Mendelian Genetics

25

A young snow leopard relaxes with his mother on a quiet afternoon. Look closely and family resemblances become clear. Compare the shape of their mouths and the pattern of black markings. The young leopard watches the landscape with the same confident eyes as his mother. You might say that he even has her nose. Family members often look alike, but why? How are traits passed from parent to offspring? This chapter will introduce you to the laws of heredity—the laws that explain how traits are passed from generation to generation.

Guide for Reading

Key words: genetics, dominant, recessive, gene, alleles, homozygous, heterozygous, genotype, phenotype

Questions to think about:

- What conclusions did Mendel reach from his experiments on pea plants?
- What laws govern how traits are inherited?
- How is the phenotype of an organism related to its genotype?

25-1 Mendel's Principles of Heredity

Section Objectives:

- *Describe* the experimental procedures that were used by Gregor Mendel.
- *State* and *give* an example of Mendel's law of dominance and his law of segregation.
- *Explain* Mendel's law of segregation in terms of chromosomes and meiosis.

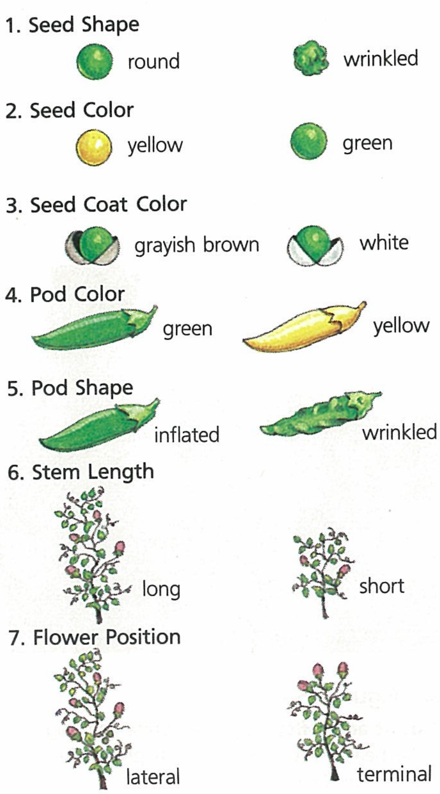
The Study of Heredity

In sexual reproduction, the new individual develops from a single cell—the zygote—which was formed by the union of two gametes, one contributed by each parent. The chromosomes of each gamete bring hereditary material to the new cell. This hereditary material controls the development and characteristics of the embryo, as well as determining the features of the adult organism. Because the hereditary material comes from two different parents, the offspring is similar to both parents in some ways but differs from both parents in other ways. The offspring has all the common characteristics of its species, but it also has its own distinct, individual characteristics that make it different from all other members of the species.

▲ **Figure 25–1**
Parent and Offspring. The white coloring of polar bears is hereditary. All offspring inherit traits from their parents.

Figure 25–2
Sugar Pea Flowers. The pea plant was the experimental subject in the first scientific study of heredity. ▶

Figure 25–3
Seven Traits Studied by Mendel. Mendel used pea plants to study seven pairs of contrasting traits. ▼



Genetics (juh NET iks) is the branch of biology that studies the ways in which hereditary information is passed on from parents to offspring. The first scientific study of heredity was carried out by Gregor Mendel (MEN dul) in the 1800s, before much was known about either chromosomes or cell division.

Mendel's Experiments

Gregor Mendel was a monk who was interested in mathematics and science. Mendel lived in a monastery in the town of Brünn in what is now Czechoslovakia. For a while, he taught science at the local high school. From 1857 to 1865, Mendel investigated the inheritance of certain traits in pea plants grown in the monastery garden. After many experiments, Mendel arrived at some basic principles of heredity that are still accepted today.

Pea plants were a good choice for Mendel's investigations. They are easy to grow, and they mature quickly. Different plants show sharply contrasting traits. For example, some are tall; some are short. Some have green pods; some have yellow pods. Each pair of traits is easily seen. In addition, the structure of the pea flower and its natural method of pollination make it easy to use in controlled experiments. Pea flowers normally self-pollinate because the stigma and anthers are enclosed by the petals, as you can see in Figure 25-2. This reduces cross-pollination in nature. By removing the stamens before they ripened, Mendel could prevent self-pollination and cross-pollinate the flower by dusting pollen from another plant onto the stigma. If he wanted certain plants to self-pollinate in the normal way, he left them alone.

Mendel kept careful records of what he did to each generation of plants. He collected the seeds from each experimental cross, and then he planted them in a definite place so that he could see the results. Mendel made a careful count of each type of offspring, and he used mathematics to understand the results. It was this use of mathematics that allowed him to draw the important conclusions that he did.

Mendel wrote a paper about his discoveries. It was published in the journal of his local scientific society and sent to other scientific organizations and libraries. Other scientists, however, do not seem to have understood its importance at the time. Mendel died in 1884, without receiving recognition for his discoveries. In 1900, however, three European scientists, all working separately, reached the same conclusions about heredity that Mendel had. Before they published their works, they read through the past scientific literature and found Mendel's papers. They gave him credit for his discoveries, and Mendel finally received the recognition he deserved.

The Law of Dominance

Mendel noticed that pea plants have certain traits that come in two forms. For example, plants are either tall or short, seeds are either yellow or green, and so on. In his experiments, Mendel studied seven pairs of contrasting traits. See Figure 25–3.

