

Course Syllabus:

1. Genetic Transmissions and Mendelian Genetics.
2. Transmission and inheritance of chromosomes.
3. Linkage and Mapping.
4. Mendelian Genetics in Corn (*Zea mays*).
5. Extensions of Mendel's laws (Extensions of Mendelian inheritance).

MENDELIAN GENETICS OF CORN**Objectives:**

By doing this part well, you will be able to:

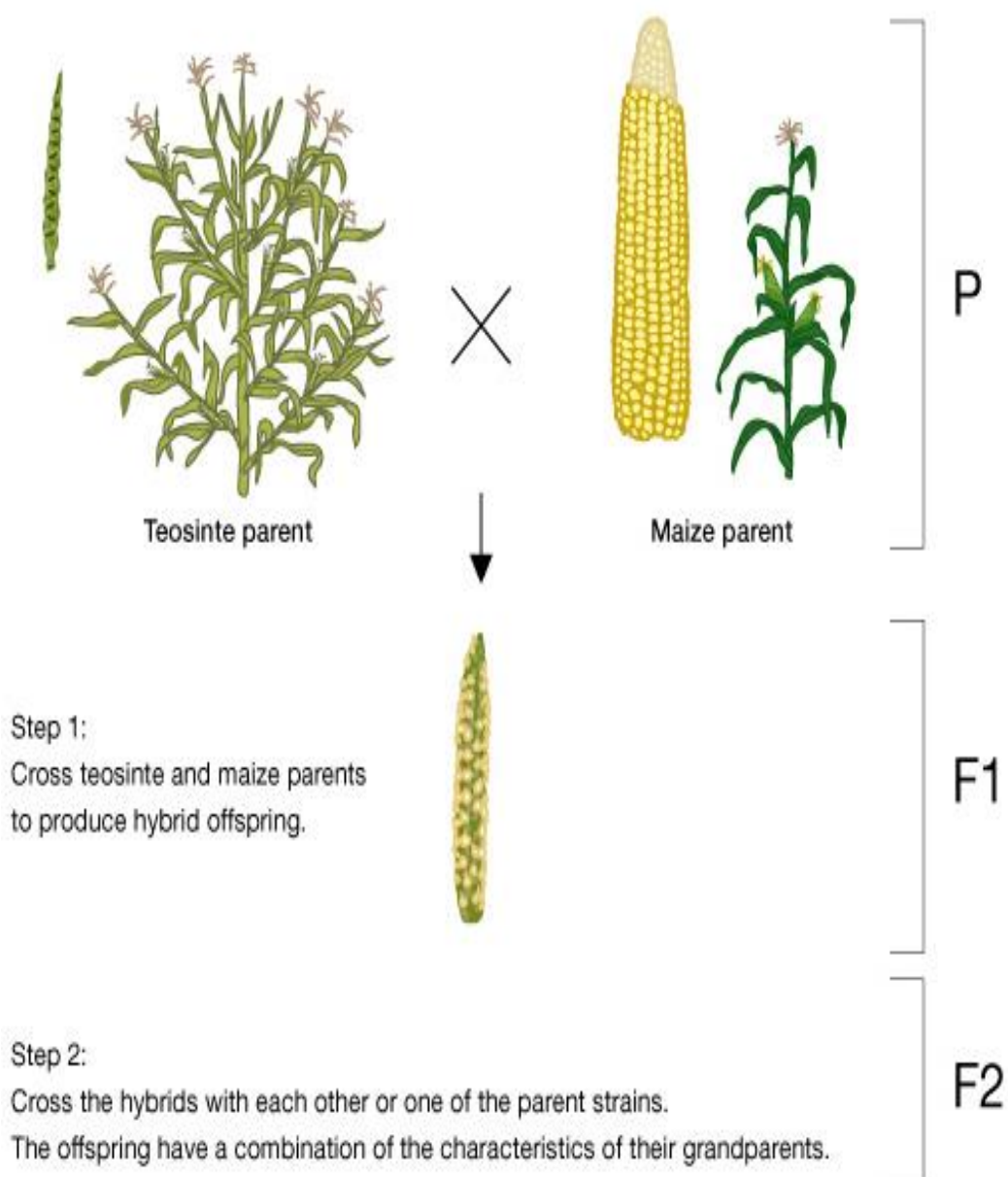
1. Know and understand the evolution of corn
2. Differentiate between Corn and its ancestor Teosinte
3. Distinguish between the different shape and color of kernel
4. Explain how the transposon genes function in Indian Kernel
5. Identify the different genes that control the shape and color of kernel
6. Know the different types of corn

