Review Article

How Mendel uncovered the mechanism of inheritance overlooked by his predecessors?

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Abstract

Gregor Mendel conducted a series of hybridization experiments on the garden pea, *Pisum sativum*, to elucidate the mechanisms of heredity. For his studies, he selected seven pairs of contrasting traits, each occurring in alternative forms. Crosses involving any single pair of traits are known as monohybrid crosses, while those in which two or three pairs of traits were followed simultaneously are termed dihybrid and trihybrid crosses, respectively. Mendel tracked these crosses for two generations, meticulously recording the number of progeny phenotypes during each stage. He observed that these traits followed a predictable pattern: the F1 generation expressed only one of the parental phenotypes, whereas the F2 generation saw the reappearance of all parental traits in specific, predictable ratios. Based on these observations, he postulated the fundamental laws of heredity: the Law of Dominance, the Law of Segregation, and the Law of Independent Assortment. This review paper explains these laws and their corresponding ratios using principles of probability. Furthermore, it provides a historical account of similar experiments carried out by Mendel's predecessors, evaluating their merits and shortcomings to examine how they ultimately helped Mendel formulate his pioneering concepts that later laid the foundation of classical genetics.

Keywords: Alleles, dominance, independent assortment, Mendelian laws, Mendelian ratios, Product rule, segregation.

Introduction

It was in 1868 that Gregor Mendel published his findings on hybridization experiments. However, the significance of his work was recognized only in 1900, laying the foundation for modern genetics. Hence, the year 1900 is considered the birth year of genetics. The preceding century is often referred to as the pre-Mendelian era in the history of genetics. Even during the pre-Mendelian period, there were several predecessors of Mendel, many of whom conducted plant hybridization experiments. Some of them made observations, obtained results, and arrived at conclusions that were similar or very close to those later proposed by Mendel. The progress in elucidating the mechanism related to heredity was, however, retarded during the pre-Mendelian period, largely due to the prevailing concepts and doctrines of heredity established by renowned philosophers and biologists of that time. This article attempts to explore these concepts and doctrines of heredity and trace the historical development of our understanding of hereditary mechanisms by examining the experiments and observations of Mendel's predecessors. Furthermore, it provides a comprehensive account of Mendel's subsequent experiments and his monumental contributions to elucidating the definitive principles of inheritance, explaining how Mendel succeeded where earlier investigators failed.

Fixity of species

The concept of the *fixity of species* was formally proposed by Carl Linnaeus (1707-1778). According to this doctrine, all species are fixed and immutable, perpetually retaining their original morphological characteristics. The central precept of this view is encapsulated in the phrase *nullae species novae* ("no new species"), asserting that no additional species have been produced since the original creation.[1,2] In terms of heredity, Linnaeus argued for the *constancy of characters*, maintaining that the "essential characters" used to identify a genus or species remained permanent and were not subject to evolutionary progression or change.[3] This perspective effectively precludes the possibility of organic evolution and suggests a static model of heredity where variation is negligible. Consequently, because species were viewed as the result of a single, divine creative act, the total number of species in existence was considered defined, finite, and unchanging. The concept of fixity of species, in fact, reflected the belief of special creation.[4]

Naturphilosophie

Naturphilosophie was a dominant philosophical movement during the late 18th and early 19th centuries, championed by German thinkers such as F.W.J. von Schelling, J.W. von Goethe, and G.W.F. Hegel. It advocated a holistic approach to understanding the natural world, conceptualizing nature as a dynamic, organic whole rather than a mere collection of mechanical parts.[5] *Naturphilosophie* significantly influenced early biology, particularly the early plant hybridization experiments. Proponents argued that isolated parts removed from an organism, as was done in hybridisation experiments, did not represent the integrated nature of the whole organism. Consequently, they maintained that interpretations derived from such reductionist experiments were unreliable, as they failed to account for the vital unity and "archetypal" form of the organism as a whole. However, by the mid-19th century, *Naturphilosophie* fell out of favour with the rise of strictly empirical and mechanistic methodologies and critics dismissed the movement as overly "speculative" and lacking in experimental rigor. [5,6]

Cell theory and atomic theory

The cell theory, primarily developed by Matthias Jakob Schleiden and Theodor Schwann, is a foundational principle of biology. It establishes that all living organisms are composed of cells, which serve as the basic structural and functional units of life. A critical later addition, popularized by Rudolf Virchow, clarified that all cells arise from pre-existing cells.[7] Parallel to these biological advancements was the atomic theory proposed by John Dalton in the early nineteenth century (1803–1808). This was the first scientific framework to define the nature of matter, asserting that all substances are composed of minute, indivisible particles called atoms.[8] While some German scientists were inspired by the "oneness" of nature—a core tenet of *Naturphilosophie*—the cell and atomic theories ultimately helped transition science towards Materialism and Empiricism. By focusing on discrete, physical building blocks, these theories moved scientific thought gradually away from the more mystical and speculative aspects of "Nature Philosophy."

