkage groups of maize and studies of accompanying genes, gene mutations and so-called chromosome aberrations in this important economic crop (Longley, *MNL* Nov. 1934, p. 18; Emerson et al. 1935; Coe and Kass 2005; Kass et al. 2005; Coe 2009; Longley MaizeGDB; Kass et al. 2019; Longley's publications, Table I).

Combined with his thorough observing skills, Longley's career demonstrated openness to new phenomena, particularly in chromosome form and behavior, and he explored these and their meanings. Recognition of Longley's outstanding work in plant cytology supported his early election to membership in the Washington Academy of Sciences (*Proceedings Washington Academy of Sciences*, 1932). He was recognized with entries in *American Men of Science* (e.g. Longley 1938, p. 869), and elected a Fellow of the American Association for the Advancement of Science (1947). He held memberships in the Botanical Society of America (1920), The Botanical Society of Mexico (1960) and the Genetics Society of America, the honor societies of Gamma Alpha and Sigma Xi, and the Camellia Society of Southern California.

Highlights of Longley's accomplishments can be summarized as follows:

Longley's (1924c) first studies of maize chromosomes demonstrated genetic consequences of chromosome pairing failure and pollen abortion in hybrids between maize and its wild relatives. Genetic segregation of carbohydrate types in pollen (Longley 1925b) showed an integral tie between chromosomes, genes, and biochemical constituents.

His review (1925a) of a new text book, *General Cytology* edited by E.V. Cowdry (1924), which contained chapters by 14 authors, criticized compartmentalization of the contents and limited coverage of chromosomes and genetics and plant biology.

Longley's discovery (1927b) of supernumerary chromosomes in maize was precedent-setting and made clear that the basic number was consistent with a chromosome haploid number of 10, resolving earlier reports of other numbers. Diminutive forms of these near-inert chromosomes were studied subsequently by Longley (1956a and b).

Continuing with studies on related grasses, basic haploid numbers in sorghums were determined (Longley 1932) to be 10 in seven species of annuals, 20 in one annual (*S. purpureo-sericeum*), 20 in the perennial *S. halepensis* (Johnson grass), and 5 in southeastern African *S. versicolor*. Such series imply relationships by origin.

Hybrids between perennial teosinte ( $n = 20$ ) and maize ( $n = 10$ ) were found (Longley 1934) to display unpaired chromosomes and produce some 10-chromosome gametes, opening the possibility of breeding into maize some of the properties of the polyploid.

Collins and Longley (1935) applied a genic marker to examine chromosome distribution in an exceptional tetraploid (20 perennial teosinte + 20 maize) and defined the degree of regularity in gamete distribution deriving from the chromosome pairing patterns.

Applying new techniques to visualize chromosome tracts, Longley (1937b, 1941a, b), determined chromosome lengths, centromere positions and heterochromatic knobs for a group of seven 10-chromosome maize relatives and 18-chromosome *Tripsacum*, and diagrammed their chromosomes with numbered ideograms of the chromosomes arranged from longest to shortest to show relationships among them. This tour-de-force of cytological characterizations

was accompanied in 1938 and 1939 with ideograms, measurements and frequencies among 33 strains of North American Indian and 41 additional indigenous varieties of Mexican maize.

These studies provided and stand as exemplary baseline characterizations (Longley 1941b, 1952b) for diversity at the fine level.

A cytologically distinct chromosome, abnormal 10, which itself has abnormal transmission, was shown to affect segregation of other chromosomes by altering transmission of knobs (Longley 1945).

Genetic and cytological studies on the effects of exposure of corn kernels to atomic bomb radiation in July 1946 at Bikini atoll documented chromosomal aberrations (Randolph et al. 1948, Anderson et al. 1949, Longley 1950 a and b, 1958-1961) and compared data for different lots to those for a range of x-ray doses. Longley transferred to the California Institute of Technology at Pasadena in 1947 as a key member of a large scientific team that carried out the latter studies under auspices of the U.S. Navy (*Bulletin Caltech* 1947, p. 28; See Fig. 1). Many mutants and hundreds of reciprocal translocations were defined and characterized in this work and are a part of the tools of genetic and cytogenetic research.