The evolution of corn

The history of modern-day maize begins at the dawn of human agriculture, about 10,000 years ago. Ancient farmers in what is now Mexico took the first steps in domesticating maize when they simply chose which kernels to plant. These farmers noticed that not all plants were the same. Some plants may have grown larger than others, or maybe some kernels tasted better or were easier to grind. The farmers saved kernels from plants with desirable characteristics and planted them for the next season's harvest. This process is known as **selective breeding or artificial selection**. Maize cobs became larger over time, with more rows of kernels, eventually taking on the form of modern maize after thousands of selective breeding. The identity of maize's wild ancestor remained a mystery for many decades,

there is no wild plant that looks like maize, with soft, starchy kernels arranged along a cob.

The earliest events in maize domestication likely involved small changes to single genes with dramatic effects. We know the events were early because there is little variation in these genes between maize varieties, suggesting that modern varieties are descended from a single ancestor, Teosinte (*Zea mays* ssp. *parviglumis*) which is the wild relative to modern corn.





Evolution

Through Genetic Archaeology We See That Teosinte and Maize are Alike

At the DNA level, the two (Maize and Teosinte) are surprisingly alike. They have the same number of chromosomes ($2n = 20$) and a remarkably similar arrangement of genes. In fact, teosinte can cross-breed with modern maize varieties to form maize-teosinte hybrids that can go on to reproduce naturally. Scientists study teosinte-maize hybrids and their offspring through the process of genetic archaeology. This process helps geneticists understand what is happening at the DNA level to make teosinte and maize so different. By combining clues from genetics and the archaeological record, scientists have pieced together much of the story of maize evolution.

The Difference Between Teosinte and Maize is About 5 Genes

Through the study of genetics, we know today that corn's wild ancestor is a grass called teosinte. Teosinte doesn't look much like maize, especially when you compare its kernels to those of corn: An ear of teosinte is only about three inches long, with just 6 to 12 kernels in two, interleaved rows protected by a hard, outer covering. Compare that to the corn we eat today, which can have as many as 20 rows or more, with numerous exposed kernels (over five-hundred). In fact, teosinte is so unlike maize in the structure of its ear that 19th century botanists failed to recognize the close relationship between these plants.

One of the first scientists to fully appreciate the close relationship between teosinte and maize was George Beadle. In the 1930s, Beadle studied teosinte-

maize hybrids and showed that their chromosomes are highly compatible. Later, he produced large numbers of teosinte-corn hybrids and observed the characteristics of their offspring. By applying basic laws of genetic inheritance, Beadle calculated that only about 5 genes were responsible for the most-notable differences between teosinte and a primitive strain of maize. Using more-modern techniques, they confirmed that about 5 regions of the genome (which could be single genes or groups of genes) seemed to be controlling the most-significant differences between teosinte and maize.

Additional Knowledge:

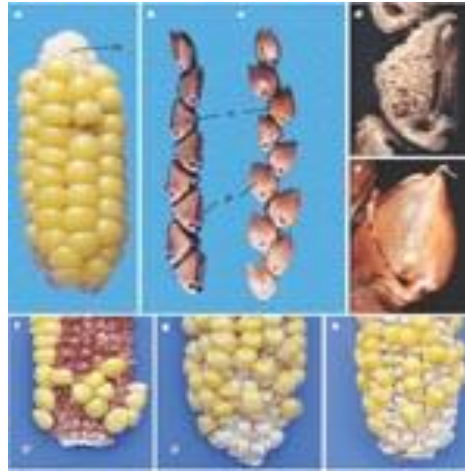
What traits were modified during domestication?

