

Barbara McClintock

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Abstract Barbara McClintock, pioneering plant geneticist and winner of the Nobel Prize in Physiology or Medicine in 1983, is best known for her discovery of transposable genetic elements in corn. This chapter provides an overview of many of her key findings, some of which have been outlined and described elsewhere. We also provide a new look at McClintock's early contributions, based on our readings of her primary publications and documents found in archives. We expect the reader will gain insight and appreciation for Barbara McClintock's unique perspective, elegant experiments and unprecedented scientific achievements.

1 Introduction

This chapter is focused on the scientific contributions of Barbara McClintock, pioneering plant geneticist and winner of the Nobel Prize in Physiology or Medicine in 1983 for her discovery of transposable genetic elements in corn. Her enlightening experiments and discoveries have been outlined and described in a number of papers and books, so it is not the aim of this report to detail each step in her scientific career and personal life but rather highlight many of her key findings, then refer the reader to the original reports and more detailed reviews. We hope the reader will gain insight and appreciation for Barbara McClintock's unique perspective, elegant experiments and unprecedented scientific achievements.

Barbara McClintock (1902–1992) was born in Hartford Connecticut and raised in Brooklyn, New York (Keller 1983). She received her undergraduate and graduate education at the New York State College of Agriculture at Cornell University. In 1923, McClintock was awarded the B.S. in Agriculture, with a concentration in plant breeding and botany. She received both master's (1925) and doctoral degrees

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(1927) from Cornell's Department of Botany, and held positions there as researcher, teaching assistant, and instructor from 1924–1931 (Kass 2000, Kass 2003). From 1931 to 1936, supported by the National Research Council, and the Guggenheim and Rockefeller Foundations, she continued the work that culminated in her discovery of transposable elements published in 1950. She held appointments at the University of Missouri (1936–1942) and then the Carnegie Institution of Washington's Department of Genetics, Cold Spring Harbor, New York, where she worked until her death in 1992 (Kass 2003).

2 The Early Years of Genetics

McClintock was awarded Cornell's "Graduate Scholarship in Botany" for 1923–1924, which provided support during her first year of graduate studies. She was elected to the graduate student's Honor Society, Sigma Xi (Kass 2000). Her Master's thesis was a literature review of cytological investigations in cereals with particular attention to wheat (McClintock 1925, Kass 1999). During this time, she did not study corn, the plant to which she would later devote her life's work, nor did she morphologically describe its chromosomes, although both stories have been widely circulated (i.e., Comfort 2001, Keller 1983).

In graduate school McClintock worked as a research assistant to L. F. Randolph, an Associate Cytologist of the United States Department of Agriculture. In the summer of 1925, she discovered a corn plant that had three complete sets of chromosomes (a triploid). Applying Belling's new chromosome staining technique they studied the meiotic behavior of the chromosomes in the pollen of this plant (Kass and Bonneuil 2004) and published their results the following February (Randolph and McClintock 1926). They described the repeated occurrence of tetraploid microsporocytes and suggested that the functioning of gametes derived from such cells might account for the origin of triploidy and conceivably of other forms of polyploidy in maize (Randolph 1927). It seems that McClintock was upset that her name appeared second on their article when she believed she had done most of the work, and soon after they ended their working relationship (Kass 2003, Kass and Bonneuil 2004).

The new focus of her Ph.D. dissertation was an investigation of the cytology and genetics of the unusual triploid corn plant, which, when crossed with normal diploid plants, produced offspring with extra chromosomes (trisomic plants). This permitted her to correlate an extra chromosome plant with a particular linkage group, although she had not yet determined the identity of the extra chromosome (McClintock 1927, 1929a, Kass and Bonneuil 2004). Her research was supported by an assistantship in the Botany Department with Lester Sharp, her Ph.D. advisor and one of the leading cytologists in the country. While McClintock was a graduate student in the Botany Department, several other women were awarded graduate degrees from Cornell's Department of Plant Breeding (Kass 2003, Murphy and Kass 2007), although it has been reported (i.e., Comfort 2001, Berg and Singer 2003) that Cornell's Department of Plant Breeding did not accept women graduate students.

3 The 10 Chromosomes of Maize

Upon completing her doctorate, McClintock became an instructor at Cornell, which afforded her faculty status with responsibilities for teaching and guiding graduate students. She continued to pursue her studies on the triploid corn plant and its trisomic offspring. Plants with extra chromosomes could be used for correlating genes with their chromosomes if one could cytologically distinguish the extra chromosome. McClintock's continued maize cytological investigations led her to devise a technique to distinguish all 10 chromosomes. She found that late prophase or metaphase in the first microspore *mitosis* (male gametophyte) provided clear chromosome observations and by June 1929 she published the first ideogram of maize chromosomes (McClintock 1929b, Kass and Bonneauil 2004).

4 Linking Genetics and Cytology

Having the ability to recognize each chromosome individually would now permit researchers to identify genes with their chromosomes. Using a technique of observing genetic ratios in her trisomic plants and comparing the ratios with plants having extra chromosomes, McClintock cooperated with and guided graduate students to determine the location of many genes grouped together (linkage groups) on six of the ten chromosomes in corn (summarized in Emerson et al. 1935; Rhoades and McClintock 1935; Kass et al. 2005). McClintock and graduate student Henry Hill were the first to identify the *R-G* linkage group with the smallest maize chromosome (10) (McClintock and Hill 1931).

McClintock was the first to observe pieces of one chromosome attached to another chromosome (interchange chromosomes) when pollen grains are produced during meiotic cell division (McClintock 1930). She used these translocation or interchange chromosomes, which she observed during the pachytene stage of meiosis, to locate the remaining four gene groups with their chromosomes (Kass 2000; Kass and Bonneauil 2004). In addition, the cooperators confirmed Belling's translocation hypothesis which offered an explanation of how translocations could confer semisterility (gametic sterility) in corn (Burnham 1930, see Rhoades and McClintock 1935).

5 Proof of Crossing Over and the Chromosome Theory of Inheritance

Also using interchange chromosomes, Instructor McClintock and graduate student Harriet Creighton (McClintock 1931, Creighton and McClintock 1931, Creighton and McClintock 1935) provided the first demonstration of cytological "crossing over," in which chromosomes break and recombine (exchange parts) to create genetic reassociations. It was the first cytological proof that demonstrated the genetic theory that linked genes on paired chromosomes (homologues) did exchange

places from one homologue to another. For this study, Creighton and McClintock used a semisterile maize plant found to be associated with a reciprocal translocation (segmental interchange) between the second and third smallest chromosomes (chromosomes 9 and 8; McClintock 1930). By means of trisomic inheritance, McClintock (1931) first observed that chromosome 9 of the monoploid complement ($n=10$) was associated with the genes of the *c-sh-wx* linkage group. Using yet unpublished interchange data of C.R. Burnham, and trisomic inheritance for the genes *wx*, *sh*, and *c*, McClintock reported the order of the genes on chromosome 9 as *wx-sh-c*, beginning at the middle of the long arm and running toward the end of the short arm. Knowing the order of the genes was critical to the demonstration of a correlation of cytological and genetical crossing over (Creighton and McClintock 1931, Coe and Kass 2005).