He continued conducting research on maize in Pasadena until retirement in 1960 and in July 1960 began three periods of research under the Rockefeller Foundation in Mexico (transitioned to the Centro Internacional de Mejoramiento de Maíz y Trigo, CIMMYT) with E.J. Wellhausen. Longley and T.A. Kato (1965), whom he had trained in cytogenetic techniques, detailed characterizations of chromosome morphology in a wide range of Latin American maize races. Kato continued his studies in maize cytogenetics, obtaining his Ph.D. in 1975, and later co-authoring an important contribution on the evolution of maize (McClintock et al. 1981, Kato Y. 2013).

Late in his career Longley conducted and guided research (1958-60) on scores of species, hybrids, and varieties of *Camellia* [common name Tea Life or Chai, Family Theaceae] and allied genera, determining chromosome numbers and potentials for breeding new horticultural traits. The work included attempts to induce mutations and to make wide crosses. His interest in *Camellia* continued long after his retirement, growing hopeful hybrids at his home in Missouri.

Longley's personal botanical interest was constant and evident, notably in Virginia with cascading azalea beds – his gardens in Virginia and California homes were showplaces and were productive. Drosophila geneticist A.H. Sturtevant, an iris fancier, took collegial interest in Longley's 1928 cytological study of iris species.

Longley moved to Columbia, Missouri in 1961 and was appointed Visiting Professor in 1967; he died at his home in Columbia October 14, 1984.



**Figure 1.** Caltech Biology Experimental Farm (Arcadia Farm). Members of the Arcadia Farm group, summer 1948.

From left to right, **Top row:** D.M. Gopinath, Jim Nishitani, Jack Beckett, Bob [Robert W. MacClowry? Lab. Asst. ?], Bob Parker, George Sands, Donald S. Robertson<sup>c</sup>

**Middle row:** Dr. Ching Hsiung Li, Dr. Ernest E. Dale<sup>a</sup>, Dr. Edgar Anderson, Dr. Herschel L. Roman<sup>b</sup>, Dr. John R. Laughnan, Earl B. Patterson<sup>d</sup>

**Front Row:** Dr. Ernest Gustav Anderson, Mary Olga Longley, Vicky Rodekor, Dr. Albert E. Longley<sup>e</sup>

<sup>a</sup>Union College 1954-1955, retired to Caltech; Nickerson and Dale *Annals of MO Bot Garden*, Sept. 1955, vol. 42 No. 3; <sup>b</sup>Gosney Fellow; <sup>c</sup>Research Asst.; Research Fellow, listed as Mr. in 1948-1949 *Caltech Catalogue*; <sup>d</sup>graduate student 1948-1949, *Caltech Catalogue*; Ph.D. 1952; <sup>e</sup>Research Associate.

### **Table I. PUBLICATIONS OF ALBERT E. LONGLEY [\*maize and maize related]**

Jeffrey, E, Longley, AE and Penland, CWT. 1922. *Science* 55(No. 1428, 12 May):517-518 Polyploidy, polyspory, and hybridism in the angiosperms

Longley, AE. 1923. *Am Nat* 57(No. 653, Nov-Dec):568-569 Cytological studies in the genera *Rubus* and *Crataegus*

Longley, AE and Darrow, GM. 1924. *J Agric Res* 27(No. 10, March 8):737-748 Cytological studies of diploid and polyploid forms in raspberries

Longley, AE. 1924a. *Am J Bot* 11(No. 4, 1 April):249-282, plus 5 plates Cytological studies in the genus *Rubus*

Longley, AE. 1924b. *Am J Bot* 11 (No. 5, 1 May):295-317, plus 2 plates Cytological studies in the genus *Crataegus*

\*Longley, AE. 1924c. *J Agric Res* 28(No. 7, 17 May):673-682, plus 3 plates Chromosomes in maize and maize relatives

Longley, AE. 1925a. *J Hered* 16(Issue 1, Jan.):25-27 Essays on cellular structure and function (A review)