In recent years, geneticists have used advanced molecular-biology tools to pinpoint the roles of some of the genes with large effects, as well as many other regions across the genome that have had subtle effects on maize domestication.

1. Glume: The teosinte kernel is surrounded by a hard coating called a glume. In the wild, this glume helps to protect the seed when passing through the digestive tract of animals or when sitting in the ground during the winter. Since this tough glume is difficult to chew and digest by humans, those plants with a softer glume were conceivably targeted during domestication. In today's maize, the glume is very reduced (you may have encountered it when eating corn-on-the-cob as it's the part that often gets stuck in your teeth). A single major locus, *teosinte glume architecture* (TGA) has been identified that controls much of this reduction in glume size.

2. Plant Architecture: In a modern maize field, you see a single stalk and ear per plant. This is not the case in teosinte, where many stalks, called tillers, are found per plant, along with many inflorescences (female ears and male tassels). By concentrating energy resources into a single stalk and ear, it was probably possible to create larger ears that were easier to harvest. John Doebley's research group has cloned this domestication gene and named it *teosinte*

branched 1 (tb1). Tga1 (Kernel covering) and tb1 (branching pattern) show us that evolution doesn't always involve gradual change over time.



Tga 1 gene

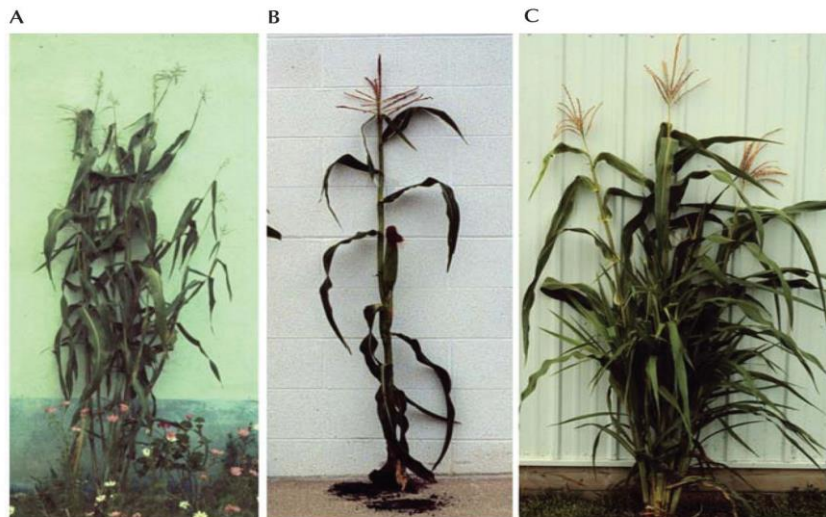


FIGURE 11.28. (A) Teosinte plant, (B) maize plant, and (C) maize *tb1* mutant plant. The teosinte (A) and maize (B) plants are quite different looking (e.g., the teosinte plant has many lateral branches, whereas maize has few or none), but the *tb1* mutant maize (C) plant has several morphological features that make it look more like teosinte, including the presence of lateral branches.