Using a chromosome pair visibly heteromorphic in two regions, one chromosome of the homologue possessing an enlarged chromatic knob on the end of the short arm of the chromosome and a piece of a non-homologous chromosome attached to the same chromosome (a translocation), both pairs of contrasting features can be observed in meiotic prophases. When a heterozygous plant (in which an interchange chromosome includes the knob, and the non-interchange chromosome is knobless) is crossed to a standard knobless plant, the combinations knobless-interchange and knobbed-standard were found in the progeny. This indicated that chromosomal cross-overs had occurred in the region between the knob and the point of interchange. By the simultaneous use of genes known to be in the cytologically marked region of the chromosome, genetic crossing-over was correlated with the occurrence of chromosomal crossing-over (Creighton and McClintock 1931, Creighton 1934). The assumption that genetic crossing-over was due to an exchange of chromosome segments thus seemed to be justified (Creighton 1934). Creighton and McClintock's significant study gave further confirmation to Thomas Hunt Morgan's chromosome theory of inheritance, for which he won a Nobel Prize in 1933 (Kass, Bonneuil and Coe 2005; Coe and Kass 2005; Kass 2005).

In the *Dynamic Genome*, a gift to McClintock on her ninetieth birthday, Nina Fedoroff commended McClintock's early achievements: "The Influence of her early work is greater than that of any of her peers. ... Had she done no more, McClintock would have become a major figure in the history of genetics" (Fedoroff and Botstein 1992). McClintock hoped for a research appointment commensurate with her qualifications. By 1931, however, the country was deep into the Great Depression, which was spurred by the stock market crash in October 1929 (Kass 2000). Research jobs at most universities were not abundant and research appointments for educated women were even more limited (Kass 2005b).

6 Chromosomal Structural Changes and the Identification of Chromosome Mutations

From 1931–1934, sponsored by two National Research Council (NRC) Fellowships, and a prestigious Guggenheim Fellowship (resulting from excellent work and reputation), McClintock traveled to a series of important research institutions

across the U.S., Germany, and back to Cornell, where she worked in the Department of Plant Breeding as an assistant to Rollins Adams Emerson, head of the department (Kass 2004, Kass and Bonneuil 2004). Invited by Lewis J. Stadler, University of Missouri, Columbia, McClintock studied the physical changes (mutations) in plants caused by X-rays and discovered that external phenotypic traits were caused by missing pieces of chromosomes in the cell (McClintock 1931). At the California Institute of Technology, as an NRC Fellow with Ernest Gustav Anderson, she employed interchange chromosomes to investigate the Nucleolar Organizer Region (NOR) in cells (McClintock 1934). Studying a translocation for chromosomes 9 and 6 (the satellite chromosome, which includes a “pyncotic body” –for the NOR) that had broken the NOR into distinct pieces, she could show that either large or small nucleoli would form in progeny cells that carried a piece of the NOR. This led her to conclude that the “pyncotic body” on chromosome 6 is a nucleolar-organizing-body, with one area more active than another. Pachytene configurations showed that the NOR was attached to the nucleolus. Microspores carrying chromosome 6 and a translocation 9⁶ chromosome developed numerous small nucleolar bodies. The nucleolus, she concluded, develops from a definite nucleolar-organizing region of chromosome 6, the distal part of which, normally more closely associated with the nucleolus, is most active; but the proximal part of which may produce a full-sized nucleolus when not in competition with more active bodies. As summarized by Clausen (1936), McClintock suggested that the “function of the nucleolar-organizing body is to organize the nucleolar substance present in each chromosome into a definite body, the nucleolus, and that the nucleolar substance is either identical with or closely related to the matrix substance of the chromosomes, which may in turn be concerned with the distribution and dispersion of the chromatin within the chromosomes into the metabolic condition.”

7 Variegated Phenotypes and Unstable Chromosomes

Returning to Missouri in 1932, she continued a research project on the cytology of X-rayed plants that she began there in 1931. This investigation of ring chromosomes in corn was influenced by a study of similar chromosomes first reported by M. Navashin (1930) in *Crepis*. McClintock had previously observed “ring fragments” in maize and hypothesized the mechanism for producing ring chromosomes (McClintock 1931; Creighton and McClintock 1932). In 1932, she correlated ring chromosomes with variegation occurring both spontaneously and in x-rayed maize plants (McClintock 1932, Anderson 1936). Since the ring chromosomes varied in size in different cells, and sometimes were totally eliminated, it was suggested that the variegation was caused by the somatic elimination of that part of the ring chromosome that carried the dominant allele. Studies of the synapsis and morphology of the different ring chromosomes and their normal homologues at the mid-prophase of meiosis [pachytene stage] gave the approximate location of the *b* and *pl* loci (Rhoades 1934). Gene *b* was found

to be situated in the mid-portion of the short arm of the *B-lg* chromosome [chromosome 2] and *pl* was located towards the middle of the long arm of the satellite chromosome [chromosome 6] (McClintock 1932).

Later, McClintock (1938a) continued her studies of ring chromosomes and found that some plants harboring ring shaped chromosomes would produce dicentric chromosome bridges at mitotic anaphase, thereby losing genetic material and uncovering recessive traits in some of the cell descendents. Sister mitotic cells would gain the genetic material that was lost in the breakage of the chromosome bridge. The broken chromosome ends would fuse again to reform a ring, ready to undergo breakage again. The repeated losses resulted in variegated plant tissues due to the continual uncovering of recessive traits (McClintock 1938a).

McClintock returned to Cornell to complete her Guggenheim Fellowship after only four and one half months in Berlin and Freiburg, Germany (1933–1934). Her decision to return was due to uncomfortable circumstances caused by the rise of the Nazi Party, which forced many of her German-Jewish colleagues to leave academe, and to health problems she suffered while in Berlin. Upon completing her Guggenheim Fellowship, R. A. Emerson convinced the Rockefeller Foundation to grant him funds to employ McClintock as his research assistant. Her project provided insights to an understanding of variegation (Rhoades and McClintock 1935) and would eventually lead to her studies of the breakage-fusion-bridge cycle (see below).

In 1936, McClintock accepted an appointment as Assistant Professor of Botany at the University of Missouri to join L. J. Stadler's genetics research group (Kass 2005, Kass 2007). Stadler (1928, 1930) was the first to use X-irradiation in plants to recover mutations. McClintock had previously performed extensive cytological examination of plants carrying Stadler's x-ray induced mutations (McClintock 1931, 1932, 1933). These studies revealed that many of these mutations were due to deficiencies or rearrangements of a chromosome segment carrying the dominant allele. This material was also the major source of chromosome rearrangements that later allowed McClintock (1938a, b) to study the behavior of broken chromosomes as well as the induction of transposable elements.

After years of understanding the consequences of mitotically unstable chromosome behavior in the form of ring chromosomes (McClintock 1931 through 1938a; see Appendix), McClintock sought to experimentally determine the process of chromosome breakage and fusion. Her 1938 studies (McClintock 1938b) of an inverted segment of chromosome 4L clearly showed that "fusion of broken meiotic chromatids does occur" resulting in anaphase bridge configurations and the formation of an acentric fragment. This curious but profound behavior of newly replicated chromosomes was termed the breakage-fusion-bridge (BFB) cycle (McClintock 1939). McClintock observed this chromosome behavior during the mitotic cell divisions in pollen cells following meiosis. The scientific question then followed, what happens to such chromosomes when they are passed into the next generation? (McClintock 1938b).

A definitive conclusion came only a year later (McClintock 1939). It was well established that deficient chromosomes would not transmit well through the haploid pollen or ovule, so a method was developed to transmit a newly broken chromosome that harbored a full complement of genes using rearrangements on chromosome 9.