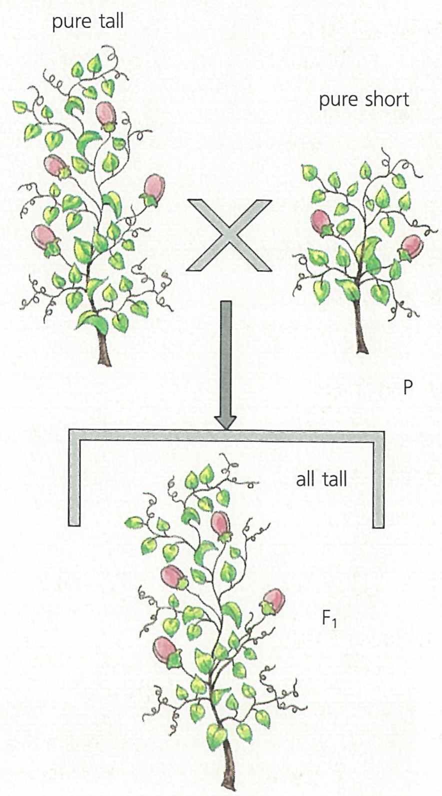
Mendel discovered that some plants "bred true" for a certain trait. For example, when short plants were allowed to self-pollinate through several generations, the offspring were always short. Mendel considered these plants to be pure for shortness. In his experiments, Mendel always started with plants that he knew were pure for the trait in which he was interested.

Mendel then wanted to find out what would happen if he cross-pollinated pure plants with contrasting traits. To do this, he stopped self-pollination by removing the stamens from a plant that was pure for one trait. He pollinated that plant with pollen from a plant that was pure for the contrasting trait. For example, he pollinated short plants with pollen from tall ones, and he pollinated tall plants with pollen from short ones. In these experiments, the pure plants made up the **parent,** or **P, generation.** Mendel collected the seeds produced by this cross-pollination, planted them, and allowed them to grow. Mendel found that all the offspring of this cross were tall. See Figure 25–4. That is, the short trait seemed to have disappeared in the **first filial,** or **F_1, generation.** The same kinds of results were obtained for all seven of the pairs of contrasting traits that Mendel investigated. The offspring of crosses between pure parents showing contrasting traits are called **hybrids.** In Mendel's experiments, the hybrids showed only one of the contrasting traits and not the other.

Mendel wanted to know if the trait of shortness had been lost forever as a result of the cross. To answer this question, he allowed the hybrid plants of the F_1 generation to self-pollinate. See Figure 25–5. When their seeds were planted and grown, about three-fourths of the offspring were tall and about one-fourth were short. The offspring of the self-pollinated hybrids made up the **F_2 (second**

Figure 25–4

A Cross of Pure Tall and Pure Short Pea Plants. All offspring in the first filial (F_1) generation are tall. ▼



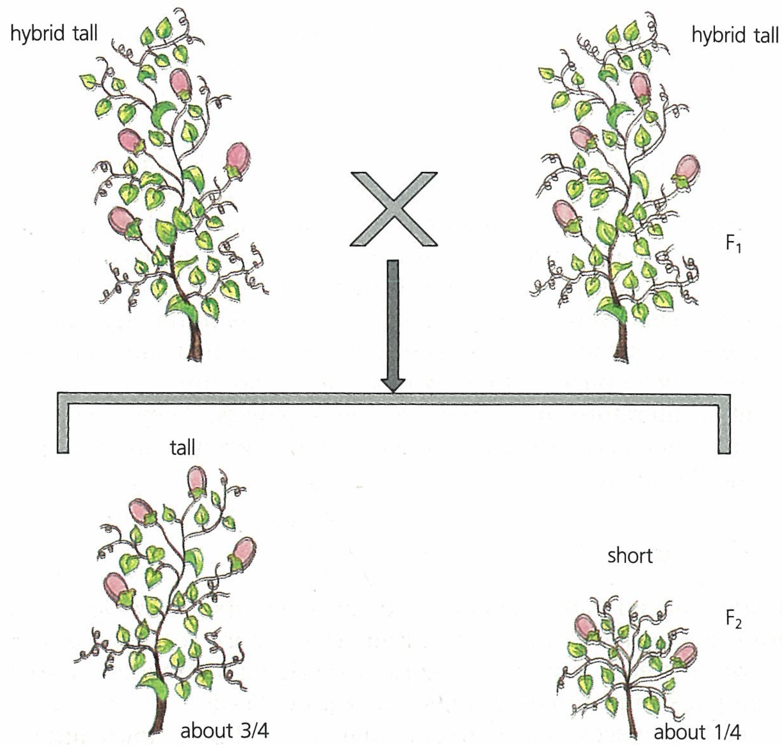


Figure 25–5
A Cross of the Hybrid Plants of the F_1 Generation. In a cross of the F_1 generation, about three-fourths of the second filial (F_2) generation are tall, and one-fourth are short. ▶

filial) generation. The appearance of short plants in the F_2 generation showed that the factor that determined shortness was still present in the F_1 generation.

Mendel described the traits that were expressed in the F_1 generation as **dominant** and the traits that were hidden in the F_1 generation as **recessive.** He concluded that *when an organism is hybrid for a pair of contrasting traits, only the dominant trait can be seen in the hybrid.* This is called the **law of dominance.**

The Law of Segregation

Mendel tried to explain why the recessive trait disappeared in one generation and appeared again in the next generation. He hypothesized that each trait in an individual was controlled by a pair of "factors." (Remember that in Mendel's time, the role of chromosomes and genes in heredity was not known.) Mendel also hypothesized that a factor could be one of two kinds. There was, for example, a factor for tallness and another factor for shortness. The factors in a pair could be alike or different. In a cross, the offspring received one factor from each parent. Thus, in a cross between a tall plant and a short plant, the offspring received both kinds of factors. However, only the dominant factor was expressed. The recessive factor was hidden.