Pre-Mendelian insights into the mechanism of heredity

During the pre-Mendelian era, the scientific community lacked a unified, mathematically sound framework for understanding how physical traits were transmitted across generations.[9] Highly speculative and often competing theories dominated the landscape, and contemporary experiments frequently led to ambiguous or indecisive conclusions.[9] One of the most widely accepted views during this period was *blending inheritance*, which speculated that parental traits mix during fertilization to produce an intermediate physical appearance in the offspring.[10] Similarly, when Charles Darwin proposed natural selection acting on individual variations as a mechanism for evolution, he lacked a definitive understanding of how these variations originated or persisted. To address this, he introduced a provisional hypothesis known as *Pangenesis* in 1868.[11] According to this model, every organ and tissue in the body sheds minute organic particles called gemmules into the bloodstream, which carry somatic characteristics and accumulate within the gametes during their formation. While numerous hereditary concepts and breeding experiments designed to follow hereditary traits emerged during the pre-Mendelian era, this review focuses exclusively on those that directly aligned with or laid the conceptual groundwork for Mendel's laws.

Plant hybridization experiments by Joseph Gottlieb Kölreuter

Joseph Gottlieb Kölreuter was a pioneering 18th-century German botanist who conducted more than 500 large- scale scientific plant hybridization experiments using *Nicotiana* species (tobacco).[12] In 1760, he performed the first successful artificial hybridization between two tobacco species, *Nicotiana rustica* and *Nicotiana paniculata*, with the former serving as the female parent and the latter as the male parent. Kölreuter observed that the resulting hybrids often exhibited superior physical characteristics compared to their parents, a phenomenon now known as heterosis, although the hybrids were frequently sterile. He regarded these hybrids as unnatural and unstable. In experiments with carnations (*Dianthus*), crosses between red- and white-flowered varieties produced pink offspring. When these pink hybrids were self-pollinated, the next generation yielded a mixture of red, white, and pink plants. Kölreuter noted that hybrids were often unstable and tended to "revert" to parental forms in subsequent generations rather than maintaining a stable hybrid state. This observation led him to consider hybrids as "unnatural" deviations from the natural order, a view consistent with the school of *Naturphilosophie*.

Kölreuter's experiments provided strong evidence for the theory of plant sexuality. Through reciprocal crosses, he demonstrated that similar results were obtained regardless of which species served as the pollen donor or the seed parent. He concluded that both male (pollen) and female (egg) parents contribute to the traits of the offspring, thereby supporting the concept of *biparental inheritance*. Although he did not formulate the laws of inheritance, his meticulous hybridization experiments laid the foundation for the later work of Gregor Mendel.[12]

Hybridisation experiments on garden peas by Knight

In 1799, Thomas Andrew Knight conducted experiments using the genus *Pisum* (garden pea). He fertilized a white-seeded variety with pollen from a grey-seeded variety.[13] The hybrid plants produced in the first generation exhibited only grey seeds. This demonstrated the dominance of one character over another, a phenomenon later formulated by Mendel as the “principle of dominance”.[13,14] However, in the second generation raised from the first-generation grey-seeded plants, both parental seed colours reappeared. This observation demonstrated that traits were not “lost” in hybrids but could re-emerge,[13] and that the two traits—grey and white—did not blend. Mendel later observed a similar pattern of inheritance, on the basis of which he proposed the law of purity of gametes. Although Knight observed these inheritance patterns, he neither counted the offspring belonging to each trait category in successive generations nor attempted to determine a numerical ratio between them.[14]

John Goss (1800–1880)