- \*Longley, AE. 1925b. *Science* 61(Issue 1686, 22 May):542-543 Segregation of carbohydrates in maize pollen
- Longley, AE. 1925c. *J Wash Acad Sci* 15(No. 14, 19 Aug.):347-351 Polycary, polyspory and polyploidy in citrus and citrus relatives
- Longley, AE. 1926a. *J Agric Res* 32(No. 6, 15 Mar.):559-568 Chromosomes and their significance in strawberry classification
- Longley, AE. 1926b. *J Wash Acad Sci* 16(No. 20, 3 Dec.):543-545 Triploid citrus
- Longley, AE. 1927a. *Mem Hort Soc New York* 3(Issued July 1927):15-17 Relationship of polyploidy to pollen sterility in the genera *Rubus* and *Fragaria*
- \*Longley, AE. 1927b. *J Agric Res* 35(No. 9, 1 Nov.):769-784 Supernumerary chromosomes in *Zea mays*
- Longley, AE. 1927c. *Science* 66 (Issue 1719, 09 Dec.):566-568 Chromosomes in *Vaccinium*
- Longley, AE. 1928. *Bull Am Iris Soc Sci Ser* 3(No. 9, Oct.):43-55 Chromosomes in Iris species
- Longley, AE and Sando, WJ. 1930. *J Agric Res* 40(No. 8, 15 April):683-719, plus plates 1-4 Nuclear divisions in the pollen mother cells of *Triticum*, *Aegilops*, and *Secale* and their hybrids
- Longley, AE and Clark, CF. 1930. *J Agric Res* 41(No. 12, 15 Dec.):867-888 Chromosome behavior and pollen production in the potato
- Longley, AE. 1932. *J Agric Res* 44(No. 4, 15 Feb.):317-321 Chromosomes in grass sorghums
- Longley, AE. 1933. *J Agric Res* 46(No. 3, 1 Feb.):217-227 Chromosomes in *Gossypium* and related genera
- Darrow, GM and Longley, AE. 1933. *J Agric Res* 47(No. 5, 1 Sept.):315-330 Cytology and breeding of *Rubus macropetalus*, the Logan and related blackberries
- \*Longley, AE. 1934. *J Agric Res* 48(No. 9, 1 May 1934):789-806 Chromosomes in hybrids between *Euchlaena perennis* and *Zea mays*
- \*Collins, GN and Longley, AE. 1935. *J Agric Res* 50(No. 2, 15 Jan.):123-133 A tetraploid hybrid of maize and perennial teosinte
- \*Longley, AE. 1935. *MNL* 9(06 March):9 From a perennial teosinte-corn hybrid has been isolated a cornlike strain with 20 chromosomes in which chromosome IX has a terminal knob on the short arm and a large internal knob on the long arm
- \*Longley, AE. 1937a. *MNL* 11(23 March):15 Recent morphological studies of the chromosomes of strains of Indian corn and of teosintes from the experiment station at Chapingo near Mexico City have shown several strains in which chromosome 10 is abnormal
- \*Longley, AE. 1937b. *J Agric Res* 54(No. 11, June 1):835-862, plus plates 1 & 2 Morphological characters of teosinte chromosomes
- \*Longley, AE. 1938. *J Agric Res* (No. 3, 1 Feb.):56:177-195 Chromosomes of maize from North American Indians
- Longley, AE and Stanton, T. 1939. *J Am Soc Agron* 31(August):733-735 Chromosome number in dwarf oats
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- Jones, JW and Longley, AE. 1941. *J Agric Res* 62(No. 7, April 1):381-399 Sterility and aberrant chromosome numbers in Caloro and other varieties of rice
- \*Longley, AE. 1941a. *J Agric Res* 62(No. 7, April 1):401-413 Knob positions on teosinte chromosomes
- \*Longley, AE. 1941b. *Bot Rev* 7(No. 5, May):263-289 Chromosome morphology in maize and its relatives