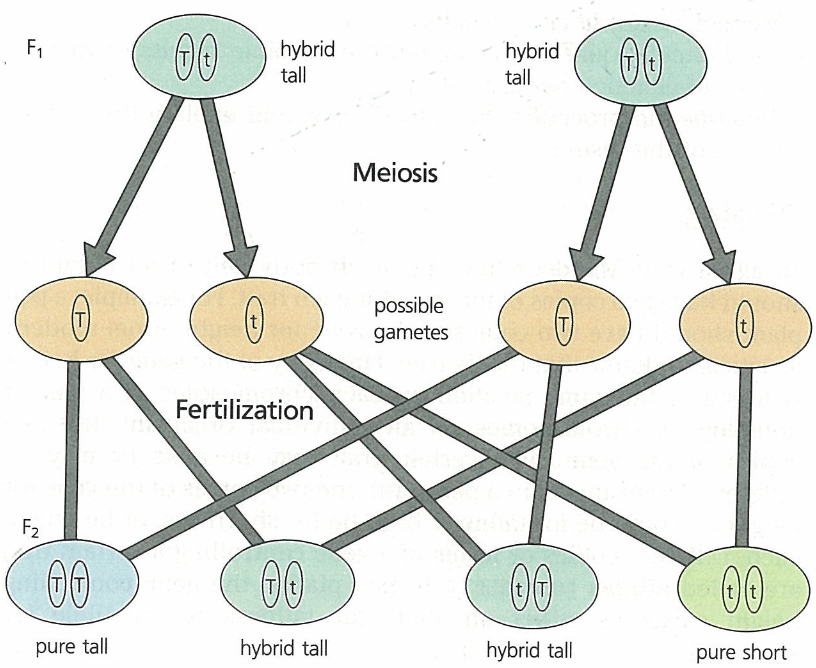
Because the factor for shortness was still present in these tall plants, it was possible for the factor to show itself in the later generations. This would happen when fertilization brought two shortness factors together in the same seed. The idea that *factors* *that occur in pairs are separated from each other during gamete formation and recombined at fertilization is called Mendel's* **law of segregation.**

The Gene-Chromosome Theory

The importance of Mendel's work may have been overlooked in the mid-1800s because little was known about chromosomes, mitosis, and meiosis. When Mendel's research was rediscovered in 1900, however, much more had been learned about cells. Chromosomes had been stained and observed in cells, and the processes of mitosis and meiosis had been described in detail.

The idea that Mendel's "factors" might be carried by homologous chromosomes was suggested first in 1903 by an American graduate student, W. S. Sutton. Sutton was studying the formation of sperm in the grasshopper. He observed the pairs of homologous chromosomes in diploid cells and the separation of the homologous chromosomes during spermatogenesis. He realized that the chromosomes that separated during meiosis were the same as the chromosomes that had united during the fertilization process that had originally produced the animal. After reviewing Mendel's work, Sutton began to think that the factors of Mendel's theory were carried on the chromosomes. Figure 25–6 shows how Sutton's chromosome theory would apply to a Mendelian cross of two tall hybrid plants.

As you can see in Figure 25–6, the separation of homologous chromosome pairs during meiosis and their recombination during fertilization would account for the separation and recombination of the Mendelian factors.



◀ **Figure 25–6**
The Gene-Chromosome Theory. T represents the factor for tallness and t the factor for shortness. Each factor is on a homologous chromosome. When the pairs of homologous chromosomes separate during gamete formation, they form two kinds of gametes: one with T, and the other with t. During fertilization, the chromosomes recombine.

Following the publication of Sutton's paper, titled "The Chromosomes in Heredity," in 1903, many experiments showed that this hypothesis was correct. At that time, the term **gene** was used in place of Mendel's "factor." Research showed not only that chromosomes carry genes but also that the genes are in a definite order along each chromosome. This work led to the modern gene-chromosome theory of heredity, which is discussed in detail in Chapter 26.

25-1 Section Review

1. Why are pea plants a good choice for genetic experiments?
2. What is a hybrid, and what is a dominant trait?
3. State Mendel's law of segregation.
4. What idea did Sutton propose?

Critical Thinking

5. What assumptions did Mendel make when he simply left plants alone that he wanted to self-pollinate? (*Identifying Assumptions*)

25-2 Fundamentals of Genetics

Section Objectives:

- *Define* the terms *alleles, homozygous, heterozygous, genotype,* and *phenotype.*
- *State* the law of probability, and explain how it applies to Mendel's experimental results.
- *Use* Punnett squares to work out the possible results of various types of genetic crosses.
- *Describe* the procedure for a test cross, and explain the significance of the results.

Alleles

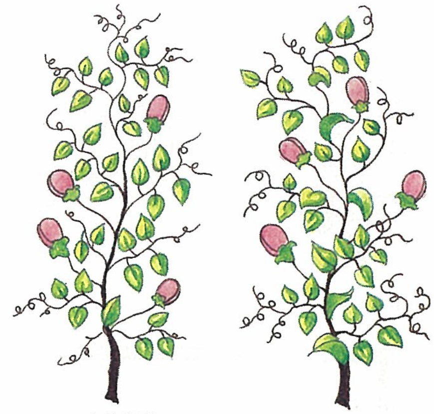
To agree with Mendel's findings, each body cell of an organism should have two copies of the gene for each trait. For example, a pea plant should have two copies of the gene for height. From modern genetics, we know that this is true. One copy of the gene for height is found at the same position on each chromosome of a pair of homologous chromosomes. In an individual organism, the two copies of the gene for a certain trait may be alike or may be different. For example, in a pea plant, the two copies of the gene for height can both be for tallness, both be for shortness, or be one of each. Different copies or forms of a gene controlling a certain trait are called **alleles** (uh LEELZ). In pea plants, the gene controlling height exists as either an allele for tallness or an allele for shortness.

If the alleles for a certain trait in an organism are the same, the organism is said to be **homozygous** (hoh muh ZY gus) for that trait. For example, a pea plant that is homozygous for tallness would have two copies of the gene for tallness. If the alleles are different, the organism is said to be **heterozygous** (het uh roh ZY gous). Therefore, a pea plant that is heterozygous for tallness has one gene for tallness and one for shortness. Homozygous means *pure*. Heterozygous means *hybrid*.

Genotypes and Phenotypes

When writing about alleles, a capital letter is used for the allele for a dominant trait. For example, the allele for tallness is represented by the symbol T. A lowercase letter is used for the contrasting recessive allele. Therefore, the allele for shortness is represented by the symbol t.

