Chapter 16

# *Genetics*

**KEY CONCEPTS**

1. The hereditary traits of an organism are determined by units of information called genes and are encoded in the base sequence of the organism's DNA. A mutation in a DNA base sequence produces a new allele of a gene, which can sometimes be identified by a detectable change in a trait.

2. In plants, DNA is divided among several chromosomes, with each gene occurring at a specific place along the length of one of the chromosomes.

3. Meiosis and fertilization work together to assure that different combinations of alleles appear in new generations.

4. The transmission of chromosomes, genes, and alleles from parents to progeny follows clear rules, so that the traits of progeny can be predicted from the traits of their parents and more distant ancestors. However, the processes of meiosis and fertilization include chance events; therefore, the predictions describe probabilities rather than certainties.

5. A knowledge of genetics allows plant breeders to develop crops with improved qualities and yields.

## 16.1 TRAITS, GENES, AND ALLELES

Plants of a particular species can be described by a series of **characters**, such as flower shape and color, stem length, leaf shape and arrangement, fruit type, and seed shape. All these characters are specified to some degree by internal factors called **genes**. Genes provide the instructions to the plant cells on how to grow and develop and how to respond to environmental cues. Genetic information is inherited--that is, passed from parents to progeny, from generation to generation in the process of sexual reproduction. **Genetics** is the study of how genes work and the rules by which they are inherited.

### Different Alleles Produce Different Traits

Some basic principles of genetics were discovered by Gregor Mendel, an Austrian monk, botanist, and teacher who used garden peas (*Pisum sativum*) as his experimental organism. His report, published in 1866, was generally unappreciated until his principles were rediscovered around 1900. One of Mendel's principles was the idea that some plant characters are determined by heritable factors. When Mendel looked at his pea plants, he noticed that certain characters occurred in more than one form. For instance, for the character of stem length, pea plants could be short or tall; the character of flower color could be red or white; seed shape could be round or wrinkled. He reasoned that the factors for those characters came in more than one form. Today, each character is called a **trait**; the factors are called genes; the alternate forms of a gene are called **alleles**. One allele of a gene for stem length makes a pea plant tall; another makes it short.

**Traits Reflect the DNA Code**

Genes are sequences of nucleotides in DNA, or **base sequences** (referring to the parts of the nucleotides that give them their identities). What we know about genes has come from the work of many scientists, but no doubt the most famous breakthrough in knowledge was made by James Watson and Francis Crick, the discoverers of the double helical structure of DNA. They recognized how the sequence of bases along a DNA molecule could act as a code to specify the sequence of amino acids in a protein. Proteins have numerous important functions in a cell, including their role as enzymes.

The functions of proteins depend on their three-dimensional structures. An example is glucosyl transferase, an enzyme needed for the synthesis of amylose, a type of starch. This protein works because it has a three-dimensional structure that binds to the reactants (uridine-diphosphoglucose--an active form of glucose--and a growing starch chain) and catalyzes the reaction that adds glucose to the end of the chain. That three-dimensional structure is a consequence of the sequence of the amino acids in the protein molecule. The sequence of the amino acids is determined by the base sequence of its gene.

Sometimes a plant with a different form, a **mutant**, may appear spontaneously in a collection of similar plants from the same parental stock. Figure 16.1 and Table 16.1 compare several mutant plants to their "normal" or **wild-type**, relatives. Different forms of a trait arise through **mutation**, changes in the base sequence of DNA. Sometimes, the mutation is as simple as a change in one base. At other times, the mutation is more drastic: a complete disruption of the base sequence by the addition or deletion of a line of bases. When a

Figure 16.1. Mutations in maize plants. (a) An albino mutant seedling among wild-type green seedlings. (b) Mature ears, in which different kernels express different combinations of alleles of genes controlling the production of anthocyanins (red and purple pigments). (c) A stripe mutant, in which chlorophyll accumulation decreases periodically as the leaf grows from the base. (d) An attached leaf mutant in which the cuticle has changed, causing the leaves to stick together as they develop.

mutation changes the base sequence of a gene that previously coded for an enzyme, the gene no longer contains the information to code for the correct amino acid sequence. Then the enzyme either is not made, or it does not function properly. For instance, a mutation in the gene encoding glucosyl transferase results in a corn plant not being able to make the functional enzyme. The mutant corn plant lacks the ability to form amylose in its seeds. Without that type of starch, the seeds appear "waxy"; therefore, the gene involved is called "waxy" (Table 16.1).

Mutations are the raw material for evolution through natural selection. Although most mutations are "bad," some may simply make a plant different; others may make a plant more suited to its environment. Once a mutation occurs, the altered DNA will be passed from the mutant organism to its progeny according to the rules that Mendel discovered. If the progeny that express the mutant trait reproduce more effectively, the mutation and its trait will spread through the population, and the population will have evolved.

**Table 16.1 A Small Selection of Mutations In Three Plant Species**

| Wild-type Form | Alternate (Mutant) Form | Name of Gene |
|---|---|---|
| ***Pisum sativum*** (garden peas) | | |
| Yellow cotyledons | Green cotyledons | *I* |
| Red flower petals | White flower petals | $A_1$ |
| Smooth seed surface | Wrinkled seed surface | *R* |
| Tall (more than 20 internodes) | Short (10–20 internodes) | *T* |
| Green foliage | Yellow-green foliage | *O* |
| Axillary flowers | Terminal flowers | *Fa* |
| Straight pod | Curved pod | *Cp* |
| Tendrils | No tendrils | *N* |
| ***Zea mays*** (maize, corn) | | |
| Filled endosperm | Shrunken endosperm (lacks sucrose synthase) | *sh* |
| Yellow endosperm | White endosperm | *y* |
| Colored (red) endosperm | Yellow endosperm | *R* |
| Normal endosperm | Waxy endosperm (altered starch-synthesizing enzyme) | *wx* |
| Dormant seed | Viviparous (germinates on cob) | *Vp* |
| Has isocitrate dehydrogenase | Lacks isocitrate dehydrogenase | *idh* |
| ***Brassica campestris*** (rapid-cycling Brassicas, fast plants) | | |
| Normal internode length | Short internode (gibberellin-insensitive) | *dwf* |
| Normal internode length | Short internode (rosette–gibberellin-sensitive) | *ros* |
| Red pigment on hypocotyl | Lacks pigment | *anl* |
| Waxy covering on leaves, stem | Lacks waxy covering (glossy) | *glo* |
| Green leaves | Yellow-green (chlorophyll deficient) | *ygr* |
| Normal internodes | Elongated internodes (lacks phytochrome B) | *ein* |

## 16.2 TRANSMISSION OF GENES

### Chromosomes Carry Genes

In plants, as in all other eukaryotic organisms, most of the DNA is found in the nucleus and is combined with proteins to form **chromatin**. The chromatin is divided into

**chromosomes**, each of which contains a single linear strand of DNA. Each gene is a portion of the DNA between 300 and 3,000 bases in length (or longer). Every gene has a particular position--its **locus**--on one of the chromosomes (Fig. 16.2). It is separated from the adjacent genes by long stretches of DNA believed to be nonfunctional. Because the DNA in a chromosome may be a hundred million bases in length, there is plenty of room for several hundred genes on one chromosome. The collection of all the genes in an organism is called the **genome**. The smallest number of chromosomes in a plant is four, found in the desert plant *Haplopappus gracilis* (a relative of the sunflower) and some other species. The coast redwood (*Sequoia sempervirens*) has nearly a hundred chromosomes; some ferns have several hundred.

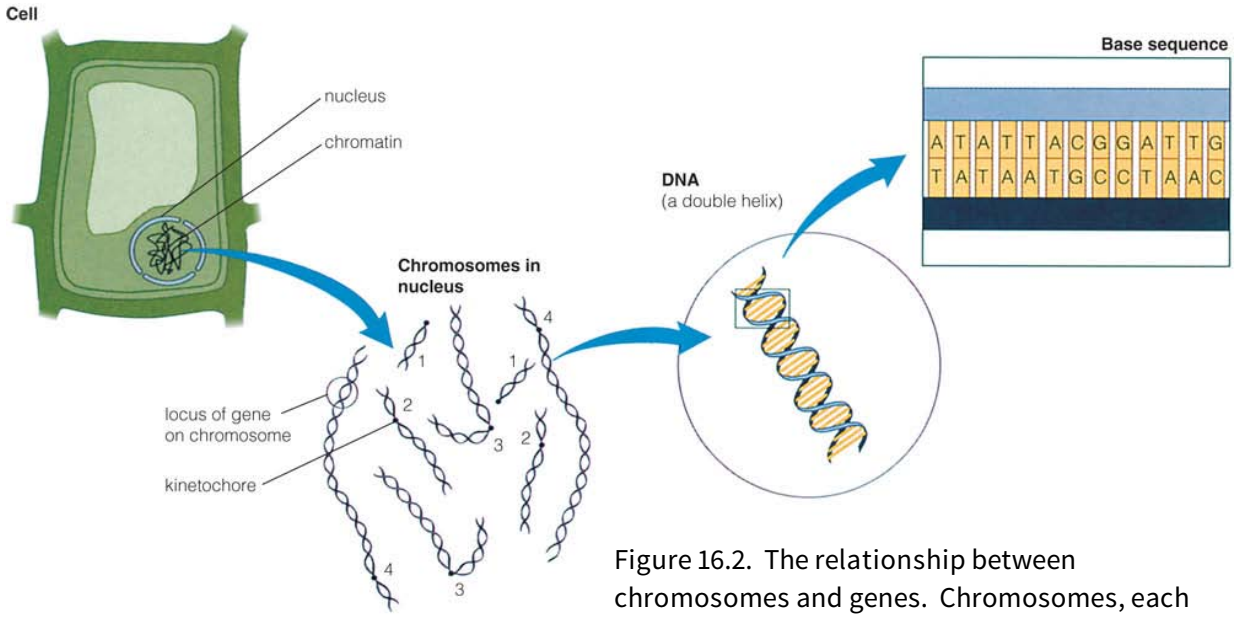


Figure 16.2. The relationship between chromosomes and genes. Chromosomes, each a long strand of DNA, reside in the nucleus of a plant cell. A gene is found at a particular site (locus) on a chromosome. Each gene has a specific sequence of bases.