These chromosome configurations were obtained from both Harriet Creighton and L. J. Stadler. One of the chromosomes was an inverted duplication of the short arm which carried a series of dominant color and starch conditioning genes that could be visualized in the kernel and plant when they were present or lost (including *Yg*, *C-I*, *Sh*, *Bz* and *Wx*). In a subsequent study, McClintock paired this chromosome with a 9S deficiency that did not pass through the male gamete. Each of these chromosomes did not transmit well (or at all) through the male gamete. Meiotic recombination of this chromosome with the 9S deficiency produced a dicentric chromosome, which ruptured after each centromere was pulled to opposite poles during anaphase. One of the ruptured chromosomes carried (at least) a full complement of 9S genes and was transmitted through the pollen. Since each of the parental chromosomes was not efficiently transmitted through the pollen, McClintock developed an exquisite method to select for a high percentage of broken chromosomes in the gametes. This method demonstrated the elegance of her experimentation, her deep understanding of the plant and the foresight she had in her studies.

Upon learning that Stadler's research unit might be eliminated, and preferring research over teaching, McClintock requested a leave of absence from Missouri in 1941 to seek employment elsewhere. In the summer of 1941, she was appointed a Visiting Professor at Columbia University (organized by M. M. Rhoades) and a Visiting Investigator at the Carnegie Institution of Washington (CIW), Department of Genetics (invited by A. F. Blakeslee), Cold Spring Harbor, Long Island, New York (Kass 2005). Soon after arriving at CIW, a former Cornell Plant Breeding student, Milislav Demerec, became Director of the Department of Genetics. He offered McClintock a permanent job commencing in 1943. The University of Missouri counter offered but she resigned effective August 31, 1942.

While with the CIW, Department of Genetics, McClintock elaborated on the behavior and characterization of chromosomes and genes in maize. She continued investigating the BFB cycle, but this time followed the fate of the broken chromosome into the progeny using the markers on the broken chromosome arm. By the patterned loss of markers in the endosperm, she definitively concluded that the BFB cycle continued in the cell divisions of the endosperm. Since the fusion of ends occurs between newly formed chromatids, McClintock referred to this type of chromosome behavior as the chromatid type BFB cycle (McClintock 1941a).

Cytological examination of the embryo and plant tissue revealed that the chromatid type BFB cycle did not continue in the somatic plant tissue or in the gametes of a plant that received such a broken chromosome. In fact, all sporophytic cells observed carried the same 9S chromosome complement suggesting that the chromosome had "healed" when passed to the embryo. Years later it was realized that the healing process is likely the formation of a telomere on the broken end of the chromosome entering the zygote (McClintock 1984a). This drastic difference in behavior of the chromosomes intrigued McClintock and further investigations on the behavior of broken chromosomes into the embryo followed. Elizabeth Blackburn (1992), who discovered the enzymes that add telomeres to chromosome ends, elaborated on the contribution McClintock made to the understanding of chromosome behavior and telomere formation.

Table 1 Description of loci and phenotypes described in the text. Note that the genes involved in anthocyanin accumulation require the presence of other genes in the pathway, including *Al* *A2* *C1* *C2* and *R1*, to confer color to the plant or kernel

Gene Name	Chromosome-arm	Allele (historical*)	Phenotype
<i>Activator</i>		<i>Ac</i>	An autonomous transposable element capable of controlling the movement of itself and the movement of <i>Ds</i> ; Increasing dosage of <i>Ac</i> delays transposition.
<i>Anthocyaninless1</i>	3L	<i>Al</i>	Red or purple anthocyanin accumulation in plant and kernel (aleurone).
		<i>al</i>	Green, or brown plants, colorless aleurone, brown pericarp; recessive to <i>Al</i> .
		<i>al-m1</i> (a^{m-1})	Pale color in the kernel (aleurone) and plant. In the presence of a functional <i>Spm</i> element the pale pigmentation becomes colorless and red revertant sectors are detected. This allele responds to a fully functional <i>Spm</i> through a non-autonomous <i>Spm</i> present at the locus.
		<i>al-m2</i> (a^{m-2})	Pale pigmentation in the aleurone and plant with fully colored revertant sectors in the presence of <i>Spm</i> . The original allele contained a fully functional <i>Spm</i> at the <i>al</i> locus.
<i>Anthocyaninless2</i>	5S	<i>A2</i>	Red or purple plants and kernels (aleurone).
		<i>a2</i>	Green, or brown plants, colorless aleurone; recessive to <i>A2</i> .
		<i>a2m-1</i> ($a2^{m-1}$)	Color in the kernel (aleurone) and plant in the absence of a fully functional <i>Spm</i> . In the presence of a functional <i>Spm</i> element the pale pigmentation becomes colorless and red revertant sectors are detected. This allele responds to a fully functional <i>Spm</i> through a non-autonomous <i>Spm</i> present at the locus.
<i>Booster1</i>	2S	<i>B1</i> (<i>B</i>)	Plant color intensifier conferring a purple plant due to the accumulation of anthocyanin in major tissues.
		<i>b1</i> (<i>b</i>)	Green plant; little or no accumulation of anthocyanins; recessive to <i>B1</i> .
<i>Bronze1</i>	9S	<i>Bz1</i> (<i>Bz</i>)	Red or purple aleurone layer of the kernel due to the accumulation of anthocyanins.
		<i>bz1</i> (<i>bz</i>)	Bronze or brownish colored aleurone layer; recessive to <i>Bz1</i> .
<i>Colored aleurone1</i>	9S	<i>C1</i> (<i>C</i>)	Red or purple aleurone layer of the kernel due to the accumulation of anthocyanins.
		<i>C-1</i> (<i>I</i>)	Color inhibitor, colorless aleurone layer; dominant to <i>C1</i> .
		<i>c1</i> (<i>c</i>)	Colorless aleurone; recessive to <i>C1</i> .

<i>c1-m1</i> (<i>c^{m-1}</i>)		Mutable color; red sectors on a colorless aleurone background in the presence of <i>Ac</i> . The red sectors are caused by restoration of the <i>c1</i> locus after <i>Ds</i> transposition whereas <i>Ds</i> still inhibits the <i>c1</i> locus in the colorless aleurone background. In the absence of <i>Ac</i> the kernel is colorless. A number following the "m" was used by McClintock to identify the next consecutively isolated mutable allele in her cultures; i.e., <i>c1-m1</i> was the first mutable allele (caused by the insertion of <i>Ds</i> at the <i>C1</i> locus).
<i>Dissociation</i>	<i>Ds</i>	First named for the phenotype of dissociation (breakage) of chromosomes in the presence of <i>Ac</i> ; First described on chromosome 9. Later shown to be a transposable element due to its ability to move (transpose) in the presence of <i>Ac</i> into and away from loci thereby disrupting or controlling their function. The presence of the element was designated <i>Ds</i> and the absence of the element was designated <i>ds</i> .
<i>Dotted</i>	<i>Dt</i>	An autonomous transposable element capable of controlling the transposition of the receptor element <i>rDt</i> at the <i>A1</i> locus. In the presence of <i>Dt</i> , <i>a1-dt</i> responding alleles are unstable and express colored dots on a colorless aleurone background. In the absence of <i>Dt</i> , the <i>a1-dt</i> alleles are stable and exhibit a colorless aleurone.
<i>Enhancer-Inhibitor</i>	<i>En-1</i>	Discovered independently by P. Peterson (1953) yet structurally and functionally the same as <i>Spm</i> . The <i>Enhancer</i> function is equivalent to the <i>Suppressor</i> function (<i>Sp</i>) of <i>Spm</i> and the <i>Inhibitor</i> function is equivalent to the <i>mutator</i> function (<i>m</i>) of <i>Spm</i> .
<i>Liguleless1</i>	2S	Leaves show normal ligule and auricle development and structure
<i>Modulator of Pericarp</i>	<i>Lg1</i> (<i>Lg</i>)	Leaf lacks ligule and auricles, leaves stand upright at base; recessive to <i>Lg1</i> .
	<i>Ig1</i> (<i>Ig</i>)	Leaf lacks ligule and auricles, leaves stand upright at base; recessive to <i>Lg1</i> .
<i>Pericarp Color</i>	<i>Mp</i>	Discovered independently by Brink and Nilan (1952) yet structurally and functionally the same as <i>Ac</i> . The transposable element was studied in association with the <i>P</i> locus where it caused the red variegated or revertant tissue sectors in the <i>P^{vv}</i> allele.
	<i>PI</i> (<i>P</i>)	Controls pigmentation accumulation in the pericarp and cob. All pericarp loci are designated <i>P</i> with superscript letters following the <i>P</i> , such as <i>P^{RR}</i> for red pericarp, red cob, <i>P^{WW}</i> for white pericarp, white cob. <i>P^{vv}</i> is variegated pericarp and cob color due to transposition of <i>Mp</i> and functional restoration of the <i>P</i> locus.