A pure tall pea plant has two alleles for tallness. Its genetic makeup is represented as TT. The genetic makeup of a pure short plant is tt, while that of a hybrid is Tt. The genetic makeup of an organism is called its **genotype** (JEE nuh typ). The physical trait that an organism develops as the result of its genotype is called its **phenotype** (FEE nuh typ). It is possible for two different individuals to have the same phenotype but different genotypes. A pure tall plant and a hybrid tall plant have the same phenotype (both are tall), but they have different genotypes (TT for the pure plant and Tt for the hybrid). See Figure 25-7. An organism that shows a recessive trait is always homozygous for that trait. Thus, a short pea plant will have two copies of the gene for shortness (tt).



pure tall (TT) hybrid tall (Tt)

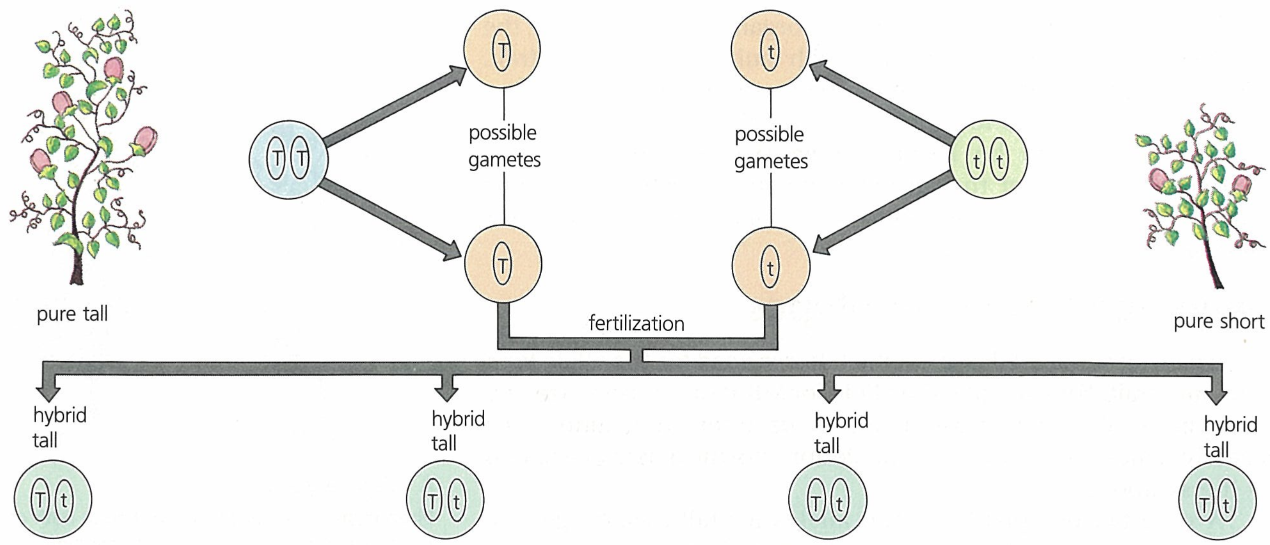
▲ **Figure 25–7**

Phenotype and Genotype. Although both of these pea plants have the same phenotype (tall), they have different genotypes (TT or Tt).

Probability in Genetics

Mendel's experiments involved hundreds of plants. He arrived at the laws of dominance and segregation by counting many, many offspring. To explain the *numerical* results of Mendel's experiments, you must understand the laws of chance. For example, if you toss a penny, you know that the chance of its turning up heads is 1 out of 2, or ½. If you toss the coin 100 times, you expect to get about 50 heads and 50 tails. That is, you expect to get about 1 head for every 1 tail. This can be expressed as a ratio of 1:1, or 1 head: 1 tail. In any real trial, the ratio of heads to tails is rarely exactly 1:1. In a short trial, say, 4 tosses, you might even get all heads or all tails. However, if you made a large number of tosses, 1000 or more for example, you would expect the ratio of heads to tails to be quite close to 1:1. Experiments have shown that the larger the number of trials, the closer the ratio comes to the expected value. This assumes, of course, that there is nothing special about the coin or the way in which it is tossed that would make one side *more likely* to turn up than the other.

Consider another example—the rolling of dice (singular, die). When a die is rolled, each face is as likely as any other to turn up. If you roll the die 600 times, you would expect to get about 100 of each face: 100 1's, 100 2's, 100 3's, and so on.



▲ **Figure 25–8**
Genetic Explanation of the Formation of Hybrids.

These are examples of the basic **law of probability,** or chance: If there are several possible events that might happen, and no one of them is more likely to happen than any other, then they will all happen in equal numbers over a large number of trials. This law allows you to predict the results of breeding experiments like those of Mendel. However, these predictions apply only when large numbers of individuals are involved.

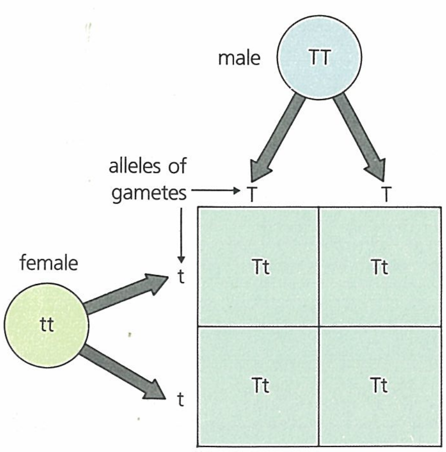
The Punnett Square

Consider how alleles separate during meiosis and then recombine during fertilization, when a pure tall pea plant is crossed with a pure short plant. The body cells of the tall plant have two alleles for tallness. Their genotype is TT. When gametes form in this plant, each gamete receives one T allele. The genetic makeup of each gamete can be shown by the single letter T. See Figure 25–8. The cells of the short plant have two alleles for the recessive trait of shortness. Their genotype is tt, and the genotype of the gametes is t. Since each parent plant is homozygous, its gametes all contain the same allele.

Suppose that we transfer pollen from the tall plant to the pistil of a short plant. Each sperm cell nucleus will be carrying one T allele. The egg cell in each ovule of the short plant will contain one t allele. When fertilization takes place, the zygotes will receive one T allele and one t allele, and their genotype will be Tt. The plants that grow from these zygotes will be hybrid tall.