All the cells that make up the root and shoot of a plant are formed from an original single cell by a sequence of mitotic cell divisions. As described in Chapter 3, mitotic cell divisions follow the S phase of the cell cycle, during which the DNA in each chromosome is faithfully replicated. Mitosis assures that each of two progeny cells has one of every chromosome. This means that every allele (mutant or wild-type) found in the original cell also will be present in all the cells of the plant. When plants reproduce by vegetative reproduction, which occurs solely through mitotic cell division, the progeny plant have the same alleles as the parent plants.

Each different type of chromosome has a different set of genes. However, as explained in Chapter 12, all diploid organisms, including flowering plants, have two copies of each type of chromosome, one from the sperm and one from the egg. The two copies are said to be **homologous** because they have the same set of genes. That does not mean, however, the genes at the same locus on two homologous chromosomes are necessarily identical; they may have different alleles.

**Meiosis Segregates Alleles, and Fertilization Combines Them**

Diploid organisms--including plants--reproduce sexually, a mechanism that offers greater genetic variety than mutation alone. As described in Chapter 12, the gametes of a plant--sperm and egg--are haploid, each having only one chromosome of each type. Their union forms a new single cell, the zygote, which has two sets of chromosomes. Thus, the zygote, and the plant that develops from it, is diploid. To reproduce, the diploid plant must form new haploid cells by meiosis.

If we assume that a plant (and thus every cell in that plant) has two different alleles (which we designate *A* and *a*) at some locus on a chromosome, we can trace the allocation of those alleles to gametes during the process of meiosis (Fig. 16.3). The preparation for meiosis begins in the preceding S phase with the synthesis of new DNA, after which each chromosome has two identical sister **chromatids** and two copies of each gene. Meiosis opens with prophase I, in which the chromosomes coil, shorten, and thicken, becoming more visible. During this period, homologous chromosomes come together to form pairs, a process called *synapsis*. The nuclear envelope disappears, a spindle forms, and in the first division, the spindle separates the homologous chromosomes. A second division separates the chromatids, so each daughter cell gets one chromatid of each type and only one copy of each gene (see anaphase II and telophase II in Fig. 16.3). The original diploid cell had different alleles for a particular gene (*A* and *a*); each resulting haploid gamete got only one of the two alleles (*A* or *a*). In Mendel's language, the two alleles segregated (separated) during meiosis. This is sometimes known as Mendel's Law of Segregation. Amazingly, even though Mendel did not know about chromosome, genes, alleles, and meiosis, he deduced from his experiments how traits are passes from parents to progeny.

An unusual process occurs during prophase I (Fig. 16.4). During synapsis, the chromatids of homologous chromosomes may exchange some corresponding pieces with each other in a process called **crossing over**. The cross formed by the chromatids during the exhange (and visible with a microscope) is known as a **chiasma** (derived from the Greek word for "cross," plural *chiasmata*). The process results in the formation of rearranged chromatids possessing fragments from both of the homologous chromosomes. This is important when we consider more than one gene. If the homologous chromosomes of the parent cells have different alleles for both genes, then crossing over produces chromatids with new combinations of alleles (Fig. 16.4), an effect known as recombination. In contrast to mutation, which actually changes alleles, recombination between genes simply forms new combinations of alleles already present in the genome.

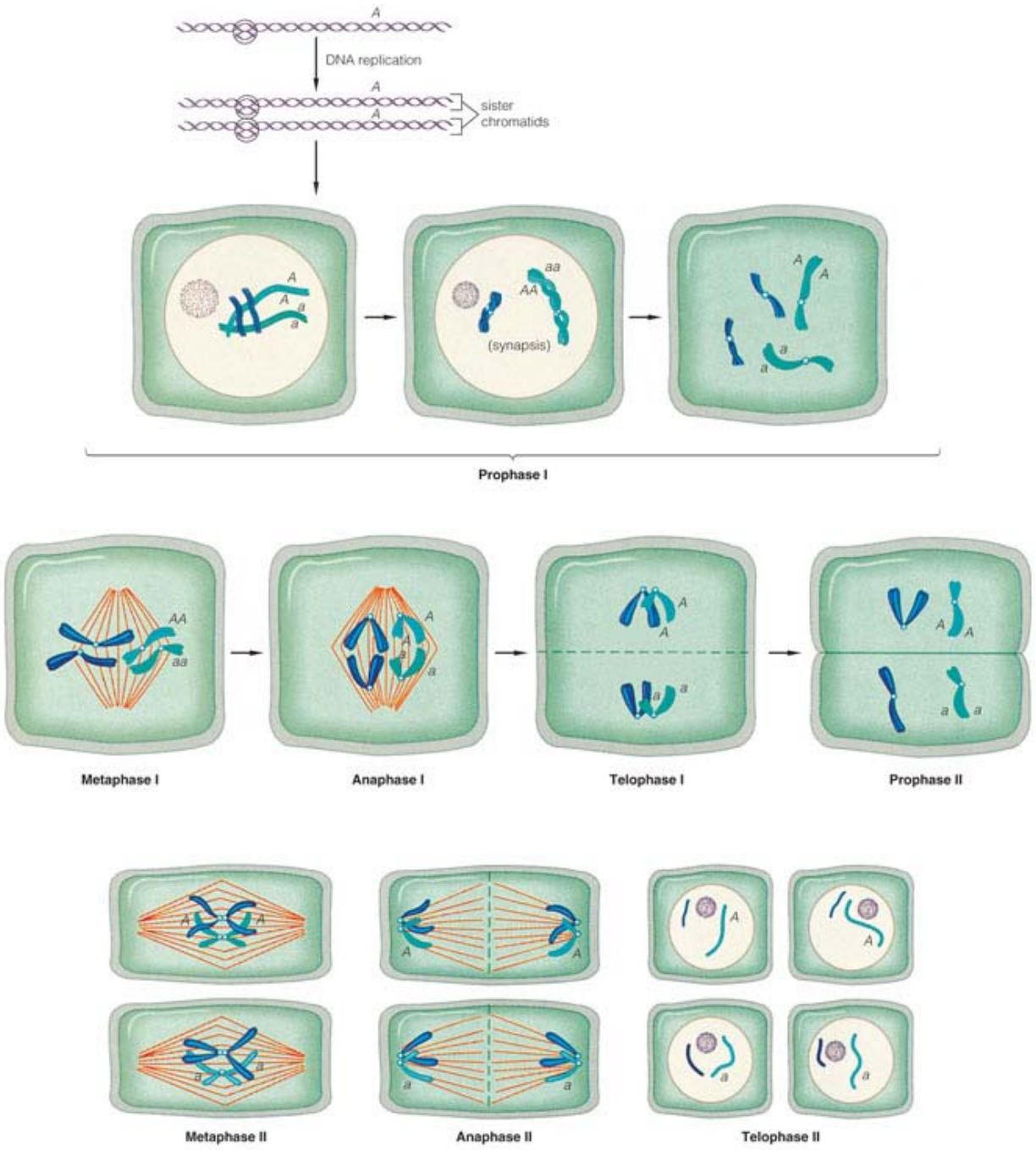


Figure 16.3. the separation of alleles of one gene (one locus on a chromosome) during meiosis. During the preceding S phase, the DNA in each chromosome is replicated. Each sister chromatid has a copy of each gene. During prophase I, the chromosomes condense, and homologous chromosomes come together (synapsis). At this point, there may be an exchange of pieces among the four chromatids in each chromosome pair (see Fig. 16.4). A spindle forms, and during anaphase I, the two homologous chromosomes separate. After intervening stages (telophase I, prophase II), a second division (anaphase II) separates the two sister chromatids of each chromosome.

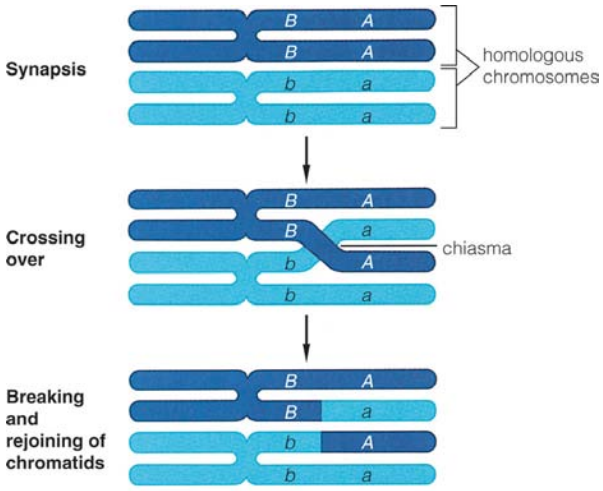


Figure 16.4. Steps leading to the recombination of alleles. Crossing over between two homologous chromosomes during prophase I of meiosis can recombine alleles for the genes on that chromosome. *A* and *a* represent different alleles of one gene; *B* and *b* represent different alleles of another gene. In the crossing over shown, non-sister chromatids exchange *A* and *a* alleles.

**Simple Crosses Yield Predictable Results**

Mendel was not the first person to study heredity, but he was the first to identify clear rules that predicted and explained the inheritance of traits. His conceptual breakthrough was the identification of several individual characters in pea plants, each of which occurred in one of two forms. Mendel grew plants that were identical except for differences in one, two, or three of these characters, so that he could focus on the inheritance of the alleles of their genes.

**SINGLE GENES** The most basic type of genetic experiment involves a mating between two plants that are genetically identical except for one character, in which they express different traits. If the character is controlled by one gene, then the two plants have different alleles for that gene.

An example comes from one of Mendel's experiments. He carefully took pollen from the anthers of a dwarf variety of peas and dusted it on the stigma of a tall variety. The resulting seeds were planted the next season. All the plants that grew from these seeds--called the F1 (first filial) generation--were tall. The same was true when pollen from tall plants was dusted on stigmas of dwarf plants. Then in a second mating, flowers of the tall progeny were self-pollinated; that is, pollen from each flower was dusted on the stigma of the same flower. The seeds resulting from these self-pollinated flowers--the F2 (second filial) generation--produced 787 tall plants and 277 dwarf plants. In other words, about three fourths of these progeny were tall, and one fourth of the progeny were dwarf.