(continued)

Table 1 (continued)

Gene Name	Chromosome-arm	Allele (historical*)	Phenotype
<i>Purple Plant1</i>	6L	<i>Pl1(Pl)</i> <i>pl1(pl)</i>	Light independent accumulation of red or purple color (anthocyanin) in major tissue of the plant. Sunlight dependent accumulation of pigmentation in the leaves and sheath.
<i>Red (Colored1)</i>	10L	<i>R1 (R.)</i> <i>r1 (r)</i>	Red or purple color in the plant and kernel. <i>R-G</i> designation refers to separate components of the locus that specifically confer color to the kernel or plant respectively. Green plant, colorless aleurone in the kernel.
<i>Shrunken1</i>	9S	<i>Sh1 (Sh)</i> <i>sh1 (sh)</i>	Plump kernel, normal starch synthesis in endosperm. Shrunken or collapsed endosperm due to reduced starch content, recessive to <i>Sh1</i> .
<i>Suppressor-Mutator</i>		<i>Spm</i>	An autonomous transposable element capable of controlling gene function as well as transposition of itself and nonautonomous <i>Spm</i> elements. The <i>Suppressor (Sp)</i> function enhances or suppresses gene expression of a locus containing a functional or defective <i>Spm</i> element, while the <i>Mutator</i> function (<i>m</i>) is necessary for transposition of the element.
<i>Waxy1</i>	9S	<i>Wx1 (Wx)</i> <i>wx1 (wx)</i>	Endosperm starch contains amylose and amylopectin; stains blue-black with iodine stain (I ₂ KI). Endosperm appears waxy, starch contains only amylopectin; stains red/brown with iodine stain (I ₂ KI); recessive to <i>Wx1</i> .
<i>Yellow Green2</i>	9S	<i>Yg2 (Yg-2)</i> <i>yg2 (yg-2)</i>	A normal green plant. Leaves of seedling and mature plant are yellow-green in color.

* Historical or alternative allelic designations for loci are indicated in parentheses.

The introduction of a broken chromosome from the male and the female gametes simultaneously into the zygote allowed McClintock to study the behavior of two newly broken chromosomes in the embryo and endosperm (McClintock 1942). From her ring chromosome studies she already realized that broken chromosomes, prior to replication into chromatids, should fuse together in embryo and plant tissue (McClintock 1938). Each of the chromosomes was distinctly marked so that she could follow the behavior of the chromosomes phenotypically in the endosperm. From such studies she realized that two broken chromosomes would fuse prior to replication in the embryo and undergo what she termed the chromosome type BFB cycle (McClintock 1942). This process was distinct from the chromatid type BFB cycle since it required two broken chromosomes. The fusion occurred prior to chromatid formation and the process occurred in sporophytic tissue. McClintock repeated experiments using her “improved method” of delivering a broken chromosome into the gametes (McClintock 1944b) to produce seed from plants that underwent either the chromatid or the chromosome type BFB cycle. Such plants were used as a system to induce new mutations by minute deletions and rearrangements of chromosome 9. Through careful cytological examination and subsequent genetic crosses, McClintock could associate new mutant “genes” to chromosome segments, a remarkable feat at the time and even today (McClintock 1945b, 1946).

In the winter of 1944 soon after her election to the National Academy of Sciences, George Beadle invited McClintock to Stanford University to study the chromosomes of the pink bread mold *Neurospora*. Beadle was a former student colleague and friend with whom she worked on corn genetics at Cornell from 1927–1930 and during her NRC years at Caltech. Within ten weeks, with the assistance of Beadle’s staff, she was able to provide a preliminary study of the fungal chromosomes and demonstrate their movement during cell division (McClintock 1945a). This work was important to an understanding of the life history of the organism and was the basis for Jesse Singleton’s Ph.D. dissertation research conducted at Caltech under McClintock’s guidance in 1946 (Singleton 1948, Singleton 1953). Beadle and his colleagues would employ the fungus to elucidate how genes control cell metabolism (Berg and Singer 2003). In 1958 Beadle and Tatum shared a Nobel Prize with J. Lederberg.

8 Unstable Mutants and the Discovery of Transposable Elements

Returning to CIW in 1945, McClintock continued to investigate the behavior of chromosomes and the effects of deletions and rearrangements. Similar to her past (and future) studies, McClintock focused her attention on unique phenotypes. Such mutant or altered phenotypes were her key to unlocking the mechanisms of chromosome behavior, responses of the genome to stress and to gene regulation. In 1945, the same year she was elected the first woman President of the Genetics Society of America, she characterized four unusual unstable mutations (McClintock 1946). These were derived from selfed plants that underwent the chromatid or chromosome type BFB cycle (a white seedling variegated, a variegated light green

seedling, a luteus seedling, and a chromosome breakage variegation pattern in the aleurone of the seed). They were all tied together by their unique, yet similar, frequency and timing of unstable phenotypes (mutability). In the plant, mutant tissue gave rise to wild type tissue in a very regular pattern. In the kernel mutant, loss of chromosome markers also occurred in the same “controlled” regular pattern. These patterns were unlike the random losses due to ring chromosomes or the usual BFB cycle and she suggested there was a different control mechanism at work.

What caught McClintock’s eye was the unique pattern on the kernels showing a regular loss of all markers distal (towards the end of the chromosome) to the *Wx1* locus (see Table 1 for descriptions of genetic symbols) on chromosome 9S. In fact, crossover data and cytological observations indicated that there was a chromosome dissociating locus (designated *Ds*) just proximal to the *Wx1* locus. Due to the segregation of this trait, it was also apparent that a second locus was required, designated *Activator* (*Ac*), to cause the chromosome breakage. Many other mutable loci, like the ones described in 1946, were isolated from these cultures, including multiple alleles of a mutable color locus (*c-1*, *c-2*) and a mutable starch conditioning mutant (*wx-1*, *wx-2*). Each mutant was used to unify the theory of gene control while delineating and further defining the capabilities of what she later referred to as controlling elements (McClintock 1956).