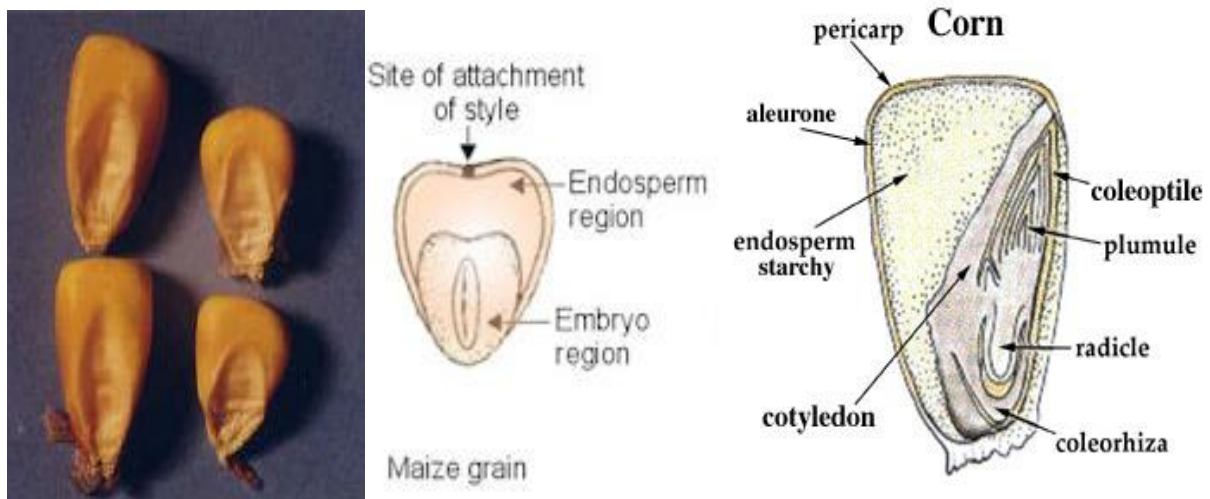
Tb1 gene

3. Other Distinguishing Traits: QTL at genes responsible for three more distinguishing traits--shattering vs. solid cobs, single vs. paired spikelets, and distichous vs. polystichous condition--are the subject of current investigation. While several regions of the genome have been identified, we have yet to definitively find those genes responsible for these traits.

4. Starch: While changes in plant shape and ear morphology were the initial focus of domestication research, many additional traits have been the target of human selection over the last few thousand years. Some traits of particular significance were yield, the size of the ear (which has increased from 2cm to 30cm), and the quality of the grain. Starch was—and is—the key product of maize, accounting for 73% of the kernel's total weight. As such, the genes involved in starch synthesis are among the most important for grain production, critical to both the yield and the quality of the grain. To date, researchers have identified three starch loci (*su1*, *bt2*, and *ae1*) as targets of selection during maize domestication and improvement.

Corn Grain (kernel)

Maize grain is not a seed, but a single-seed fruit. Its fruit-wall and seed-coat are fused into a single layer. A very slight whitish patch on one side of the grain marks the embryo. The internal tissues of the corn grain consists of 3 layers: the pericarp (outermost layer), the aleurone (middle single-celled proteins/fats layer), and the endosperm (innermost starchy or sugary layer). The shield-shaped single cotyledon is known as scutellum, in which the grain embryo is embedded in (depression part).



Different Shape and color of Kernel (common and Indian ears) and genes controlling them

1. Common ear (corn):

Two traits commonly used in genetic studies of corn are kernel shape and kernel color. Some of the different possible phenotypes for these two traits are listed below:

Trait #1: Kernel Color (Aleurone pigmentation)

1. red (red pigment in kernel cells)
2. purple (purple pigment in kernel cells)
3. yellow (carotenoids in kernel cells)
4. white (no pigments present in cells)



Yellow kernel



Purple kernel



Red kernel



White kernel

Many genes determine the phenotypes of the 3 tissues that control the color of a corn kernel. These tissues are the pericarp, the aleurone and the endosperm. In our known corn, the pericarp is always colorless, but the aleurone may be colorless, purple, or red, and the endosperm yellow or white.

The presence of purple anthocyanin pigments (Y) in the aleurone layer is dominant to the lack of such pigments (y). A grain with a genotype of YY or Yy will express the purple phenotype, whereas a grain with the yy genotype will appear with yellow to white color, because the translucent aleurone allows the color of the underlying starch layer to show through.

If the aleurone is colorless, the kernel color will be that of the endosperm, either yellow or white. Normal corn endosperm color (yellow) occurs when the allele Y causes the production of carotenoid pigments in the endosperm. In the recessive condition (yy) carotenoids are not produced and the endosperm is

white. The *Y* alleles are masked by the presence of a colored aleurone (**epistasis**).