Why were all the plant tall in the offspring of the first mating if one of the parents was dwarf? And how did some of the plants from the second mating come to be dwarf when none of their parents were? These results can be explained by the model shown in Figure 16.5. Because there are two traits for this character, tall and dwarf, we can assume that there are two alleles involved, called *T* (for tall) and *t* (for dwarf). Every adult diploid plant has two copies of each gene because it has two sets of chromosomes. Mendel took pains to make sure that his varieties were genetically homogeneous; therefore, the tall variety had two tall alleles, and the dwarf variety had two dwarf alleles. Geneticists call the visible traits of an organisms its **phenotype** and its collection of alleles its **genotype**. In this case , the plant with the tall phenotype had the genotype *TT*, and the plant with

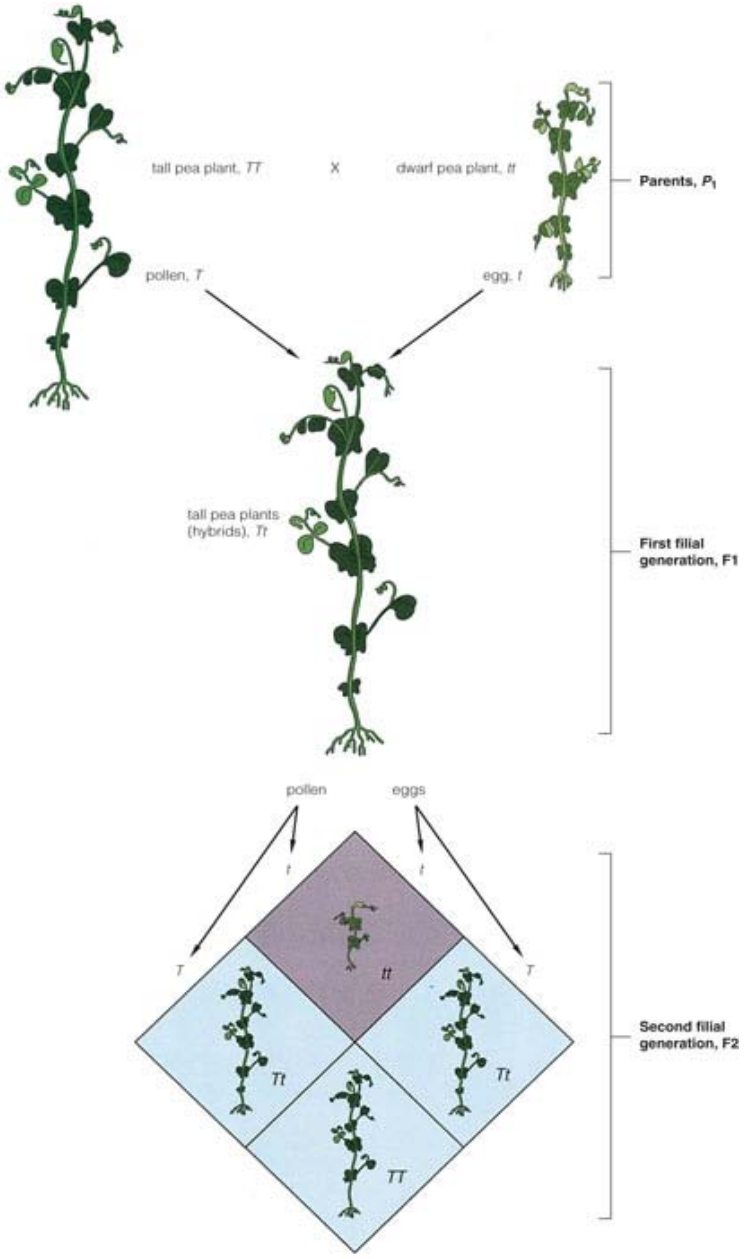


Figure 16.5. Diagram of a cross between tall (*TT*) and dwarf (*tt*) pea plants. All plants in the first filial generation (F1) are heterozygous (*Tt*), meaning that the zygote, and therefore all the cells, have both alleles of the trait, one from each parent. The dwarf allele (*t*) is not outwardly visible in the F1 plants, which all exhibit the tall phenotype. When the F1 plants are self-pollinated, the second filial generation (F2) produces on average three plants with the tall phenotype to every one with the dwarf phenotype.

the dwarf phenotype had the genotype *tt*. Plants with two copies of the same allele are called **homozygous** for that allele because the zygotes from which all of the plants' cells originated had two copies of the same allele. When plants form gametes, every gamete gets one allele from the parent, in this case, *T* or *t*, depending on which parent. Gametes

from a homozygous parent all carry the same allele. The genotype of a zygote is the combination of the alleles from the two gametes that fused to form that zygote.

In the first mating, the progeny all received one *T* allele and one *t* allele, and so they all had the genotype *Tt*. Plants that have different alleles of a gene are said to be **heterozygous**. The model suggests that the progeny all had the same genotype; this fits with the observation that they all had the same phenotype.

But why were they tall, if they had copies of both alleles? To explain why the progeny were tall, we have to assume that the expression of the tall allele in some way overshadowed the expression of the dwarf allele. We say that the tall allele was **dominant**; the dwarf allele was **recessive**. This means that the presence of one *T* allele is enough to produce the tall phenotype. Only a *tt* genotype will produce a dwarf plant.

The relationship among alleles is not always dominant-recessive; for some genes, heterozygous plants show traits that are intermediate between those of the parental homozygotes. In these cases, the alleles are said to be **codominant** or **incompletely dominant.** For instance, in snapdragons (*Antirrhinum majus*), the combination of a red allele and a white allele for the flower color gene produces pink flowers.

To explain the results of the second mating, additional assumptions need to be made. The first assumption is that the two alleles in the *Tt* parent are distributed randomly to their gametes; therefore; half the gametes receive a *T* allele, and half receive a *t* allele. The second assumption is that the gametes fertilize randomly, so that combinations of alleles are formed in proportion to their frequency in the gametes.

According to the model, the *Tt* parent that donated pollen produced half *T* and half *t* pollen. The *Tt* parent that was pollinated produced half *T* eggs and half *t* eggs. At fertilization, there were four combinations, and they occurred in equal proportions. One-fourth had the *TT* genotype, half had the *Tt* genotype, and one-fourth had the *tt* genotype. Because the *TT* and *Tt* genotypes yield tall plants, three-fourths of the progeny were tall; the remaining one-fourth of the progeny were dwarf.

A Punnet square (named for the genetics professor who popularized it) is useful for keeping track of the combinations of alleles formed during fertilization. It is constructed by drawing a square and listing alleles of the male gametes available for the mating along one side of the square and those of the female gametes along the perpendicular side (Fig. 16.5). The combinations of alleles at the intersections of the columns and rows show the expected genotypes of the progeny. The mathematical principles of probability can be used to make quantitative predictions about the phenotypes and genotypes of the progeny (see the endnote "IN DEPTH: Probability and Mendelian Genetics").

Performing this experiment with two plants that differ in one trait constitutes a test of the assumptions we have made. If the progeny of the first cross were not all identical, we would have to abandon the assumption that the parents were homozygous. If the progeny of the first cross were identical, but the proportions of the second cross did not come out 3:1, we would need to question the assumption that the trait was controlled by a single gene.

**TWO GENES** Plants, like other organisms, are guided by thousands of genes acting in concert. The overall phenotype--for instance, the branching pattern of a tree together with the shape of its flowers--is determined by combinations of alleles of many genes, rather than by the allele of a single gene. How are combinations of alleles inherited? Mendel simplified this question by studying the inheritance of pairs of genes.

What will be the result of mating two pea varieties that differ in two characters--for instance, height (tall or dwarf) and form of seeds (round or wrinkled)? Let us assume that we have available a strain of plants that breeds true for tall plants and round seeds and one that breeds true for dwarf plants and wrinkled seeds. When we mate these plants, we will find--as Mendel did--that the resulting progeny are all tall and have round seeds. This fits a model in which one strain has a genotype of *TTRR*--it is homozygous for both the dominant (tall) allele for height and the dominant (round) allele for seed form--and the other strain has the genotype *ttrr*--it is homozygous for the recessive (dwarf) allele for height and the recessive (wrinkled) allele for seed form. The progeny would all have the genotype *TtRr*, representing the combination of the genes from *TR* and *tr* gametes. These are **dihybrid** plants, meaning that these offspring are the combination (hybrid) of plants that differ in their alleles for two genes. Because both the tall (*T*) allele of the height gene and the round (*R*) allele of the seed gene are dominant, all the F1 progeny will have round seeds and will be tall.

What happens when these dihybrid progeny plants are used as parents? When cells undergo meiosis, the alleles from these two genes (*TtRr*) are distributed so that each gamete receives one allele of each gene. There are four possible combinations in the gametes: *TR, Tr, tR,* and *tr*. If the two genes are on different chromosomes (which act independently in meiosis), the alleles will be distributed randomly and the four combinations of alleles will occur in approximately equal numbers. If such a plant is mated with the homozygous recessive parent (*ttrr*), the phenotypes of the progeny will reflect the genotypes of the gametes from the dihybrid (Fig. 16.6)--that is, four different phenotypes will occur in equal numbers. Mating an experimental plant, such as the dihybrid just described, with a plant known to be homozygous recessive in all the genes of interest is called a **test cross**, because the phenotypes of the progeny indicate the genotypes of the gametes from the plant to be tested. It is an easy technique for determining whether combinations of alleles are produced in equal numbers in the gametes of a dihybrid plant.

A more complicated case occurs if we use dihybrid plants for both parents. In this case, there are four possible genotypes for both the male and the female gametes. Combining these genotypes at fertilization gives 16 possible genotypes in the zygote (Fig. 16.7). The Punnett square now becomes a useful tool for arranging the zygote genotypes and grouping the phenotypes for the different genotypes. We find that the mating of two dihybrids gives tall plants with round seeds, tall plants with wrinkled seeds, dwarf plants with round seeds, and dwarf plants with wrinkled seeds in the ratio 9:3:3:1. The 9:3:3:1 ratio is typical for all crosses in which both parents are dihybrid for dominant-recessive alleles for the same two genes.