A number of additional remarkable conclusions came from these early studies (McClintock 1946, 1947, 1948, 1949, 1950). The pattern of mutability of the reverting loci (*c1-m1*, *c1-m2*, *wx-m1*, see Table 1) was strikingly similar to the patterned loss of *Ds* and both types of loci were under the control of *Ac*. McClintock was convinced that a unifying mechanism was underlying these phenotypic similarities. In addition, somatic sectors and germinal changes in the plant and kernel were readily detected that altered the pattern of mutability in all descendent somatic cells. These heritable alterations were called “changes in state” of the locus, rather than simply mutations, since they occurred frequently and, at times, were twinned (one daughter cell gained what the other cell had lost). She also saw that the patterned loss of the distal third portion of chromosome 9S, including markers *C*, *Bz*, *Wx* could heritably change in a few kernels. The marker loss pattern in these derived kernels now clearly showed that marker losses were occurring at a new location on the chromosome. The *Ds* had moved (transposed) to a new position on chromosome 9.

McClintock hypothesized how the *Ds* element could move. Large chromosome rearrangements were often associated with the *Ds* locus since it was causing chromosome breaks. McClintock reasoned that in some instances, rather than a large, visible rearrangement, a submicroscopic chromatin segment carrying *Ds* was cut out and reinserted to the new position on the chromosome, not unlike larger rearrangements that she had observed in early studies. Similarly, she hypothesized that by the same *Ac* controlled mechanism, *Ds* could transpose to a position within or near a normal gene (the *C1* locus; McClintock 1948) thereby disrupting or inhibiting its function (*c1-m1*; McClintock 1949). McClintock also explained how the mutant *c1* locus could be restored in somatic and germinal tissues. She stated, “An event leading to removal of the inserted *Ds* segment from the *C* locus would give rise to two broken ends in the chromatid. Fusion of these broken ends would re-establish the former normal genic order, and remove the inhibitory action on the *C* locus induced by the inserted

segment; and as a consequence a mutation from *c* to *C* would be evident.” (McClintock 1949). This single hypothesis of *Ds* transposition unified many of the observations of *Ds* behavior, including the similarity in patterns of mutability of reverting loci (*C* and *Wx*) and the patterned loss and movement of *Ds* along the chromosome. It was for this discovery, 35 years later, that she was awarded the Nobel Prize in 1983.

9 Control of Gene Action

Transposition of the elements allowed McClintock to discover and study another key aspect of gene action, that of gene regulation. The observations that these transposable elements could influence the regulation of many genes was intensively studied over the next 15 years, particularly using an element designated *Suppressor-Mutator* (*Spm*).

By 1954 (McClintock 1954) the two-element mutation-controlling system designated *Ac/Ds* was well studied by McClintock and, like the *Dt* system described earlier by Rhoades (Rhoades 1938), investigators at other institutions were characterizing mutable systems, including *Mp* at the *P* locus (Brink and Nilan 1952). At this time McClintock switched much of her attention to a new and unique mutable system which she discovered was controlling the *A1* locus.

The new system, designated *Spm* for *Suppressor-Mutator* (McClintock 1954), had characteristics both similar to and distinct from the *Ds-Ac* system. Similarly, the *A1* somatic mutations were controlled by a two-element system that could transpose, although the instability was not controlled by the *Ac* or *Dt* loci. In addition, chromosome breaks were not detected with the *Spm* system. What was unique about *Spm* was the added layer of gene regulation that was not observed with *Ds-Ac*. The newly controlled allele of the *A1* gene (designated *a1-m1*) was lightly colored in the kernel or plant. Only upon introduction of a fully functional *Spm* element elsewhere in the genome in conjunction with the *a1-m1* allele, did the pale pigmentation turn to colorless. In addition, intensely colored sectors appeared much like the somatic reversion mutations recognized with other transposable elements. The function responsible for the trans-acting inhibition of pigmentation was termed the suppressor function (*Sp*). Likewise, the function responsible for the somatic reversion was designated the Mutator function (*m*). Independently, Peterson (1953) published on a transposable element system designated *En-I* (*Enhancer-Inhibitor*) which was later recognized as the same element system as *Spm* (Peterson 1965).

A second allele of *A1* under the control of *Spm* demonstrated a distinct suppressor regulation of gene function. In the case of the *a1-m2* allele a fully functional *Spm* element was originally identified at the locus (subsequently many defective derivatives were produced). When the element was functioning, the kernel exhibited pale pigmentation and fully colored sectors. The pale pigmentation in the presence of a functional *Spm* element was opposite of what was observed with the *a1-m1* (and *a2-m1*) *Spm* controlled alleles. Utilizing other unique behaviors of *Spm*, McClintock showed that the *A1* locus expression was now dependent on the suppressor function of *Spm*; when *Sp* was active, the *A1* gene was expressed and when *Sp* was shut off, the *A1* gene was also inactivated giving rise to a colorless phenotype. Numerous

cases were studied over the years to demonstrate and dissect the gene controlling action of the *Spm* system (McClintock 1965).

The fact that these elements could differentially regulate endogenous genes solidified McClintock's concept that they were truly "controlling elements". It was also clear that McClintock believed that by selecting for certain transpositions or other genic-altering events she could uncover gene regulation mechanisms that were not previously recognized but were an inherent component of the genome. Over the next 15 years or so, McClintock continued to uncover the complexities and intricacies of the *Spm* system and therefore the complexities of gene regulation in the nucleus of cells.

Further insights into gene regulation came with the description of reversible inactivation of controlling elements. After years of describing heritable and stable changes to genes and elements, McClintock realized that both *Spm* and *Ac* could undergo a cyclical change (designated phase change) in activity during plant and kernel development (McClintock 1957, 1958, 1964). She described cases in which both *Spm* and *Ac* activity could turn off and on during plant and kernel development. While this phase change seemed random, it was not; certain alleles were "programmed" to turn on and off with a given frequency and timing. Because this phenomenon could occur with different element families and did not involve movement of the element or irreversible changes to the locus, McClintock realized that phase change was a unique layer of gene regulation not previously accounted for. Since the advent of molecular biology it has been realized that elements and genes are regulated through multiple, complex mechanisms involving modifications to the DNA and chromatin structure. Controlling element phase change demonstrated a key process in this epigenetic gene regulation and is still under investigation today (Schwartz and Dennis 1986, Chomet et al. 1987, Banks et al. 1988, Lippman et al. 2003).

10 The Races and Varieties of Maize

Other areas of maize biology were of interest to McClintock. For over 20 years, she trained students and conducted research on the evolution and migration of varieties of corn in the Americas, which was initiated in the late 1950's (McClintock 1978, McClintock et al. 1981, Timothy 1984). Utilizing cytological knobs as polymorphic markers, she, and two of the students she trained at North Carolina State University in the 1960s, investigated and published a study of variation in chromosome constitutions for over 1,200 races, strains and varieties of maize. Far ahead of her time and predating the idea of restriction fragment length polymorphisms (1980), McClintock and associates utilized the shape and distribution of chromosomal knobs, the incidence of the abnormal 10 chromosome, and the number of B chromosomes to infer the makeup and predominance of certain maize varieties and relate them across geographical boundaries in the Americas. The distribution and frequency of knobs or chromosome components are interpreted in terms of where maize developed initially and when, where, and how it was introduced into other parts of the Americas,

and its fate following introductions (McClintock et al. 1981, Timothy 1984). McClintock et al. (1981) develops a coherent theme on the evolution of maize races. For example, the distribution and frequency of knobs on chromosomes 4 and 5 link some Mexican races to one another and knobs on chromosome 7 were used to trace the migration routes by which maize from one area was carried to another. Additionally, groups of special knobs revealed the relationship of maize to teosinte, and geographical areas where some of the early diverse racial types developed. They also discuss the origins of knob complexes and their significance in association with migration pathways, introductions and introgression (for an excellent book review of McClintock et al. 1981, see Timothy 1984).