- \*Longley, AE. 1943. *Agric in the Americas* 3(No. 7, July):139 Gifts of the Americas. Maize
- \*Longley, AE. 1945. *Genetics* 30(No. 1, Jan.):100-113 Abnormal segregation during megasporogenesis in maize [r
- \*Longley, AE. 1948. *MNL* 22(8 March):3-6 Translocations in progenies showing chromosomes involved and giving in per cent of the arm length the distance from the centromere to the breakage point
- \*Randolph, LF, Longley, AE and Li, Ching Hsiung [Li, Jing Xiong]. 1948. *Science* 108(Issue 2792, 2 July):13-15 Cytogenetic effects in corn exposed to atomic bomb ionizing radiation at Bikini
- \*Longley, AE. 1949. *MNL* 23(10 March):17 A total of 385 translocations now have been analyzed cytologically to determine the position of the breaks
- \*Teas, HJ, Newton, A, Stehse, M, Wildman, SG, Cameron, JM, Patterson, EB, Robertson, DS, Longley, AE and Anderson, EG. 1949. *MNL* 23(10 March):18-19 We are undertaking a genetical-biochemical study of the development of the endosperm of maize, centering about the "indole cycle" involving tryptophane, auxin, niacin, protein and carbohydrate relationships
- \*Anderson, EG, Longley, AE, Li, Ching Hsiung [Li, Jing Xiong] and Retherford, KL. 1949. *Genetics* 34 (No. 6, Nov.):639-646 Hereditary effects produced in maize by radiations from the Bikini atomic bomb. I. Studies on seedlings and pollen of the exposed generation
- \*Longley, AE. 1950a. *MNL* 24(17 March):7-8 Chromosomal rearrangements from exposure to radiation
- \*Longley, AE. 1950b. *In: Report of Naval Medical Research Section, Joint Task Force ONE, on Biological Aspects of Atomic Bomb Tests, Appendix No. 10 (mimeograph). 60 pp. [10 June 1950] Cytological analysis of translocations in corn chromosomes resulting from ionizing radiation of the Test Able Atomic Bomb and X-rays and of translocations from other sources*
- \*Anderson, EG and Longley, AE. 1951. *MNL* 25(17 March):2 Translocations
- \*Anderson, EG and Longley, AE. 1952. *MNL* 26(17 March):15-19 List of translocations preceding the Bikini and Eniwetok series
- \*Longley, AE. 1952a. *MNL* 26(17 March):20-21 Preferential segregation in translocations
- \*Longley, AE. 1952b. *Bot Rev* 18(No. 6, June):399-412 Chromosome morphology in maize and its relatives
- \*Anderson, EG, Kramer, HH and Longley, AE. 1954. *MNL* 28(17 March):13-16 Patterns of recombination suppression in heterozygous translocations involving chromosomes 4, 6, and 10
- \*Prywer, C, Longley, AE and Anderson, EG. 1954. *MNL* 28(17 March):17 Translocation B-9a
- \*Longley, AE. 1954. *MNL* 28(17 March):18 Preferential segregation due to a paracentric inversion
- \*Longley, AE. 1955a. *MNL* 29(17 March):3 Non-disjunction in the Generative Nucleus of the pollen of T-B 10a
- \*Longley, AE. 1955b. *MNL* 29(17 March):3-4 Pollen transmission from plants heterozygous for ab 10 and a paracentric inversion of chromosome 7
- \*Anderson, EG, Kramer, HH and Longley, AE. 1955a. *Genetics* 40(No. 4, July):500-510 Translocations in maize involving chromosome 4
- \*Anderson, EG, Kramer, HH and Longley, AE. 1955b. *Genetics* 40(No. 4, July):531-538 Translocations in maize involving chromosome 6
- \*Longley, AE. 1956a. *Am J Bot* 43(No. 1, Jan.):18-21 The origin of diminutive B-type chromosomes in maize
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translocations preceding the Bikini and Eniwetok series

- \*Longley, AE. 1956b. *MNL* 30(15 March):135-136 The origin of diminutive B-type chromosomes in maize
- \*Longley, AE. 1957. *MNL* 31(15 March):19-20 The gametophyte factor of chromosome 5
- \*Anderson, EG and Longley, AE. 1957. *MNL* 31(15 March):20-28 List of translocation stocks
- \*Longley, AE. 1958a. *U.S. Dept. Agr., Agr. Res. Serv. ARS 34-4*, 31 pp. July 1958 Breakage points for two corn translocation series
- Longley, AE. 1958b. Chromosomes and their relation to *Camellia* breeding. Pp. 383-390, *In: Tourjé, EC (Ed.) Camellia Culture*, The Macmillan Co., New York, NY
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- Longley, AE and Tourjé, E. 1960b. *Am Camellia Yearb* :70-72 Chromosome numbers of certain *Camellia* species and allied genera -- Supplementary report for 1960
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