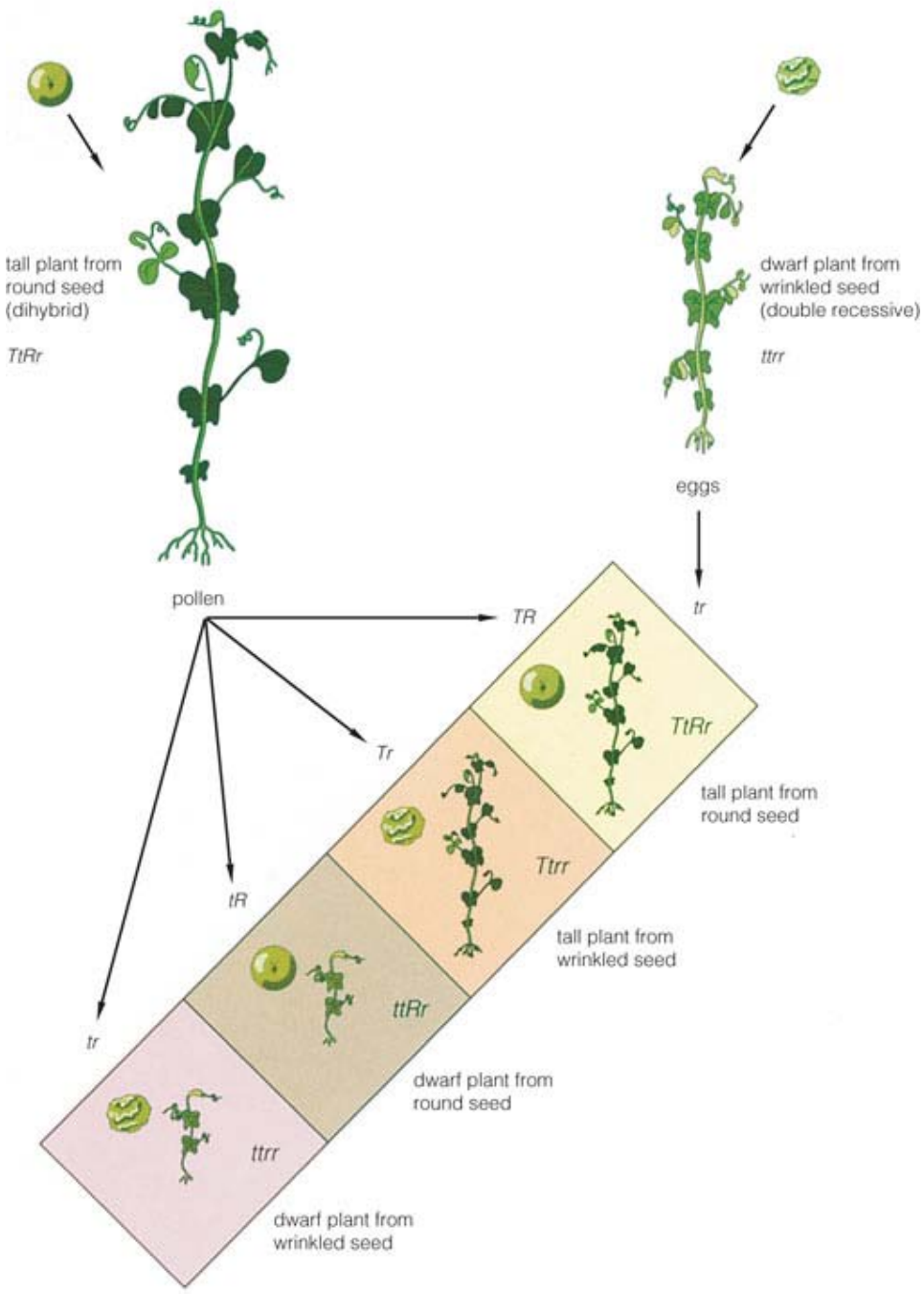


Figure 16.6. Inheritance of combinations of alleles of unlinked genes (genes on different chromosomes. *R* is the round allele for seed shape; *r* is the wrinkled allele. *T* is the tall allele for height; *t* is the dwarf allele. A cross between a dihybrid pea plant, heterozygous for two unlinked genes (*RrTt*), with a plant that is homozygous recessive for both genes (*rrtt*) gives progeny with four different genotypes and phenotypes. The phenotypes of the progeny reflect the genotypes produced by the dihybrid parent.

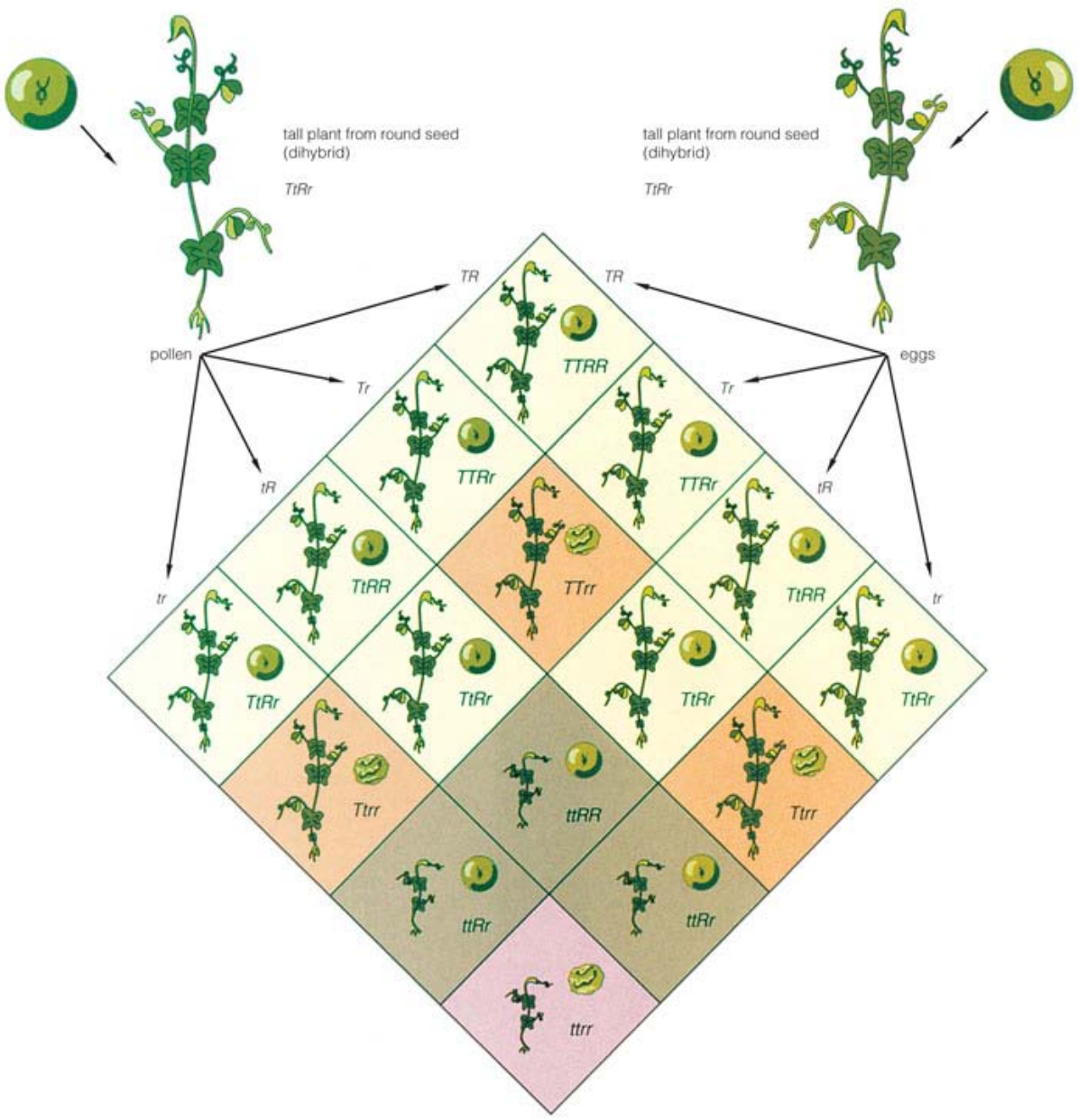


Figure 16.7. Inheritance of combinations of alleles of unlinked genes (part 2). A cross between two dihybrid pea plants, both heterozygous for two unlinked genes (*RrTt*), gives progeny with 16 different possible combinations of alleles and four different phenotypes. Because each of the possible combinations (squares on the Punnett square diagram) is equally likely, the phenotypes are expected to occur in the ratio 9:3:3:1.

Mendel, who knew nothing of meiosis or chromosomes, correctly interpreted data from crosses such as these to mean that pairs of heritable factors assort independently in gamete formation. (This is sometimes called Mendel's Law of Independent Assortment.) Today, it is said that two genes that are independently assorted are *unlinked*, meaning that they are on different chromosomes or that they are so far apart of the same

chromosome that they need not be transferred together during meiosis. The next section explains how two genes on the same chromosome might be independently assorted.

**When Genes Are Linked, Traits Are Inherited Together**

What happens if, in a test cross of a dihybrid plant, equal numbers of the four possible genotypes are not found in the progeny? This result may mean that the two genes are on the same chromosome. In this model (Fig. 16.8), one chromosome of the dihybrid parent carries the dominant alleles of two genes--for example, genes for tendrils and seed shape--and the homologous chromosome carries the recessive alleles. We say that genes are linked because during the formation of gametes, these alleles migrate as a unit rather than independently. So, in an uncomplicated course of events, when the chromatids separate in meiosis, half the gametes receive the two dominant alleles, and the other half receive the two recessive alleles (Fig. 16.8a). The plants that come from round seeds have tendrils; the plants that come from wrinkled seeds do not.