11 Recognition

Many persons have wondered why it took so long for McClintock's work to be recognized by the extensive scientific community. Although McClintock employed cytogenetic techniques to study corn chromosomes, other researchers studied simpler organisms (bacteria and their viruses) and used molecular techniques to investigate genes and inheritance. From 1944 through 1952, molecular genetic studies demonstrated that DNA was the hereditary material. This discovery launched the field of molecular biology to the forefront of scientific investigations. McClintock's experiments were complex, laborious, taking months or even years to explain results. Molecular studies in simpler organisms gave almost instant gratification and quickly answered questions about the hereditary material that had been unsolved for years. Additionally, McClintock's findings contradicted the prevailing view that all genes were permanently in a linear sequence on chromosomes.

McClintock's conclusion that genes could move from place to place in the maize genome was accepted, although the concept did not seem applicable to other organisms until transposable elements were found years later in prokaryotic (*E. coli*) and eukaryotic organisms (*Drosophila*, humans, etc.). Because McClintock was a very respected researcher (she received the Botanical Society of America Merit Award in 1957 and the National Academy of Science Kimber award in 1967), her work with corn was accepted but it was considered anomalous. In other words, even if genes did move around in corn the mechanism was probably not universally relevant to all organisms. Researchers in corn genetics however, immediately understood, explored, and expanded on her initial studies (Neuffer 1952, Brink and Nilan 1952, Dollinger 1954, Kreizinger 1960). During the 1970's, transposable elements were found in a number of other organisms; first in bacteria and then in most organisms studied by geneticists. This work has led to the revolution in modern recombinant DNA technology that has played a large role in medicine and agriculture, and which society now takes for granted. When McClintock's work was "rediscovered," she was recognized and rewarded for her great insights (Table 2, National Medal of Science 1970, Nobel Prize in Physiology or Medicine 1983, etc.). It is a lesson to be learned that new ideas in science, which contradict the

Table 2 Chronological list of Barbara McClintock's Major Awards and Recognitions

Undergraduate	
1923	Phi Kappa Phi, Honorary Scholastic Society
Graduate Student	
1923–1924	Cornell University Graduate Scholarship in Botany
1923–1924	Elected to Sigma Xi, Honorary Society
Postdoctoral	
1931–1933	National Research Council, National Academy of Sciences, Fellowship
1933	First recognized in <i>American Men of Science</i>
1933–1934	Guggenheim Memorial Foundation Fellow
Academic, Professional and Public Recognition	
1939–1940	Vice President, Genetics Society of America
1944	Elected to National Academy of Sciences
1944	Starred in Botany in <i>American Men of Science</i>
1945	President, Genetics Society of America
1946	Elected to American Philosophical Society
1947	Achievement Award, American Association of University Women
	Honorary Sc.D., University of Rochester
1949	Honorary Sc.D., Western College for Women, Oxford, OH
1953–1954	Visiting Professor, California Institute of Technology
1957	Merit Award, Botanical Society of America
1958	Honorary Sc.D. Smith College, Amherst, MA
1959	Elected Fellow American Academy of Arts and Sciences, MA
1965–1974	A.D. White Professor-at-Large, Cornell University
1967	Kimber Award, National Academy of Sciences
1967–1992	Distinguished Service Member, Carnegie Institution of Washington, Cold Spring Harbor, NY
1968	Honorary Sc.D., University of Missouri, Columbia, MO
1970	National Medal of Science, USA
1972	Honorary Sc.D., Williams College, Williamstown, MA
1973	McClintock Laboratory dedicated at Cold Spring Harbor Laboratory, Cold Spring Harbor, NY
1978	Lewis S. Rosensteel Award for Distinguished Work in Basic Medical Research, Waltham, MA
	Louis and Bert Friedman Foundation Award for Research in Biochemistry, New York Academy of Sciences

1979	Honorary Sc.D., The Rockefeller University, Bronx, NY Honorary Sc.D., Harvard University, Cambridge, MA Barbara McClintock Professorship of Genetics established, Rutgers, The State University of New Jersey, Rutgers, NJ
1980	Salute from the Genetics Society of America
1981	Thomas Hunt Morgan Medal, Genetics Society of America Wolf Prize in Medicine, Wolf Foundation, Israel MacArthur Prize Fellow Laureate, John D. and Catherine T. MacArthur Foundation Honorary D.H.L., Georgetown University, Washington, DC
1982	Albert Lasker Basic Medical Research Award, New York, NY Louisa Gross Horwitz Prize for Biology or Biochemistry, Columbia University, NY Charles Leopold Mayer Prize, Academie des Sciences, Institut de France, Paris Honorary Sc.D., Yale University, New Haven, CT Honorary Sc.D., University of Cambridge, Cambridge, England Outstanding Alumni Award, Cornell University, Ithaca, NY
1983	Honorary Sc.D., Bard College, Annandale-on-Hudson, NY Honorary Sc.D., State University of New York, Stonybrook, NY Honorary Sc.D., New York University, Manhattan, NY Nobel Prize in Physiology or Medicine, Stockholm, Sweden
1984	Honorary Sc.D., Rutgers, The State University of New Jersey, Rutgers, NJ
1986	Elected to National Women's Hall of Fame, Seneca Falls, NY
1989	Elected Foreign Member, Royal Society UK, London, England
Posthumous Awards	
1993	Benjamin Franklin Medal, Carnegie Institution of Washington, Wash. DC
2004	Barbara McClintock Professorships established at Cornell University, Ithaca, NY
2005	Barbara McClintock US Postal Service American Scientists Commemorative Postage Stamp
2007	Barbara McClintock Society [a philanthropic society], established by the Carnegie Institution of Washington, Wash, DC, 5 May 2007.

prevailing model (dogma or paradigm), are not easily accepted. Barbara McClintock died on September 2, 1992 in Huntington, Long Island, New York, yet her memorable words still resonate in the hearts and minds of the maize community:

“Because I became actively involved in the subject of genetics only twenty-one years after the rediscovery, in 1900, of Mendel’s principles of heredity, and at a stage when acceptance of these principles was not general among biologists, I have had the pleasure of witnessing and experiencing the excitement created by revolutionary changes in genetic concepts that have occurred over the past sixty-odd years. I believe we are again experiencing such a revolution. It is altering our concepts of the genome: its component parts, their organizations, mobilities, and their modes of operation. Also, we are now better able to integrate activities of nuclear genomes with those of other components of a cell. Unquestionably, we will emerge from this revolutionary period with modified views of components of cells and how they operate, but only, however, to await the emergence of the next revolutionary phase that again will bring startling changes in concepts” (McClintock 1984).

Acknowledgments LBK acknowledges the National Science Foundation (Grants SBR9511866 & SBR9710488), and the American Philosophical Society Library, Mellon Resident Research Fellowship and the Lilly Library, Helm Fellowship for support of archival research. And thanks the Department of Plant Biology and the Department of Plant Breeding and Genetics, Cornell University for logistical support. Special thanks to our colleagues Ed Coe, Royse P. Murphy, Kathleen Gale and Richard H. Whalen for helpful suggestions on revising the manuscript.