A diagram called a **Punnett square** is a helpful way to show the results of any cross. The Punnett square for the cross we have just discussed is shown in Figure 25–9. In this diagram, the alleles of the possible male gametes are written at the heads of the columns of boxes. The alleles of the possible female gametes are written at the sides of the rows of boxes. (The positions of the male and

Figure 25–9
Punnett Square for Cross of Pure Dominant (Tall) with Pure Recessive (Short). ▼



female gametes can be interchanged.) Each box contains the genotype of the zygote that forms when the allele at the top of the column and the allele at the left of the row are brought together at fertilization.

In this case, there is only one combination of alleles. All the zygotes are alike. The results are 100 percent hybrid tall (Tt).

The Punnett Square for a Hybrid Cross

A Punnett square is even more useful for a more complicated case in which hybrid tall plants either self-pollinate or are cross-pollinated. The genotype of the tall hybrids is Tt. Because they contain two different alleles for plant height, they produce two types of gametes—one type with T and the other with t. Since the T and t alleles are present in equal numbers, the two types of gametes

Critical Thinking in Biology

Reasoning Conditionally

Suppose that a friend invites you to a picnic but tells you that if it is raining, the picnic will be cancelled. On the day of the picnic, you look out the window and notice that it is raining. Therefore, you reason that the picnic will be cancelled.

This type of reasoning is known as reasoning conditionally. When you reason conditionally, you draw a conclusion based on a conditional (if-then) statement and some factual information. The conditional argument above can be set up formally:

Premise: If it is raining, then the picnic will be cancelled.
Given: It is raining.
Conclusion: Therefore, the picnic will be cancelled.

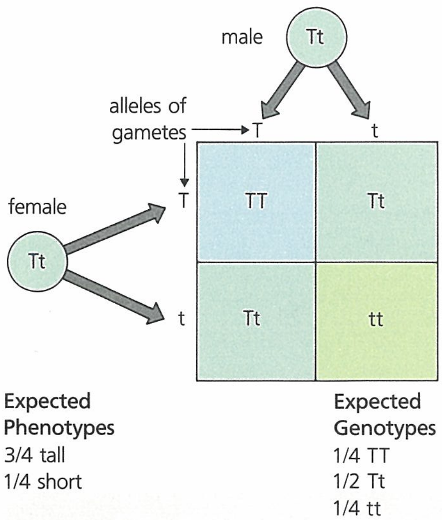
1. In pea plants, purple flowers are dominant over white flowers. Suppose you mated a homozygous, purple-flowered pea plant (PP) with a white-flowered pea plant (pp). Using the conditional argument above as a model, construct a conditional argument to show what proportion of the offspring would have purple flowers.

2. During a meeting with your biology teacher, he tells you that if you receive a grade of 70 or more on your genetics exam, you will pass the course. Suppose you receive a grade of 80. Construct a conditional argument to show whether you will pass the course. Then, suppose you receive a grade of 60. Can you construct a conditional argument in this case? Why or why not?

3. What is wrong with the following conditional argument?

Premise: If I cross two homozygous tall pea plants (TT × TT), then I will have all tall pea plants.
Given: I have all tall pea plants.
Conclusion: Therefore, I crossed two homozygous tall pea plants.

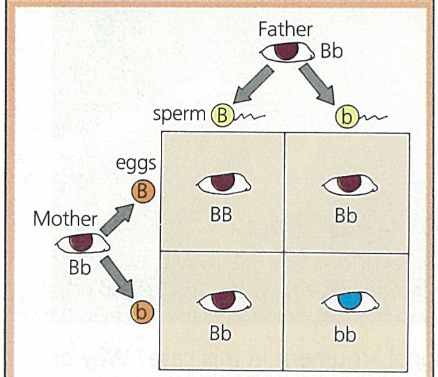
4. Think About It Explain your thought processes as you answered question 1.



▲ **Figure 25–10**

Punnett Square for Crossing Two Hybrids. Of the offspring produced, about one-fourth should be pure tall (TT), one-half hybrid tall (Tt), and one-fourth short (tt).

Can You Explain This?



A brown-eyed couple, both heterozygous for eye color (Bb), have three brown-eyed children and are expecting a fourth child. The mother insists that the child she is carrying will have blue eyes. She draws a Punnett square (see above) to back up her belief.

■ ***Do you agree with the mother? What do you think are the chances of the fourth child having blue eyes? Explain.***

are produced in equal numbers. This is true for both male and female gametes, and it is an important fact for the discussion that follows.

The Punnett square for the fertilizations that take place between these gametes is shown in Figure 25–10. Each letter at the head of a column stands for one type of male gamete that is formed. Each letter at the left of a row stands for one type of female gamete. Remember that these types of gametes are produced in equal numbers.

Each box in the diagram stands for a possible union of a male gamete with a female gamete. Since the types of gametes are present in equal numbers, each combination is just as likely to happen as any other. The law of probability tells us that each of the four zygotes is equally likely to appear if there is a large number of pollinations and fertilizations.

The Punnett square shows the four possible combinations. Given a large number of fertilizations, all four combinations should happen in about equal numbers. Among a large number of offspring, you would expect about ¼ to be TT (pure tall), about ½ (¼ + ¼) to be Tt (hybrid tall), and ¼ to be tt (pure short). Therefore, the genotype offspring expected ratio would be 1:2:1. In terms of the way they appear, or phenotype, about ¾ would be tall and ¼ would be short. Thus, the expected phenotype ratio of the offspring of this cross would be about 3:1 (3 tall to 1 short).

You can see that the law of probability, combined with a Punnett square, allows you to explain the results that Mendel got with his experimental crosses.

The Test Cross

As you now know, it is not possible to tell from appearance alone whether an individual showing a dominant trait is pure for the trait (homozygous) or hybrid (heterozygous). Breeders often need to know the genotypes of plants and animals. A test cross can be used to find out.

In a **test cross,** an individual of unknown genotype is mated with an individual showing the contrasting recessive trait. The genotype of the individual showing the recessive trait must be homozygous. The genotype of the individual with the unknown genotype may be homozygous or heterozygous. The test cross will show which is the case.