But it is not quite that simple. In prophase I, chromatids may exchange alleles through crossing over (Fig. 16.4). This can result in **recombination**, the formation of chromatids with recombinant combinations of alleles (Fig. 16.8b). In the situation we postulated, in which the two dominant and two recessive alleles are the original (parental) combinations, a recombinant combination of alleles would be the dominant allele of one gene and the recessive allele of the other. Some plants from round seeds will lack tendrils, and some from wrinkled seeds will have them. Notice, however, that the situation could be reversed if different parents had been chosen: the parental combinations could be the dominant allele of one gene and the recessive allele of the other.

The probability of crossover events occurring depends on how close together the genes are on the chromosome. Assuming that crossing over occurs randomly along the chromosome, the farther apart two genes are, the more likely crossing over will occur between them, breaking their linkage and forming recombinant combinations of alleles. However, no matter how far apart the two genes are, the fraction of gametes with recombinant combinations is never greater than the fraction of gametes with the parental combinations of alleles (that is, never greater than 50%).

**Maternal Inheritance Involves Organellar Chromosomes**

Some characters do not follow the rules of inheritance described in the preceding sections. One of these is the response to the herbicide atrazine. Atrazine is a chemical that blocks electron flow in photosynthesis. Most plants are sensitive to it and will die after an atrazine treatment and exposure to light; a few mutant plants, however, show resistance. Atrazine sensitivity ($atr^s$) and atrazine resistance ($atr^r$) are inherited traits. They represent alleles of one gene.

If an atrazine-sensitive stigma is pollinated with pollen from an atrazine-resistant plant, all the progeny plants will be sensitive (Fig. 16.9). If, in contrast, an atrazine-resistant stigma is pollinated with pollen from an atrazine-sensitive plant, all the progeny plants will be resistant. This is not at all what would be expected under the Mendelian model described earlier. Regardless of whether the sensitive allele or the resistant allele was dominant, or both alleles were codominant, the results of these two matings should

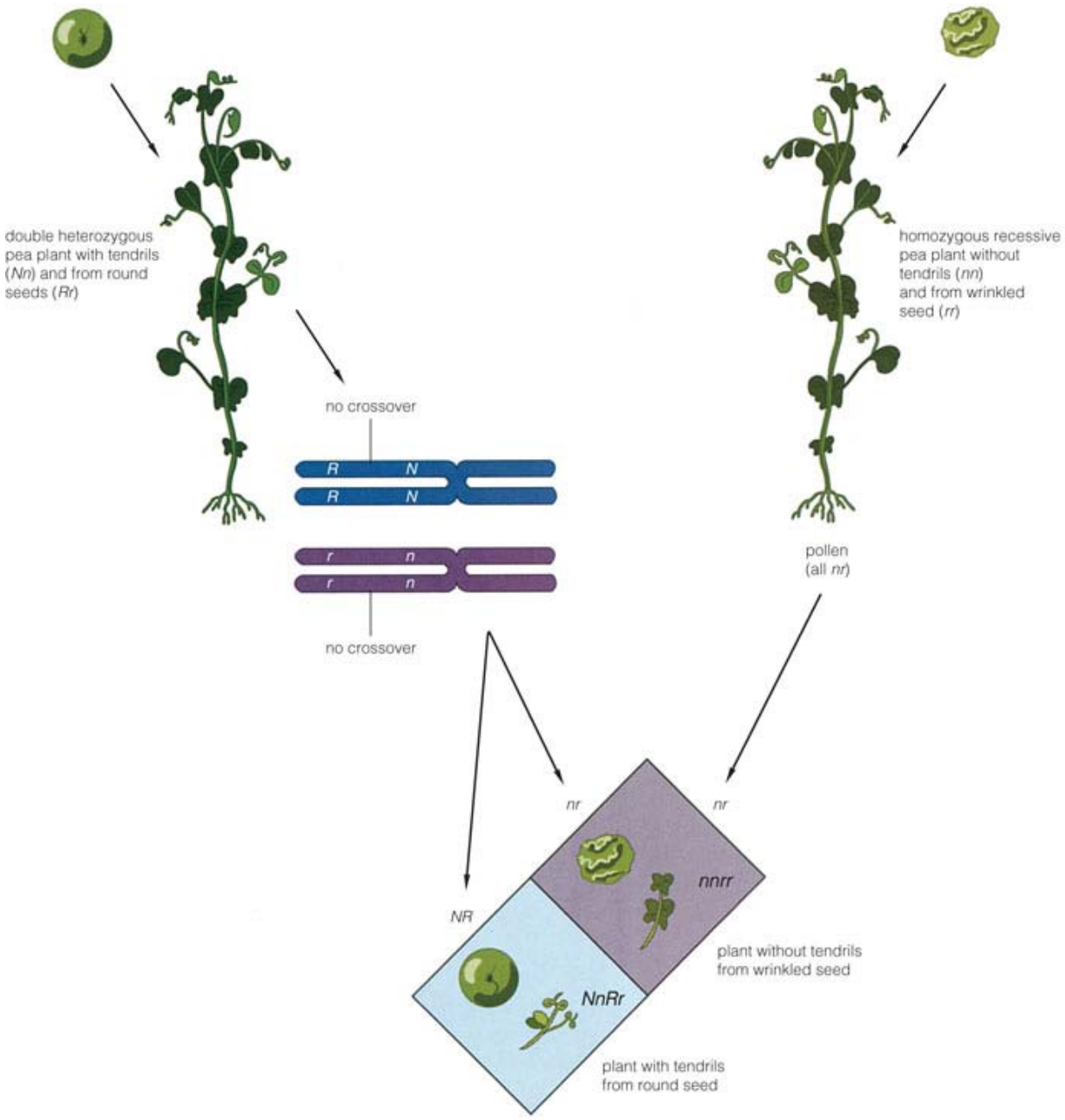


Figure 16.8. Inheritance of linked genes. *N* is the allele for possession of tendrils; *n* is the tendril-less allele. *R* is the round allele for seed shape; *r* is the wrinkled allele. In the cross between a dihybrid pea plant, heterozygous for linked genes (*NnRr*), with a plant that is homozygous recessive (*nnrr*), the parental combinations of alleles (*NR* and *nr*) are passed to gametes together unless crossing over occurs during meiosis. (a) Without crossing over between the *N* and *R* genes in the formation of the pollen (the more common situation). (b) (next page) With crossing over (the less common situation).

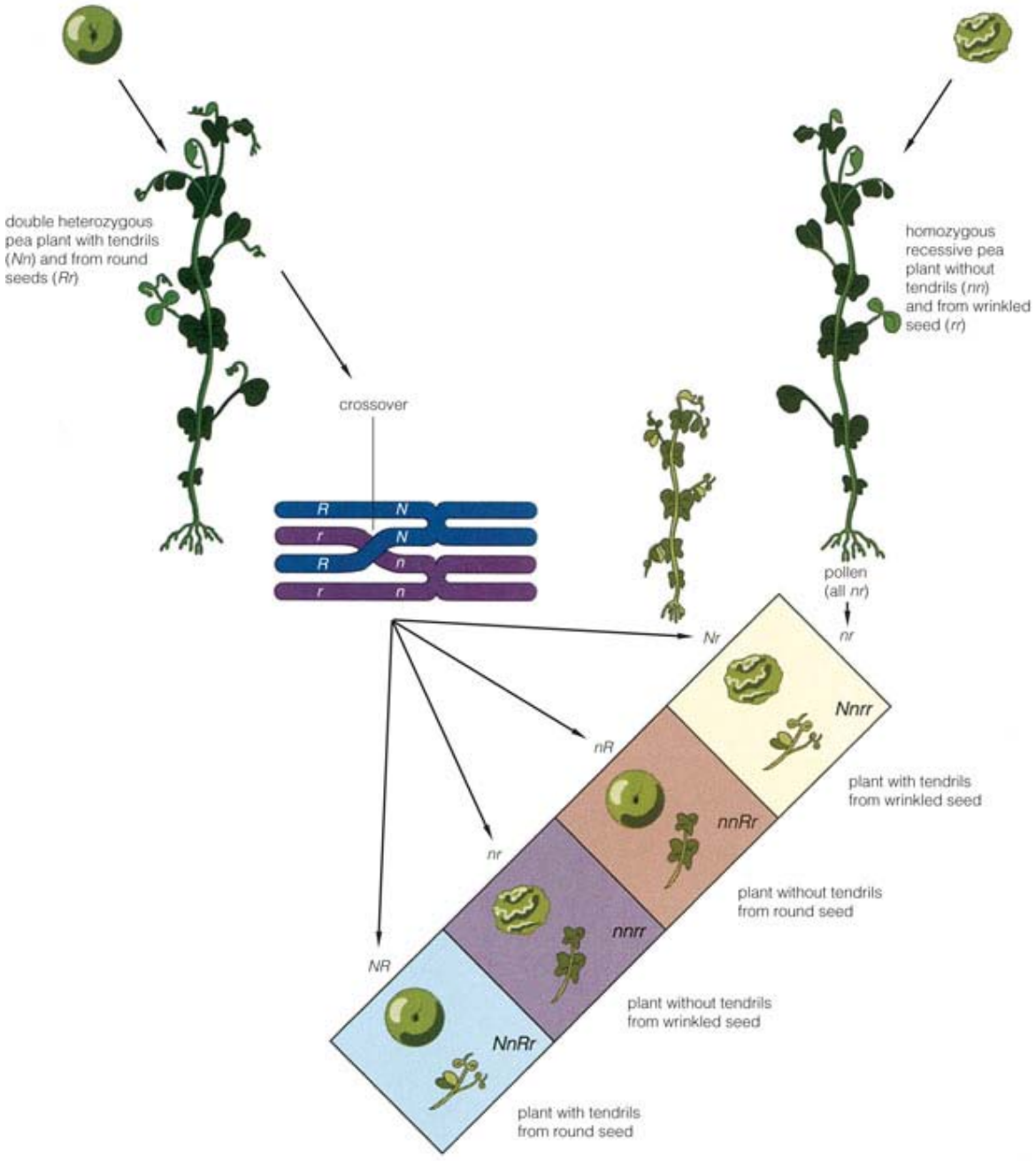


Figure 16.8 (b)

have been the same. Instead, it seems that the progeny inherited their sensitive (or resistance) allele only from the maternal parent.