Appendix I

Current List of Barbara McClintock’s Publications

(Modified from Kass, L. B. 1999. Current list of Barbara McClintock’s publications. *Maize Genetics Cooperation Newsletter* 73: 42–48. Available online, 1998: <http://www.agron.missouri.edu/mnl/73/110kass.html>)

In 1987, Moore edited and reprinted a collection of Barbara McClintock’s papers for the Great Books in Experimental Biology Series. McClintock’s publications relevant to the discovery and characterization of transposable elements are reprinted in that work. The volume also includes a list of McClintock’s published papers under the heading “Numbered List of Publications” (Moore 1987). I examined the journals, symposia, etc., where all of McClintock’s papers appear. In the course of my research, I found 14 additional contributions. I subsequently compiled a chronological list of all known contributions published by McClintock, which are listed below.

My list updates and amends Moore’s (1987) published list and brings the total number of publications to 93. I annotated citations to include, when available, dates when the papers were received, and the month they appeared in print. In some cases the publication date and inclusive pages were revised to reflect accurately these citations. This may be important for scholars who do not have direct access to the publications. I gratefully acknowledge Dr. Edward Coe for his support with this project.

Reference cited:

Moore, John A. (ed.) 1987. *The Discovery and Characterization of Transposable Elements. The Collected Papers of Barbara McClintock*. Great Books in Experimental Biology, Garland Publishing Co. New York.



Fig. 1 Gerry Neuffer, Om Sehgal, Barbara McClintock, Ed Coe at a party celebrating McClintock's honorary Sc.D. from University of Missouri (Columbia, MO), in 1968. (Used with permission of G. Neuffer, ID's Ed Coe)



Fig. 2 Barbara McClintock at Upland Farms, Cold Spring Harbor, NY, during the summer of 1986. Maize genetics was reinvigorated at Cold Spring Harbor Lab in the early 1980's by Steven Dellaporta and associates. McClintock was a mentor and teacher both in the field and in the lab for undergraduates, graduate students and post doctoral researchers. Shown here is (L to R): Scott Bernstein (undergraduate), Barbara McClintock, Brenda Lowe (Post doc), Jychien Chen (Post doc), and Paul Chomet (graduate student). (Used with permission of Paul Chomet)

ANNOTATED CHRONOLOGICAL LIST OF THE PUBLICATIONS OF BARBARA MCCLINTOCK

Note: This list uses dates of publication as referenced by McClintock; i.e., the 1951 *Cold Spring Harbor Symposia on Quantitative Biology* is cited here as 1951, although the copyright date for the symposium is 1952. Additional pertinent information is enclosed in brackets.

*Appears in Moore's (1987) "Numbered list of publications," pgs. xiii–xv. I add month of publication and submission dates in brackets. I list publications chronologically and add letters following dates for more than one publication in the same year. I add subheadings following titles for *Carnegie Institution of Washington Year Book* reports, and complete titles for other publications. Inclusive years for *Carnegie Year Book* reports are in brackets.

**Appears in Moore (1987) and edited for accuracy; i.e., titles, page numbers, or dates corrected.

No Star(*) = additions to "Numbered list of publications" (Moore 1987).

McClintock, Barbara. 1925. *A Resume of Cytological Investigations of the Cereals with Particular Reference to Wheat*. Ithaca, NY. 52 pgs. plus 25 unnumbered pgs. of tables and bibliographies. [Thesis, M. A. Cornell University. A literature review; no original research. Acknowledges Prof. L. W. Sharp.]

*Randolph, L. F. and B. McClintock. 1926. Polyploidy in *Zea mays* L. *American Naturalist* LX (666) [Jan./Feb. 1926, received — no date given]: 99–102.

McClintock, Barbara. 1927. *A Cytological and Genetical Study of Triploid Maize*. Cornell University, Ithaca, New York. 104 pgs. plus 39 unnumbered pgs. of tables, plates, and bibliographies. [Thesis, Ph.D. Acknowledges L.W. Sharp and A.C. Fraser.]

*Beadle, G. W. and Barbara McClintock. 1928. A genic disturbance of meiosis in *Zea mays*. *Science* 68 (1766) [2 November 1928, received - no date given]: 433. [This became George Beadle's dissertation research project.]

*McClintock, Barbara. 1929a. A cytological and genetical study of triploid maize. *Genetics* 14 (2) [11 March 1929, received 11 July 1928]: 180–222. [Publication of 1927 Ph.D. thesis. *Genetics* was issued bimonthly at this time.]

*McClintock, Barbara. 1929b. A method for making aceto-carmin[e] smears permanent. *Stain Technology* IV (2) [April 1929, received - no date given]: 53–56. [In this publication carmine is incorrectly spelled in the title, throughout the text, and in the citation to Belling 1926.]

*McClintock, Barbara. 1929c. A 2N-1 chromosomal chimera in maize. *Journal of Heredity* XX (5) [May 1929, received - no date given]: 218. [McClintock annotated the reprint she sent to T. H. Morgan indicating that only one photograph was intended to be published. She apparently submitted two exposures with the intent that the best one would be printed. The citation to Blakeslee and Belling *Science*, 55, is incorrect; the year, 1924, is missing, and the volume number should be 60 (LX) not 55.]

- *McClintock, Barbara. 1929d. Chromosome morphology in *Zea mays*. *Science* 69 (1798) [14 June 1929, submitted - no date given]: 629. [The first published ideogram of Zea chromosomes. The chromosomes were identified in the “first division in the microspore” (Mitosis) not at pachytene of Meiosis I as described by some text book authors. The citation for McClintock *Genetics*, 14, is incomplete. The year, 1929, is missing.]
- McClintock, Barbara and Henry E. Hill. 1929 [ABSTRACT]. The cytological identification of the chromosomes associated with the ‘R-golden’ and ‘B-liguleless’ linkage groups in *Zea mays*. *Anatomical Record* 44 (3) [25 December 1929]: 291. [The paper was “read by title” at the Joint Genetics Sections of the American Society of Zoologists and the Botanical Society of America, held with the AAAS, Des Moines, and Ames, Iowa, December 1929 - January 1930. Resulting manuscript submitted March 1930, and published one year later in *Genetics* 16: 175–190, March 1931. See McClintock 1933a (pg. 209) for correction of B-lg linkage group association with Chromosome 2 not Chromosome 4.]
- *McClintock, Barbara. 1930a. A cytological demonstration of the location of an interchange between two non-homologous chromosomes of *Zea mays*. *Proceedings of the National Academy of Sciences* 16 (12) [15 December 1930, communicated 6 November 1930]: 791–796.
- McClintock, Barbara. 1930b [ABSTRACT]. A cytological demonstration of the location of an interchange between two non-homologous chromosomes of *Zea mays*. *Anatomical Record* 47 (3) [25 December 1930]: 380. [Paper presented on 30 December 1930, at the Joint Genetics Sections of the American Society of Zoologists and the Botanical Society of America, held with the AAAS, Cleveland, Ohio, December 1930 - January 1931. Two weeks prior to these meetings, the results were published in *PNAS* 16: 791–796, December 1930.]
- *McClintock, Barbara and Henry E. Hill. 1931. The cytological identification of the chromosome associated with the R-G linkage group in *Zea mays*. *Genetics* 16 (2) [16 March 1931, received 1 March 1930]: 175–190.
- *McClintock, Barbara. 1931a. The order of the genes C, *Sh*, and *Wx* in *Zea mays* with reference to a cytologically known point in the chromosome. *Proceedings of the National Academy of Sciences* 17 (8) [15 August 1931, communicated 7 July 1931]: 485–491. [Communicated the same date and issued as one reprint with Creighton and McClintock 1931. The results reported in McClintock 1931a are necessary for an understanding of Creighton and McClintock 1931, which follows directly in the Journal. These papers were intended to be read together. McClintock 1931a ends with the following statement: “It was desired to present briefly the evidence at this time, since it lends valuable support to the argument in the paper which follows.” Creighton & McClintock, 1931 state: “In the preceding paper it was shown that the knobbed chromosome