For the aleurone to be colored, alleles *C* and *R* must be present. The homozygous recessive of either allele (*cc* or *rr*) disrupts anthocyanin production and results in a colorless aleurone. The dominant *C'* allele also inhibits anthocyanin production, giving a colorless aleurone. Genes *C* and *R* are located on separate chromosomes and segregate independently. The allele *Pr* interacts with alleles *C* and *R* to produce a purple aleurone. The homozygous recessive condition (*prpr*) interacts with *C* and *R* to produce a red aleurone.



Figure 7 Cross of R and SU alleles.



Figure 8 Pr, C, and R alleles.

Trait #2: Kernel Shape (Endosperm starch to sugar ratio)

1. Smooth or full kernel (starch present in kernel)
2. Wrinkled or shriveled (sugar present in kernel)



Starchy kernel



Sugary kernel

Normal corn endosperm is high in amylose starch. The gene *su* in the homozygous recessive condition (*su su*) produces endosperm that is high in sugar. As corn dries, its sugary endosperm loses water, and its kernels wrinkle.

The gene *Su* in the homozygous recessive condition (*SuSu*) causes the production of amylopectin starch in the endosperm and pollen. The endosperm of this kernel is opaque with a hard, waxy texture.

The presence of a high ratio of starches to sugars (*Su*) is dominant to the presence of a high ratio of sugars to starches (*su*) in the inner endosperm layer. Starchy grains (*Susu* or *SuSu*) are smooth when dry, and sugary grains (*susu*) are very wrinkled when dry. Later changes in the evolution of modern maize involved many genes (perhaps thousands) with small effects over time.

These minor changes include the following:

- Types and amounts of starch production
- Ability to grow in different climates and types of soil
- Length and number of kernel rows
- Kernel size, shape, and color
- Resistance to pests

Over thousands of years, selective breeding generated the broad diversity of corn varieties that are still grown around the world today.

Trait #3: Mixed color and/or shape of Kernel of ear in ratio 3:1 and 9:3:3:1.



3Purple:1Yellow Monohybrid.

An F_2 ear resulting from a P_1 having the genotypes *RR* and *rr*.



3Starchy:1Sweet.

An F_2 ear from a cross between a starchy (*SuSu*) and a sweet (*susu*) parent. The sweet seed are wrinkled and the starchy seed are smooth.



9 Purple Dent: 3 White Dent: 3 Purple Sweet: 1 White Sweet Dihybrid.

F_2 generation resulting from a parental cross between a plant homozygous dominant for both alleles and a plant homozygous recessive for both alleles by the assortment of two independent characteristics.



9 Purple Starchy:3Purple Sweet:3Yellow Starchy: 1Yellow Sweet dihybrid.

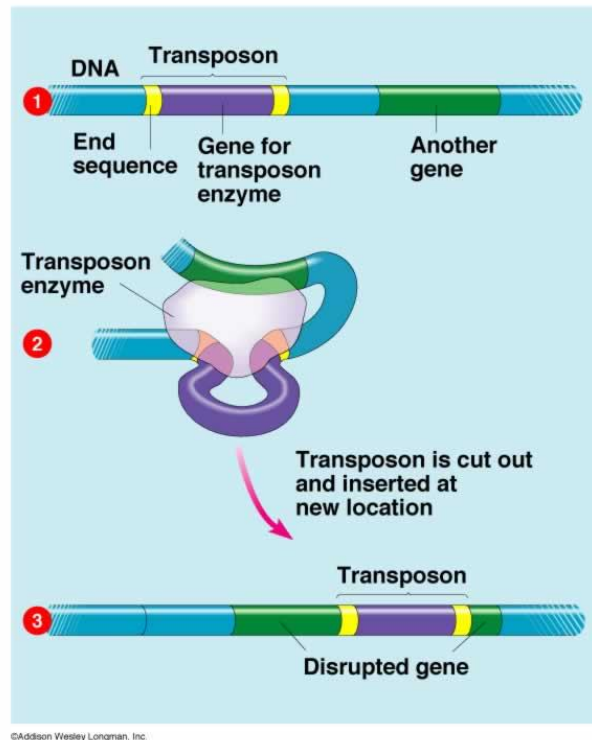
An F_2 ear resulting from a P_1 having the genotypes *RR SuSu* and *rr susu*.