To understand how the test cross works, suppose a breeder wants to know whether a tall pea plant is homozygous (TT) or heterozygous (Tt). The plant with the unknown genotype is crossed, by artificial pollination, with a short plant, which must be homozygous (tt). The Punnett squares in Figure 25–11 show the results of the two possible cases.

You can see that if the test plant is pure tall (TT), all offspring of the cross will be tall. If the test plant is heterozygous tall, half the offspring, on the average, will be short. That is, the test cross shows that the recessive allele is present in the tall parent being tested. The advantage of this method is that you do not need to test and count large numbers of phenotypes. One short offspring shows that the test plant carries one recessive allele. Thus, by crossing an individual of unknown genotype with a homozygous recessive individual and looking at the offspring, it is possible to determine whether the test individual is homozygous or heterozygous.

25-2 Section Review

1. Define the terms *allele, genotype,* and *phenotype.*
2. Why is it important to use a large number of fertilizations and offspring when studying Mendelian genetics?
3. What is a Punnett square used for?
4. How can you tell whether an organism showing a dominant trait is pure or hybrid?

Critical Thinking

5. According to the law of probability, if a coin is tossed and comes up heads 10 times in a row, what are the chances of heads coming up on toss number 11? (*Predicting*)

25-3 Other Concepts in Genetics

Section Objectives:

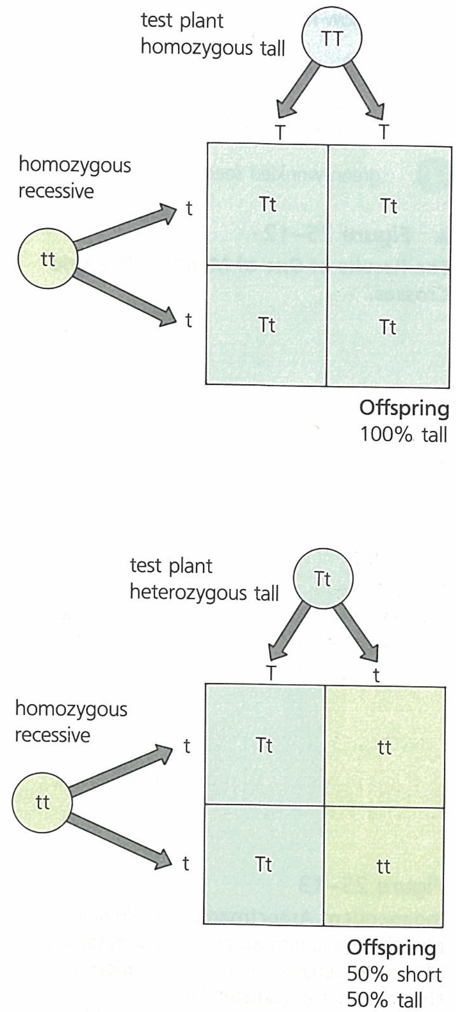
- *Explain* Mendel's law of independent assortment in terms of genes and meiosis.
- *Use* Punnett squares to predict the phenotype ratios in a dihybrid cross.
- *Describe* incomplete dominance, codominance, and multiple alleles and give examples of each.

Laboratory Investigation: *Examine* the monohybrid and dihybrid inheritance patterns in corn (p. 512).

The Law of Independent Assortment

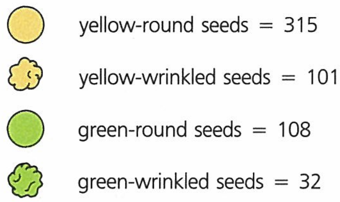
The hybrid cross discussed in the last section is called a **monohybrid cross** because only one pair of contrasting traits is being studied. Mendel first experimented only with monohybrid crosses. In experiments on tallness and shortness, for example, he did not record the other traits of the plants. After a time, however, Mendel decided to follow two pairs of contrasting traits at the same time. From the experiments he did before, he knew that yellow color (Y) was dominant over green color (y) in pea seeds and that round seed shape (R) was dominant over wrinkled seeds (r). Using this information, Mendel made crosses in which he kept track of both seed color and seed shape.

As he had done before, he started with plants that were pure, or homozygous, for these traits. For one parent, he used plants that were pure for both dominant traits. They produced yellow, round



▲ **Figure 25–11**

A Test Cross. An individual showing a dominant trait is crossed with an individual showing the contrasting recessive trait. If any offspring show the recessive trait, the test individual must be hybrid.



▲ **Figure 25–12**

The Results of One of Mendel's Dihybrid Crosses.

seeds. The other parent plants were pure for both recessive traits. They produced green, wrinkled seeds. He artificially pollinated one type of plant with pollen from the other type and then observed the seeds that were produced. The results were as expected. All the seeds of the F_1 generation showed only the two dominant traits. That is, they were yellow and smooth. No green or wrinkled seeds appeared.