To explain this unusual type of inheritance, we must recognize that although most of the genes in a plant cell are located on the nuclear chromosomes, not all of them are. There are chromosomes of DNA in the plastids and in the mitochondria, as well. These

organellar chromosomes are smaller than those in the nucleus, and they are different in other ways. But they do contain genes, and those genes can mutate. During fertilization, only the chloroplasts and mitochondria from the egg are incorporated into the zygote. Chloroplasts and mitochondria from the sperm cells either do not enter the egg or degenerate during the fertilization process. Thus, the chloroplast and mitochondrial genes in the zygote all come from the egg, and all the alleles of these genes show maternal inheritance.

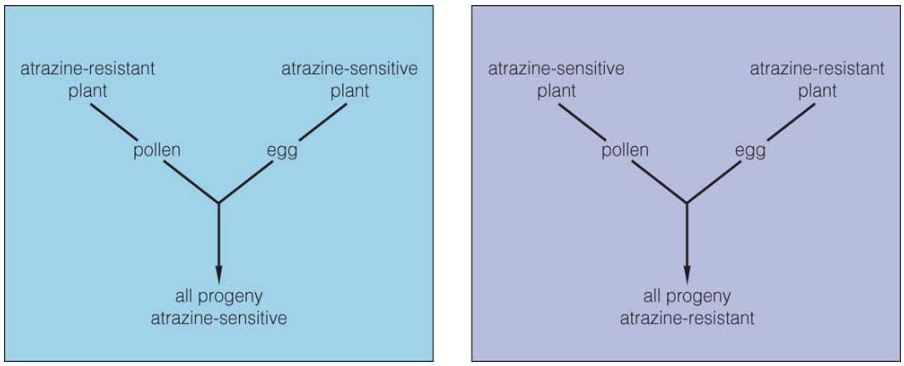


Figure 16.9. Maternal inheritance of a gene. The gene for resistance to the herbicide atrazine is on chloroplast DNA. Chloroplasts and chloroplast DNA in an embryo come only from

## 16.3 PLANT BREEDING

In the last 30 years, the earth's population has doubled. Despite the increase in population, the amount of food produced per person is more than it was in the 1950s. The ability of farmers to increase their output results in great part from the breeding of new, more productive plants. New varieties have been formed with characteristics that make them easier to grow or harvest, with resistance to disease or stress, or with edible parts that are more attractive or nutritious. For instance, modern rice (*Oryza sativa*) varieties are shorter and less likely to fall over when the grain is mature. (Plants hat fall over are difficult to harvest, and their grain is more likely to mold.) Modern tomato (*Solanum lycopersicum*) varieties are bred with resistance to *Verticillium* and *Fusarium* fungi.

### Mating Plants Combines Useful Traits

The principles of genetics are used extensively to develop plants with new and useful traits (Fig. 16.10). However, there are some tricks to plant breeding that go beyond the basic genetic principles.

Suppose we want to breed a tomato variety that will resist infection by a fungus that has recently appeared. We may mate a successful but fungus-susceptible commercial variety with a wild variety that shows resistance but has inedible fruit. If the resistance allele is dominant (let us assume that it is), the progeny will be resistant, but they probably will have inedible fruit. We then would mate the progeny with the commercial variety (a back-cross) and test the progeny of that mating for resistance. By chance recombination, some of the resistant progeny also will have acquired some of the genes needed for edible fruit. The most resistant progeny would again be mated with the commercial variety, and the most resistant progeny again selected. After several cycles, a strain that has both commercial fruit and resistance to the fungus would result.

**Multiple Genes Explain Continuous Variation**

The traits discussed in the previous paragraphs occur in one of two (or three or four) forms; there are said to have *discrete variation*. Many important traits, however, vary continuously over a certain range; these are said to have *continuous variation*. Examples in crop plants are size of the harvested organ (Fig. 16.11), sugar content, or firmness of the fruit.

Figure 16.10. Breeding trials for maize varieties at a research farm of Pioneer Hi-Bred International, Inc. Each plot represents a different stage in the development of a new variety or a test of different varieties under different conditions (for example, soil type or amount of fertilization or irrigation).

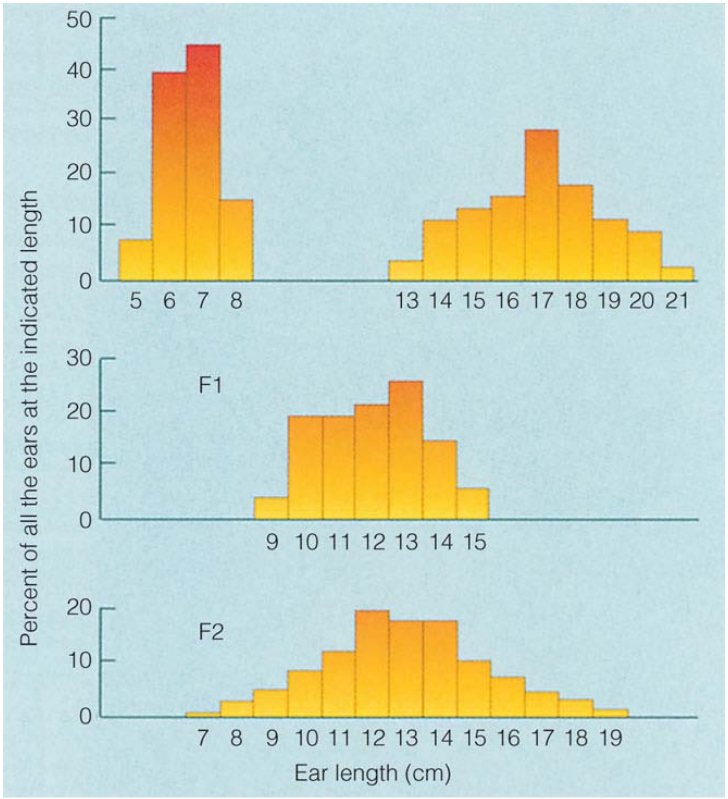


Figure 16.11. Distribution of ear lengths among two maize varieties and their progeny. Both of the parental varieties (top) and the F1 (middle) and F2 (bottom) progeny show wide and continuous variation in ear lengths, probably because several genes contribute to the trait.

There are several factors that can lead to a continuous variation. First, the most important factor is the involvement of multiple genes, each of which influences the trait of interest. Individually, alleles of the different genes may have rather small effects on the phenotype. Together, they can combine to provide a wide range of variation. If there are many genes, there are many combinations of alleles, and this situation leads to a distribution of phenotypes in which the differences among any individual forms are small, relative to the total range of possibilities. Genetic experiments have shown that the length of the corolla of a *Nicotiana* flower is controlled by at least four genes. Second, sometimes a gene has multiple alleles, each with a different degree of activity. The *R* gene of peas occurs in several allelic forms, which give different seed colors. Third, environmental effects may alter the form of the phenotype. For instance, crowded conditions produce shading and tend to make bean plants grow longer internodes; hot, dry conditions will give grape berries a greater sugar concentration. The randomness of environmental effects tends to blur the distinction among genotypes.

The inheritance of multiple genes involved in a continuously variable trait is not different from that of other genes. Alleles can be combined by mating plants with different phenotypes, and progeny can be selected on the basis of their phenotypes for further matings with one another. It must be recognized, however, that if the number of genes is unknown, how many genes are heterozygous and how many are homozygous also is unknown. Obtaining a strain in which all the relevant genes are homozygous may be important (such a strain will breed true). But with a continuously variable trait it may be difficult to tell when this has been achieved.

**Heterosis Can Give Vigorous Progeny**

It is sometimes found that the progeny from the mating of two inbred (highly homozygous) strains are much larger and healthier than either of the parents. This effect is called **hybrid vigor** or **heterosis**. Most corn (*Zea mays*) planted in the United States comes from hybrid seed. It poses a special problem for breeders because hybrids (heterozygotes) do not breed true--that is, then mated with themselves, they produce both heterozygous and homozygous progeny.

One solution is to produce new hybrid plants solely through vegetative reproduction. Potato (*Solanum tuberosum*) varieties that are reproduced by germinating buds cut from potato tubers all have the same genotype as the plant that produced the tubers.

Another solution is to produce hybrid seed by mating two homozygous strains. To do this, seed companies have developed strains that are male-sterile: they do not produce anthers or viable pollen. When a homozygous male-sterile strain of corn is planted close to another homozygous strain, it gets pollen only from the other strain, and all its seed will be heterozygous.

**Plants Often Are Polyploid**

In contrast to animals, plants become polyploid relatively easily. **Polyploidy** means having more than two sets of chromosomes. This may occur spontaneously, when a cell reduplicates its DNA and separates the resulting chromatids, but then fails to complete cell

division. This commonly occurs in the last stages of development of tracheary elements and storage tissues, although it is less common in the meristems. If a meristematic cell becomes polyploid, the new nucleus, with twice the original number of chromosomes (tetraploid, if the parent cell was diploid), can undergo new rounds of DNA synthesis and mitosis. It may take over the meristems and produce a shoot whose cells are all polyploid. The cells are still capable of undergoing meiosis; therefore they can form spores, and the spores can form gametes. If a polyploidy plant fertilizes itself, its progeny also will be polyploid.

Plant breeders have found that polyploid plants often are larger and more vigorous than their parental types. They also have found that certain chemicals that interfere with the formation of the spindle in mitosis (colchicine, for example) can increse the probability of forming polyploid cells. These chemicals have been used to produce new horticultural varieties. In nature, polyploids seem more tolerant of such environmental stresses as short, cool growing seasons, aridity, or high temperatures.

In plants, it is sometimes possible for different species to interbreed--that is, to form viable progeny. Often, the original progeny are sterile, but they can become fertile if their cells become polyploid (Fig. 16.12). The most important requirement for fertility is successful meiosis, and this requires that each chromosome be present in two copies. This is automatically true in a polyploid cell. The common bread wheat (*Triticum aestivum*) is hexaploid, having six copies of each chromosome, and it is thought to have arisen in the Middle East by hybridization of three species from two related genera.