- carries the genes for colored aleurone” etc. Unfortunately the “preceding paper” (McClintock 1931a) is neither cited nor referenced.]
- *Creighton, Harriet B. and Barbara McClintock. 1931. A correlation of cytological and genetical crossing-over in *Zea mays*. *Proceedings of the National Academy of Sciences* 17 (8) [15 August 1931, communicated 7 July 1931]: 492–497. [Communicated the same date and issued as one reprint with McClintock 1931a; see annotation for McClintock 1931a.]
- *McClintock, Barbara. 1931b. Cytological observations of deficiencies involving known genes, translocations and an inversion in *Zea mays*. *Missouri Agricultural Experiment Station Research Bulletin* 163 [December, authorized 23 December 1931]: 1–30. [McClintock NRC Fellow at Missouri and Cal Tech, investigation conducted at Missouri beginning June 1, 1931; L. J. Stadler suggested the problem and furnished all the material in the growing state.]
- McClintock, Barbara. 1932a [ABSTRACT]. Cytological observations in *Zea* on the intimate association of non-homologous parts of chromosomes in the mid-prophase of meiosis and its relation to diakinesis configurations. *Proceedings of the International Congress of Genetics II* [24–31 August 1932, preface dated 26 July 1932]: 126–128. [McClintock NRC Fellow at Cal Tech with E.G. Anderson. This paper was presented at the 6th International Congress of Genetics as a Sectional Paper in the session titled “Cytology I, Saturday August 27.” McClintock presented paper number 6 of 11 papers. Resulting manuscript submitted in April 1933 and published in *ZZMA* 19:191–237, September 1933.]
- Creighton, Harriet B. and Barbara McClintock. 1932 [EXHIBIT]. Cytological evidence for 4-strand crossing over in *Zea mays*. *Proceedings of the International Congress of Genetics II* [24–31 August 1932, preface dated 26 July 1932]: 392. [This was an exhibit that was part of the section on “General Cytology” in the “General Exhibits.” The section was organized by Ralph E. Cleland.]
- *McClintock, Barbara. 1932b. A correlation of ring-shaped chromosomes with variegation in *Zea mays*. *Proceedings of the National Academy of Sciences* 18 (12) [15 December 1932, communicated 2 November 1932]: 677–681. [McClintock NRC Fellow at Missouri with L. J. Stadler; her address is given as U of Missouri; Contribution from Dept of Field Crops, Missouri Agricultural Experiment Station Journal Series No. 355.]
- **McClintock, Barbara. 1933a. The association of non-homologous parts of chromosomes in the mid-prophase of meiosis in *Zea mays*, with 51 figures in the text and plates VII–XII. *Zeitschrift für Zellforschung und mikroskopische Anatomie* 19 (2) [22 September 1933, received 21 April 1933]: 191–237. [McClintock NRC Fellow in the biological Sciences, University of Missouri with L. J. Stadler and California Institute of Technology with E. G. Anderson; investigations conducted at Missouri and at Cal Tech.]

- McClintock, Barbara. 1933b. News Items from Ithaca: 11. Brown midrib1 (bm1) *Maize Genetics Cooperation News Letter* 4 [18 December 1933]: 2.
- McClintock, Barbara. 1933c. News Items from Ithaca: 12. A new narrow leafed character is linked with a1. *Maize Genetics Cooperation News Letter* 4 [18 December 1933]: 2.
- **McClintock, Barbara. 1934. The relation of a particular chromosomal element to the development of nucleoli in *Zea mays* with 21 figures in the text and plates VIII–XIV. *Zeitschrift für Zellforschung und mikroskopische Anatomie* 21(2) [23 June 1934, received 2 March 1934]: 294–328. [McClintock NRC Fellow in the biological sciences, California Institute of Technology with E. G. Anderson; investigation conducted at Cal Tech. Paper written while McClintock was a Guggenheim Fellow in Berlin and Freiburg, Germany and submitted just prior to leaving Germany.]
- *Creighton, Harriet B. and Barbara McClintock. 1935. The correlation of cytological and genetical crossing-over in *Zea mays*. A corroboration. *Proceedings of the National Academy of Sciences* 21 (3) [15 March 1935, communicated 9 February 1935]: 148–150. [Written while McClintock was a research assistant in the Department of Plant Breeding, Cornell University (address Botany Department).]
- *Rhoades, Marcus M. and Barbara McClintock. 1935. The cytogenetics of maize. *Botanical Review*. 1 (8) [August 1935, received - no date given]: 292–325. [Written while McClintock was a research assistant in the Department of Plant Breeding, Cornell University.]
- McClintock, Barbara. 1936a. Cornell University, Ithaca, N.Y. — 8. Mosaic plants in part heterozygous and in part homozygous for a chromosome 5 deficiency. *Maize Genetics Cooperation News Letter* 10 [4 March 1936]: 5–6.
- McClintock, Barbara and Harriet Creighton. 1936. Cornell University, Ithaca, N.Y. — 9. Several inversions ... chromosome 9 ... and chromosome 4, ... detected and isolated by Creighton and [McClintock]. *Maize Genetics Cooperation News Letter* 10 [4 March 1936]: 6.
- McClintock, Barbara. 1936b. Cornell University, Ithaca, N.Y. — 10. Disjunction studies on interchanges show that sister spindle fiber regions do not separate in I, *Maize Genetics Cooperation News Letter* 10 [4 March 1936]: 6.
- McClintock, Barbara. 1936c. [ABSTRACT PREPRINT] The production of maize plants mosaic for homozygous deficiencies: Simulation of the bm1 phenotype through loss of the Bm1 locus. Abstracts of papers presented at the December 29–31, 1936 meetings of the Genetics Society of America, Atlantic City, New Jersey; Preprinted from *Genetics* 22:183–212, 1937, in *Records of the Genetics Society of America*, Number 5, 1936. [Paper delivered 29 December 1936.]
- **McClintock, Barbara. 1937a. [ABSTRACT] The production of maize plants mosaic for homozygous deficiencies: Simulation of the bm1

- phenotype through loss of the Bm1 locus. [In Abstracts of papers presented at the 1936 meetings of the Genetics Society of America, M. Demerec, Secretary.] *Genetics* 22 (1) [January 1937, presented 29 December 1936]: 200. [Investigations funded by the Rockefeller Foundation and conducted in Department of Plant Breeding, Cornell University; McClintock's address - Cornell University. In September 1936, McClintock left Cornell to begin her Assistant Professor appointment at U of Missouri. Results reported are part of a manuscript submitted February 1938 and published in *Genetics* 23: 315–376, July 1938. Note subheadings for sections V and VI in published paper are exactly the same as title of this abstract.]
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Handbook of Maize

Genetics and Genomics

Bennetzen, J.L.; Hake, S.C. (Eds.)

2009, XII, 800 p. 94 illus., 46 illus. in color., Hardcover

ISBN: 978-0-387-77862-4