2. Indian ear (corn):

Transposons (Jumping Genes): A Simplified Explanation For Jumping Genes And Their Effect On The Kernel Color Of Indian Corn

Grains of Indian corn come in different colors, such as purple, yellow and white. Sometimes the individual grains are purple with white streaks or mottling. This mottling effect defies Mendel's basic principles of genetics because individual grains may be multicolored rather than a single color. The movement of transposons on chromosomes may result in colored, non-colored and variegated grains that do not fit traditional Mendelian ratios based solely on chromosome assortment during meiosis and random combination of gametes. The explanation for this phenomenon involves "**jumping genes**" or **transposons**, and earned Dr. Barbara McClintock the prestigious Nobel Prize in Medicine in 1983 for her life-long research on corn genetics (table 1).

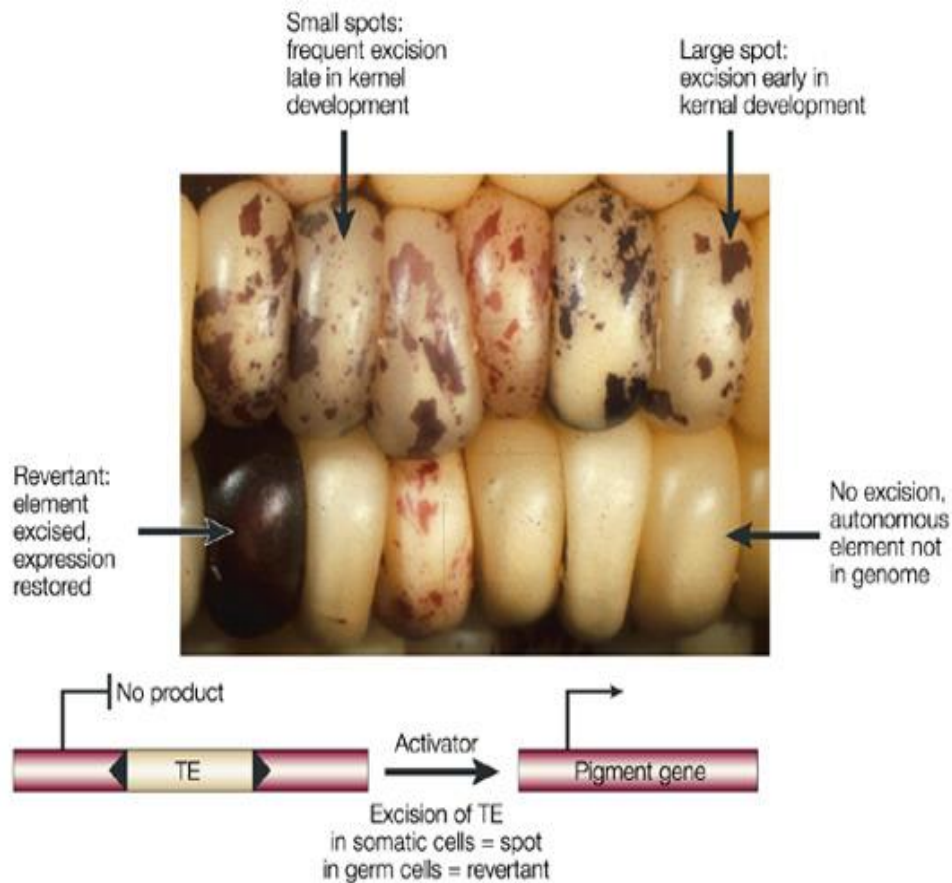




Transposons are genes or DNA sequences that move from one location to another on a chromosome within the genome sometimes creating or reversing mutations and altering the cell's genome size.