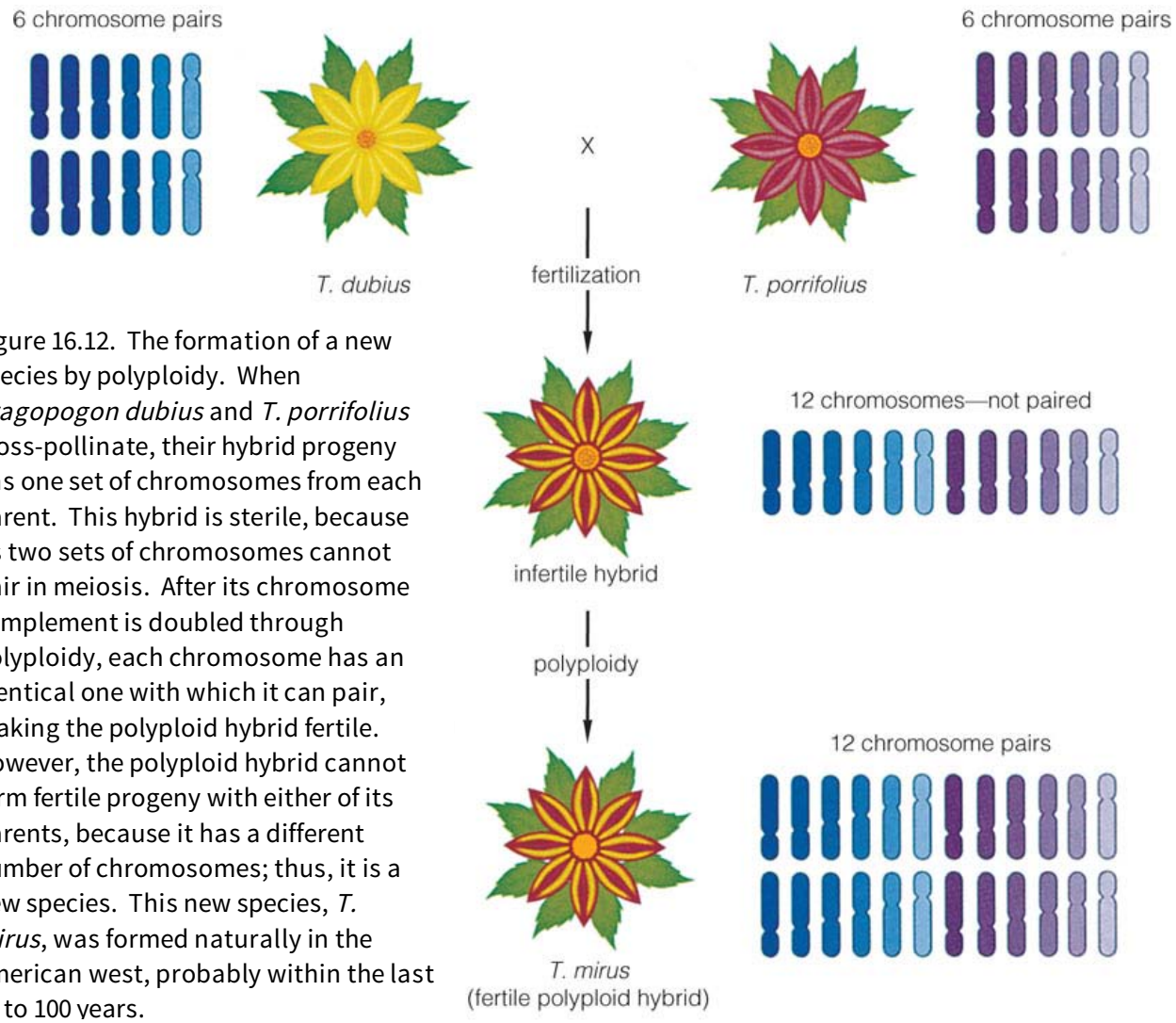


Figure 16.12. The formation of a new species by polyploidy. When *Tragopogon dubius* and *T. porrifolius* cross-pollinate, their hybrid progeny has one set of chromosomes from each parent. This hybrid is sterile, because its two sets of chromosomes cannot pair in meiosis. After its chromosome complement is doubled through polyploidy, each chromosome has an identical one with which it can pair, making the polyploid hybrid fertile. However, the polyploid hybrid cannot form fertile progeny with either of its parents, because it has a different number of chromosomes; thus, it is a new species. This new species, *T. mirus*, was formed naturally in the American west, probably within the last 50 to 100 years.

**KEY TERMS**

alleles
base sequences
characters
chiasma
chromatids
chromatin
chromosomes
codominant
crossing over
dihybrid
dominant
genes
genetics
genome
genotype
heterosis
heterozygous
homologous
homozygous
hybrid vigor
incompletely dominant
locus
mutant
mutation
phenotype
polyploidy
recessive
recombination
test cross
trait
wild-type

**SUMMARY**

1. The characters of plants are controlled by genes. Different alleles of a gene (mutant or wild-type) produce different traits, alternate forms of the character. The alleles, and thus the traits, are inherited.

2. Chemically, genes are made of DNA, and they control the production of proteins, which serve many functions in the cell.

3. Mutations are changes in the base sequence of the DNA. The modified base sequence may then change the amino acid sequence of an enzyme, or it may affect the rate or timing of expression of another gene.

4. Each gene is found at a particular locus on a chromosome. Different plants have different numbers of chromosomes, but each diploid cell in a plant has two copies of each chromosome.

5. Mitosis preserves the number of chromosomes and the alleles that are found on each chromosome. Vegetative reproduction occurs through mitosis and yields progeny that are genetically identical to the parent plant.

6. The sexual life cycle is dependent on meiosis. In meiosis, the two alleles of a gene in the diploid cell segregate (separate), so that half the haploid gametes receive one allele from the parent and half receive the other allele.

7. If two genes are on different chromsomes, the segregation of the alleles of one gene does not affect the segregation of the alleles of the other. This means that if there are four possible combinations of alleles from the two genes, each combination is equally likely, and one-fourth of the gametes will receive each combination.

8. If two genes are linked (on the same chromosome), they tend to move into a gamete as a unit, rather than separately. The result is that the two parental combinations of alleles are more likely to occur in gametes than the two recombinant combinations of alleles. Recombinant combinations of alleles can be formed by crossing over of chromatids during meiosis.

9. Genetic techniques can be used to combine useful alleles of different genes in agricultural plants, even if the relationship between genes and traits is not simple.

10. Continuously variable traits can be explained by the influence of multiple genes, by the possibility of several different alleles, and by environmental effects. Even if a desired trait is controlled by several genes, a series of matings (with careful selection of progeny) can usually isolate plants with the desired combination of alleles.

11. Hybrids (heterozygotes) often are particularly vigorous. Special techniques are needed to produce hybrid seed for agricultural use.

12. Polyploidy (formation of plants with more than two chromosomes of each type) sometimes produces particularly vigorous plants. Polyploidy can also allow hybrids of distantly related plants to be fertile and form new plant species.

***Questions***

1. Provide the appropriate terms:
   a. Gene is to character as _____ is to trait.
   b. Phenotype is to character as genotype is to _____.
   c. A base sequence is to a gene as _____ is to a protein.
   d. _____ chromosomes have similar sets of genes.
   e. _____ organisms have two identical alleles for one gene.
   f. _____ organisms have two different alleles for one gene.
   g. A new allele can be produced by _____.
   h. A new combination of alleles can be produced by _____ during meiosis.

2. Trace the pathway by which information in the genes becomes a visible trait by listing (in order) the processes that must occur.

3. Some wild radish plants have white flowers, whereas others have yellow flowers. Explain what you would do to determine whether the flower color is controlled by one gene with two alleles.

4. Explain why it takes plant breeders many growing seasons to produce a new variety of crop plant (for instance, and tomato plant) with both desirable fruit and a new useful trait, such as disease resistance.

***Genetics Problems***

The abstract but regular nature of heredity has led biology teachers to adopt a tradition of assigning word problems in genetics. Following are some problems, all concerning plants, that will test your understanding of the concepts described in this chapter.

1. In peas, the dominant allele of the $A_1$ gene for flower color gives red flowers; the recessive allele $a_1$ (when homozygous) gives white flowers. Which is more likely: two plants with red flowers producing progeny plants with white flowers, or two plants with white flowers producing progeny plants with red flowers?

2. The wild-type dominant allele of the *ein* gene in a mustard plant produces phytochrome, and the phytochrome regulates growth so that the plants have normal-length internodes. The recessive allele is associated with elongated internodes. In a greenhouse full of normal-sized mustard plants, one plant stands higher than the rest. If you assume that the increased height of this plant is because of a mutant allele of *ein*, then do you also assume that the plant is homozygous or heterozygous for this allele?

3. The color of pea cotyledons is controlled by several genes. One gene (probably the one that Mendel studied) has a dominant allele that suppresses the green color and gives yellow cotyledons. The recessive allele gives green cotyledons when it is homozygous. Assume that this is the gene involved in the following problem: A plant that grew from a green seed is pollinated with pollen from a yellow-seeded plant; a yellow seed from this mating is grown, and the resulting plant is pollinated with pollen from a plant that grew from a green seed. When the pods from this second mating mature, what proportion of the seed will be yellow? What proportion will be green?

4. A geneticist collected seeds from a pea plant whose genetic constitution she did not know. All the seeds had yellow cotyledons. One pea plant, which grew from one of those yellow seeds, self-pollinated; the first pod she opened had one green and nine yellow seeds. She then collected 100 more seeds. Of those 100, how many did she expect would be green? Would she expect the same proportion of green seeds in a second self-pollinated plant grown from another of the original yellow seeds?

5. The flower color of sweet peas is controlled by two genes, *C* and *P*. To have red flowers a plant must have a dominant allele of each gene (for example, *CCPP, CCPp, CcPp, CcPP*; note that the dominant alleles are capitalized). If a plant has two recessive alleles for either or both genes (for example, *ccpp, ccPP, CCpp, ccpP, Ccpp*), its flowers will be white. Two white plants were mated, and they produced 100% red-flowered progeny. What were the genotypes of the parents?