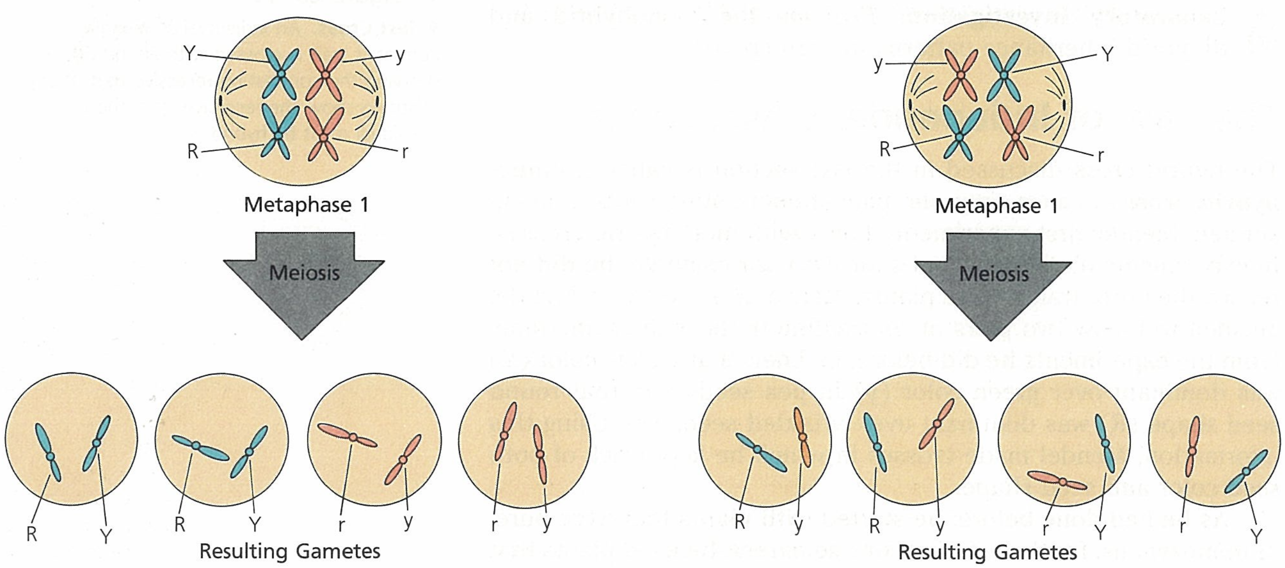
The next step was to plant the hybrid seeds and let the plants that grew from them self-pollinate. This would produce the F_2 generation of seeds. As expected, recessive traits appeared again in some of these seeds. Many seeds still showed both dominant traits. Some, however, were yellow and wrinkled (dominant-recessive), some were green and smooth (recessive-dominant), and a few were green and wrinkled (recessive-recessive). A breeding experiment like this one, involving two different traits, is called a **dihybrid cross.**

The data from one of Mendel's dihybrid crosses are given in Figure 25–12. Each trait considered by itself is close to the 3:1 ratio expected in a monohybrid cross. There are 416 yellow seeds and 140 green seeds. The ratio of 416 to 140 is 2.97:1, which is close to the expected 3:1 ratio. There are 423 round seeds and 133 wrinkled seeds. This ratio is 3.18:1, which is also close to 3:1. Note that there is about the same number of yellow, wrinkled seeds (dominant of one trait, recessive of the other) as green, smooth seeds (recessive of one trait, dominant of the other).

From data of this kind, Mendel concluded that different traits were inherited independently of one another. This principle is known as the **law of independent assortment.** In modern terms, this means that during meiosis, *genes for different traits are separated and distributed to gametes independently of one another.* See Figure 25–13. Today, we know that this is not always true. The reasons why are discussed in Chapter 26.

Figure 25–13

Independent Assortment. The alignment of homologous chromosomes during metaphase I of meiosis determines the combination of chromosomes in gametes. ▼



Phenotype Ratios in a Dihybrid Cross

With a Punnett square, you can predict the phenotype and genotype ratios expected in a dihybrid cross. First, make the diagram for the cross between the pure dominant for both traits and the pure recessive for both traits. See Figure 25–14. Note that spaces are provided for four gametes from each parent. According to the law of independent assortment, four different but equally probable combinations of two alleles, one from each of the two genes involved, can end up in the same gamete. In this case, all four possible allele combinations in the gametes have the same genotype, but they are the result of four different pairings. In the second cross, this point will be important.

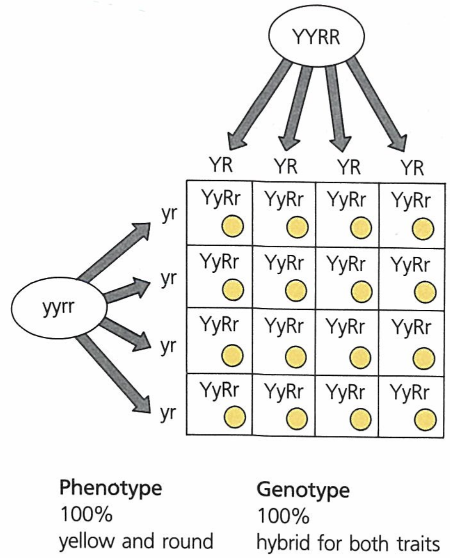
As you might expect, the phenotypes of the offspring in the F_1 generation are 100 percent dominant for both traits (yellow and smooth). The genotype is 100 percent hybrid for both traits (YyRr).

Now consider the Punnett square for a cross between the F_1 dihybrids. This time, the four possible gametes will be different: YR, Yr, yR, and yr. By the law of probability, there should be equal numbers of the four types of gametes. The zygotes produced by this cross are shown in Figure 25–15.

Again, by the law of probability, all 16 of the possible zygotes will be present in equal numbers. The Punnett square shows ratios of the types of offspring produced when large numbers are involved. The phenotypes are as follows:

- 9 yellow-round (dominant-dominant)
- 3 yellow-wrinkled (dominant-recessive)
- 3 green-round (recessive-dominant)
- 1 green-wrinkled (recessive-recessive)

This phenotype ratio of 9:3:3:1 is the ratio that is seen in dihybrid crosses when the numbers of offspring are large enough. Note that each trait considered by itself has the expected 3:1 phenotype ratio. There are 12 yellow seeds to 4 green. There are 12 round seeds to 4 wrinkled.

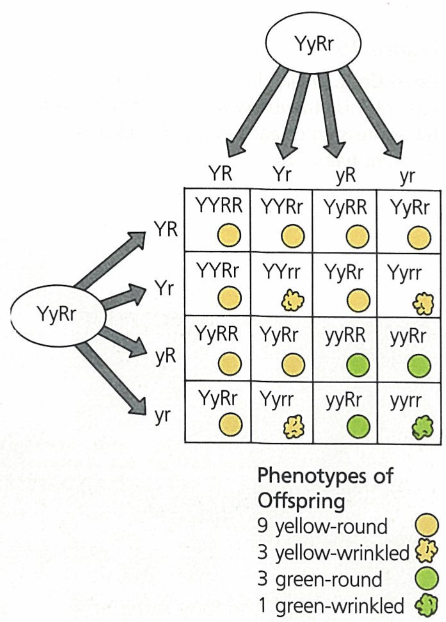


▲ **Figure 25–14**

Cross of Parents Pure for Two Contrasting Traits. All offspring are hybrid dominant for both traits.