In the pigmented aleurone layer of corn grains, the position of transposons may inhibit or block pigment production in some cells. For example, if the transposon moves to a position adjacent to a pigment-producing gene, the cells are unable to produce the purple pigment. This results in white streaks or mottling rather than a solid purple grain. The duration of a transposon in this "turned off" position affects the degree of mottling. If the pigmentation gene is turned off long enough by a transposon, the grain will be completely unpigmented. The reddish-purple patterns caused by transposons may be blotches, dots, irregular lines and streaks.





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When a transposon moves to different positions within cells of the corn kernel, the coloration gene is "turned on" or "turned off" depending on whether it lands in a position adjacent to the pigmentation gene.



Table 1: Maize Genes Studied by Barbara McClintock

Gene	Description
<i>C'</i>	Dominant allele on the short arm of chromosome 9 that prevents color from being expressed in the aleurone layer of the maize kernel, causing a so-called "colorless" phenotype (which is actually white or yellow in color). This is also known as the inhibitor allele.
<i>C</i>	Recessive allele on the short arm of chromosome 9 that leads to color development.
<i>Bz</i>	Dominant allele on the short arm of chromosome 9 that leads to a purple phenotype.
<i>bz</i>	Recessive allele on the short arm of chromosome 9 that leads to a dark brown phenotype.
<i>Ds</i>	Genetic location on the short arm of chromosome 9 at which chromosomal breakage occurs.
<i>As</i>	A factor of unknown location (at least when McClintock was conducting her research) that impacts the expression of <i>Ds</i> .

Additional Knowledge: Transposons may also have a profound effect on embryonic development and tumor formation in animal cells. Oncogenes (genes that cause tumors) may be activated by the random reshuffling of transposons to a position adjacent to the oncogene. Transposons may also be useful in genetic engineering with eukaryotic cells, by splicing in transposons to activate certain genes.

Others: <http://www.tradewindsfruit.com/corn/>

Types of ears (corns):

The thousands of maize varieties grown around the world provide food for people and livestock. The following varieties are distinguished (by starch amount, shape and size of the kernel):

- **Dent corn** (*Zea mays* var. *indentata*): derives its name from the dent or depression that is visible when dried, matured kernel. This dent is caused by

the shrinking of the soft, floury starch within the hard starch which is contained to one side of the kernel. Most dent corn is yellow or white in color and is used primarily a livestock feed.

- **Flint corn** (*Zea mays* var. *indurata*): thick, horny upper layer of kernel, small, soft endosperm due to a limited to non-existent amount of soft starch contained within the hard endosperm. It ranges in color from white to deep red. Flints also store more durably than other varieties because the kernels absorb less moisture and are more resistant to fungi and insects.
- **Sweet corn** (*Zea mays* var. *saccharata* and *Zea mays* var. *rugosa*): A wrinkly, translucent genetic variant kernel which are typically white or yellow accumulates more sugar and less starch in the ear, high fat and protein content and is consumed as a vegetable wrinkled kernels,
- **Waxy corn** (*Zea mays* var. *ceratina*): kernel solely of amylopectin without the 22% amylose giving waxy appearance.
- **Amylomaize** (Starch corn, soft corn, *Zea mays* var. *amylacea*): mostly white or blue in color, endosperm loose and very high in starch but low in protein, floury; specially suitable for starch production
- **Striped maize** (*Zea mays* var. *japonica*):
- **Baby corn**: has a crisp texture and a subtle, slightly sweet corn flavor. simply immature ears from regular-sized corn plants
- **Pod corn** (*Zea mays* var. *tunicata* Larrañaga ex A. St. Hil.): is grown almost exclusively for scientific research in an effort to trace the genetic roots of corn.
- **Popcorn** (*Zea mays* var. *everta*): small, hard kernels almost completely consisting of horny starch, high in protein.
- **Pearl popcorn**: round kernels
- **Rice popcorn**: pointed kernels, heating causes expansion and makes the husk burst.



References: from students' presentations

Animation:

Terosin to corn evolution

<http://www.dnatube.com/video/573/From-teosinte-to-corn>

<http://www.dnatube.com/video/12181/Breeding-Corn-from-Teosinte>