6. In corn, the genes for red endosperm and shrunken endosperm are unlinked. The dominant allele of the red gene gives red seeds (*RR, Rr*); homozygous recessive seeds (*rr*) are yellow. The dominant allele of the shrunken gene gives normal-shaped seeds (*ShSh, Shsh*); homozygous recessive seeds (*shsh*) are shrunken. A plant that is heterozygous for the red gene and homozygous recessive for the shrunken gene is used to pollinate the silks (stamens) of a plant that is homozygous recessive for the red gene and heterozygous for the shrunken gene. What will be the genotypes and phenotypes of the seeds in the resulting cob, and in what proportions will they be expected to appear?

7. A corn plant that is heterozygous for three genes (*AaBbCc*) is crossed with a plant that is homozygous recessive for all three genes (*aabbcc*). Four phenotypes of progeny seedlings are found, in equal numbers. The four phenotypes correspond to the following combinations of alleles: *ABC, aBC, Abc, abc*. Which genes are linked, and which are unlinked?

8. In corn, the gene for red endosperm, *R*, is located on the same chromosome as the gene for white seedling, *W2*. A test cross of a plant that was heterozygous for the two genes with a homozygous recessive plant produced progeny with the following genotypes and in these numbers: *RrW2w2*, 20; *Rrw2w2*, 172; *rrW2w2*, 180; *rrw2w2*, 28. (*R* and *W2* are the dominant alleles; *r* and *w2* are recessive.) Draw a diagram of the homologous chromosome in the heterozygous parent, showing which alleles were on which chromosomes. (That is, show the parent combinations of alleles.) What fraction of the pollen produced by the heterozygous parent was recombinant?

9. As a breeder of tomatoes, you have discovered a strain of wild tomato that is resistant to a destructive virus. The resistance is controlled by the dominant allele of a single gene (*Rv*). Unfortunately, the wild tomato has bad-tasting fruit and other undesirable traits; therefore , you want to breed a domestic tomato with only the resistant gene from the wild strain. You cross the wild tomato with a domestic tomato (cross 1) and select resistant progeny; you cross the progeny from the first cross with the domestic tomato (cross 2) and select resistant progeny; and so on. What fraction of the progeny of cross 1 will be resistant? Of cross 2? Of cross 10? What fraction of the progeny of cross 1 will have alleles from the wild tomato of genes unlinked to *Rv*? Of cross 2? Of cross 10?

10. Several years ago, corn geneticists isolated a mutant in which anthers did not develop. The mutant was called *male-sterile*. They pollinated this mutant with wild-type pollen; all the resulting plants were also male-sterile. They pollinated these plants with wild-type pollen; all these progeny plants also were male-sterile. At this point, the geneticists decided that the gene for male-sterility was maternally inherited. Explain why they drew this conclusion.

**IN DEPTH:** *Probability in Mendelian Genetics*

One of Mendel's most important innovations was his use of the concepts of mathematical probability and statistics in the study of heredity. These concepts, first developed by Blaise Pascal and Pierre de Fermat to analyze games of chance, can be applied to any event or experiment in which the results are subject to both random fluctuations and well-ordered processes. The purposes of such application are to separate the well-ordered features of the experiment from the random features, to identify the patterns that the experiment follows, and to use these patterns to predict future results.

A critical concept in probability is the idea of the *outcome* of an event or experiment. The outcomes are unit results, only one of which can occur at any one trial of the experiment and all of which together constitute all possible results of the experiment. If we toss a coin to see which side lands up, the outcomes are "heads" and "tails." If we mate two parents and observe the sex of a resulting offspring, the outcomes are "male" and "female."

A basic operation in the analysis of probability is to assign numbers to each of the various outcomes, numbers that indicate our feeling about the likelihood that each outcome will occur. If we are certain that a particular outcome will occur, we assign it a probability of 1.0 (denoted $P = 1.0$); if we are certain that an outcome will not occur, we assign it a probability of 0.0 ($P = 0.0$); if we feel an outcome will occur half the time, we assign it a probability of 0.5 ($P = 0.5$).

Some of the principles useful in assigning and interpreting numerical probabilities are described below, together with examples taken from problems in Mendelian genetics.

1. In an experiment with $n$ equally likely outcomes, the probability of the occurrence of any one outcome is $1/n$.

Example: In the mating of two hybrid plants with genotypes *Gg*, a Punnett square diagram indicates that the progeny may have any of four different genotypes (that is, outcomes): *GG*, *Gg*, *gG*, and *gg*. The probability of any one occurring is ¼.

2. If the probability of a particular outcome is $1/n$, then in a large number of trials, that outcome will tend to represent $1/n$th of the total.

Example: In the experiment described above, the probability of finding the *gg* genotype in any one seed is ¼. If we looked at 1,000 progeny seeds, we would expect to find ¼(1000) = 250 seeds with the *gg* genotype. We also would expect to find 250 seeds each with the *GG*, *Gg*, and *gG* genotypes. Notice, however, that if we look only at small numbers of seeds, we should not be surprised if the outcomes do not reflect their respective probabilities. If we look at 10 seeds, we do not expect 2.5 seeds with each genotype; if we

look at 100 seeds, we do not expect *exactly* 25 seeds with each genotype. But the more seeds we consider, the closer the relative frequency of appearance of each genotype should be to its probability.

3. The probability of an occurrence represented by two or more different (mutually exclusive) outcomes is the sum of the probabilities of the separate outcomes.

Examples: Assume that the experiment above refers to seed color. The dominant allele, *G*, give yellow seeds; the recessive allele, *g*, gives green seeds when present in a homozygote. The occurrence, "A seed is yellow," is represent by three different outcomes, the genotypes *GG*, *Gg*, and *gG*. The three outcomes are mutually exclusive because only one can occur in any one seed. The probability that a seed is yellow, therefore, is the sum of the probabilities for these three genotypes.

$P$(seed is yellow) = $P(GG) + P(Gg) + P(gG) = ¼ + ¼ + ¼ = ¾$

Likewise, the probability that the seed is heterozygous is:

P(seed is heterozygous) = $P(Gg) + P(gG) = ¼ + ¼ = ½$

4. If the probability of a certain outcome in one experiment is $1/n_1$, and the probability of another outcome in a second (independent) experiment is $1/n_2$, the probability that *both* outcomes will occur is $(1/n_1)(1/n_2)$.

Examples: In the experiment describe above, the probability of finding a green seed, genotype *gg*, is ¼; the probability of finding a yellow seed, genotype *GG* or *Gg* or *gG*, is ¾. Each seed represent an independent mating event, so the probability that the first seed investigation is green *and* the second seed investigated is yellow is:

$P$(first seed green *and* second seed yellow) = $P(gg) \cdot P(GG$ or $Gg$ or $gG)$

$= ¼ \cdot ¾ = 3/16$

The probability that the first seed, the second seed, and the third seed are all green is:

P(first seed green *and* second seed green *and* third seed green) = P(gg) · P(gg) · P(gg)

$= ¼ \cdot ¼ \cdot ¼ = 1/64$

**BIOTECHNOLOGY:** *Plant Breeding and the Green Revolution*

In 1970, the Nobel Peace Prize was awarded to Norman Borlaug, a plant breeder and plant pathologist who, funded by the Rockefeller Foundation, had started a program of breeding high-yield corn and wheat in Mexico. His ideas about breeding, irrigation, and fertilization spread throughout much of the world. Internationally recognized centers such as CIMMYT (the abbreviation of the Spanish name for the International Maize and Wheat Improvement Center) in Mexico and IRRI (International Rice Research Center) in the Philippines produced new varieties that tripled yields between 1950 and 1990. The director of the United States Agency for International Development coined the term *Green Revolution* to point out the spectacular increases in productivity resulting from the application of scientific knowledge to farming.

Much of the advantage of the new varieties of wheat and rice came from breeding for a seemingly simple morphological change: height. The original varieties grew very tall. It is possible that height gave these plants an evolutionary advantage in dispersing pollen, because their flowers are at the top of the stalk and their pollen is carried by the wind. However, there is an agricultural disadvantage to tall grasses. They tend to fall over ("lodge") when disturbed by wind, rain, animals, or when they are too crowded. The Green Revolution breeding programs selected much shorter plants. These resisted lodging, and the extra energy not used in growing upward could be used to produce more seed mass.

Another advantage from breeding programs lies in the development of pathogen resistance. Fungi and bacteria can account for the loss of a large fraction of a wheat or rice harvest. There are, however, strains that develop resistance to infection by a specific pathogen, and the genes that produce the resistance can be transferred to varieties in combination with other desirable traits. This is an ongoing activity, because new fungal or bacterial strains that overcome the resistance continually arise through mutation, recombination, and natural selection. One of the goals of biotechnologists (see Chapter 17) is to analyze the molecular mechanisms of resistance and develop methods that are less easily circumvented by pathogen evolution.

A plant breeding project starts by identifying genetic plants with new or improved traits. These might come from spontaneous mutations in a population of crop plants, from chemical or physical mutagenic treatments, or from wild relatives. To find wild plants with useful traits, it is important to know the center of origin of the crop of interest (Figure below). Once a plant with a valuable trait is located, it is crossed to the best crop plants, and progeny with the desired trait are selected for subsequent matings ("backcrosses") to the crop. It is important to perform many cycles of backcrosses to ensure that the valuable traits of the crop plant are not lost. Because the desired trait may be recessive, or even dependent on several alleles, so that its phenotype does not appear in the initial progeny, it may be necessary to use molecular techniques for selecting plants with the appropriate alleles. Chapter 18 discusses some useful molecular methods for selection.


Maize, bean,
squash, pepper,
cotton, cacao
Potato, cassava,
bean, cotton, pepper,
peanut, pineapple
Sorghum melon,
coffee, oil palm
Wheat, barley,
pea, lentil
Rice, peach,
soybean, tea
Rice, banana,
sugar cane,
coconut, cucumber

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CO http://www.itsokaytobesmart.com/post/23169485289/genetics-of-the-beautiful-glass-gem-corn-corn
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