Figure 25–15

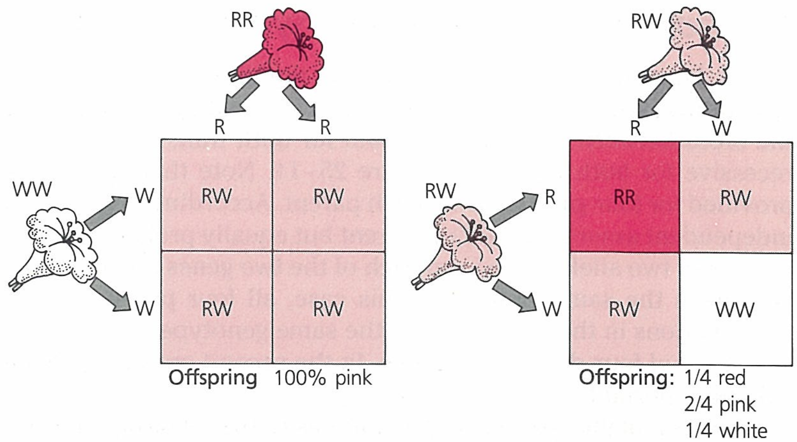
Predicting the Results of a Dihybrid Cross. The phenotype ratios agree fairly well with Mendel's experimental results. ▼



Incomplete Dominance

While many genes follow the patterns outlined by Mendel's laws, many do not. For example, in some organisms, both alleles contribute to the phenotype of a heterozygous individual to produce a trait that is not exactly like either parent. This is known as **incomplete dominance.** For example, the inheritance of flower color in the Japanese four-o'clock plant does not follow the pattern of dominance. A cross between a plant with red flowers and one with white flowers produces offspring with pink flowers. See Figure 25–16. Note that genotypes for incomplete dominance can be written using the capital initial letter of each allele, since both alleles influence phenotype. In this case, red is represented by R and white by W. Individuals with red or white flowers are always homozygous (RR or WW). Individuals with a heterozygous genotype (RW) have an

Figure 25–16
Incomplete Dominance. The hybrids of the F_1 generation (left) show a trait different from both pure traits. When these hybrids are crossed (right), one-fourth of the offspring are pure dominant, one-fourth pure recessive, and one-half hybrid intermediate. ▶



intermediate color. When two pink hybrid four-o'clocks are crossed, a 1:2:1 ratio of red to pink to white flowers is produced in the F_2 generation.

There is also a variety of chicken, called Andalusian, in which a cross between pure black and pure white chickens produces offspring that appear blue. When the blue chickens are crossed, the F_2 generation has a 1:2:1 ratio of black to blue to white chickens. When there is incomplete dominance, the F_1 generation has a phenotype different from that of either of the parents. Also, when there is incomplete dominance, the F_2 generation shows a phenotype ratio of 1:2:1 rather than the 3:1 ratio seen in normal Mendelian inheritance.

Codominance

In **codominance,** two dominant alleles are expressed at the same time. This is different from incomplete dominance, in which neither allele is completely dominant or completely hidden. One example of codominance is the roan coat in some cattle. A cross between homozygous red shorthorn cattle and homozygous white shorthorn cattle results in heterozygous offspring with a roan coat. The roan coat consists of a mixture of all red hairs and all white hairs. See Figure 25–17. Because each hair is either all red or all white, the condition shows codominance.

Capital letters with superscripts are often used to represent genotypes in codominance. For example, the symbol

Figure 25–17
Roan Coat. White hairs and red hairs in the coat of this strawberry roan horse show the full expression of each dominant allele in different hairs. ▼

C^R can represent the allele for red coat in shorthorn cattle, and the symbol C^W can represent the allele for white coat. The genotype for homozygous red coat is then symbolized as C^RC^R, and the genotype for homozygous white coat is C^WC^W. The heterozygous animal with a roan coat has a genotype of C^RC^W.

Codominance also occurs in human heredity. The inheritance of AB blood type is an example of codominance found in humans. Blood type inheritance is discussed in the next section.

Multiple Alleles

For some traits, there are more than two alleles in the species. They are referred to as **multiple alleles.** Although a single individual cannot have more than two alleles for each trait, different individuals can have different pairs of alleles when multiple alleles exist in a population.

The alleles for human blood type are an example of multiple alleles for a trait. The ABO blood group system is described in Chapter 10. The existence of multiple alleles explains why there are four different blood types. There are three alleles that control blood type. These alleles are called A, B, and O. O is recessive. A and B are both dominant over O, but neither one is dominant over the other. When A and B are both present in the genotype of an individual, they are codominant; that is, both alleles are expressed in the individual.

The usual way to write alleles in a multiple allele system is to use the capital letter I to show a dominant allele and the lowercase i to show a recessive allele. A superscript letter then stands for each particular dominant allele. Thus, I^A stands for the dominant allele A. I^B stands for the dominant allele B. Finally, i is understood to stand for the recessive allele O.

Since there are three alleles, there are six possible genotypes: I^AI^A, I^AI^B, I^Ai, I^BI^B, I^Bi, and ii. Figure 25-18 shows the blood types and their associated genotypes.

Rh blood factors are another example of multiple alleles in human genetics. See Chapter 10.

ABO Blood Group System

Genotype	Blood Type
I^AI^A or 1^Ai	A
I^BI^B or I^Bi	B
I^AI^B	AB
ii	O

▲ **Figure 25–18**
Multiple Alleles in the ABO Blood Group System. I^A and I^B are each dominant over i but not over each other. When both dominant alleles are present, the blood type is AB. Type 0 blood is produced only when neither dominant allele is present (genotype ii).

25-3 Section Review

1. State the law of independent assortment in modern terms.
2. What phenotype ratios would you expect as the result of a dihybrid cross?
3. Give one example each of incomplete dominance and codominance.
4. Name a trait that is controlled by multiple alleles.

Critical Thinking

5. Compare and contrast incomplete dominance and codominance. (*Comparing and Contrasting*)