Goss’s work during the 1820s provided some of the clearest early evidence of what is now recognised as Mendelian segregation. He pollinated a blue-seeded pea variety (“Blue Prussian”) with pollen from a yellowish-white variety (“Dwarf Spanish”).[14] To his surprise, all the seeds produced in the first filial generation (F1) were yellowish-white, resembling the male parent.[13,14] In the second filial generation (F2), raised from these hybrids, the pods contained a mixture of both blue and white seeds. Goss further observed that the blue seeds, representing the recessive trait, bred true and consistently produced only blue seeds, whereas some of the white-seeded plants produced only white seeds while others yielded a mixture of blue and white seeds.[13,14] Although these observations closely paralleled the inheritance patterns later described by Gregor Mendel, Goss lacked a mathematical framework for analysing heredity and, like Knight, did not record the numerical proportions of the different seed types.[14]

Charles Victor Naudin

Charles Victor Naudin conducted several hybridization experiments during the 1850s and 1860s, providing a more theoretical understanding of hybridity.[15] He worked with various plant species, including members of the gourd family (Cucurbitaceae) and the nightshade family (Solanaceae). Naudin observed that the first generation of hybrids was often uniform and resembled one of the parents, a pattern previously observed by Knight and Goss, and later systematically studied by Mendel.[16]

One of the most significant outcomes of Naudin’s experiments was his proposal that gametes contain distinct “essences” responsible for different characters, and that these essences separate during the formation of pollen and ovules in hybrids. He believed that this process of “disjunction” was responsible for the reappearance of the original parental forms in subsequent generations.[15,16] Mendel later referred to these hereditary units as “factors.” Naudin’s concept of “disjunction” closely anticipated the law of segregation later formulated by Mendel. What prevented Naudin from proposing a proper mechanism for the inheritance of characters was his adherence to the contemporary concept of the “fixity of species,” according to which the tendency of hybrids to revert to parental forms represented nature’s mechanism for preventing the formation of new, permanent species through hybridization.[15]

Gartner’s plant hybridization experiments

Carl Friedrich von Gärtner (1772–1850) was a German botanist who carried out one of the largest studies on plant hybridization before the work of Mendel. Inspired by the earlier experiments of Kölreuter, Gärtner spent more than 25 years performing systematic plant-crossing experiments. He conducted nearly 10,000 artificial cross- pollination experiments involving about 700 plant species from more than 80 genera, producing around 250–350 hybrids.[17] His studies included plants such as *Nicotiana* (tobacco), *Dianthus*, *Aquilegia*, *Verbascum*, *Oenothera*, and *Malva*. To prevent self-fertilization, he carefully removed the male parts of flowers before pollination and then manually transferred pollen from one plant species to another. He closely recorded characteristics such as flower shape, plant growth, fertility, and the inheritance of parental traits. His main aim was to understand whether hybrids could return to their original parental forms or develop into new stable species. One of Gärtner's important observations was that hybrids usually showed characteristics intermediate between the two parents. He also noticed that some hybrids were more vigorous than their parents, producing larger flowers and stronger growth. This is the same phenomenon of hybrid vigour (heterosis) mentioned earlier. However, he observed that this vigour often decreased in later generations. Gärtner found that many hybrids between different species were partly or completely sterile, which supported the nineteenth-century belief that species were fixed and distinct. He also observed that intraspecific hybrids often reverted to parental forms in later generations, especially when repeatedly crossed back with one of the parent species. He called this gradual return of parental characters "transformation." According to his experiments, repeated backcrossing could eventually produce offspring almost identical to one parent species.

In corn, Gärtner crossed varieties with different seed colours, such as yellow, white, and striped seeds. He observed that pollen from one variety could directly influence the colour of the grain and suggested that the male parent could visibly affect the female reproductive structures. Gärtner's experiments with corn and garden pea (*Pisum sativum*) were especially important because they later influenced Mendel's work on inheritance. Mendel carefully studied Gärtner's writings and cited them in his own famous paper. Gärtner noticed that hybrids often showed a stronger expression of one parent's traits than the other, an observation related to what later became known as dominance. He also observed that hybrid characteristics often disappeared in later generations, with plants returning to the parental forms, a process he described as the "Law of Reversion."[17]

Although Gärtner collected a huge amount of experimental data, he did not develop a clear theory of inheritance. Unlike Mendel, Gärtner provided mainly qualitative descriptions of "types" and no quantitative data, such as numerical counts of offspring. A major conceptual limitation of his work was his belief that fertilization involved a qualitative struggle between parental "essences" rather than the inheritance of discrete hereditary units. Similarly, like many botanists of his time, he believed in the fixity of species and interpreted sterility and reversion as natural mechanisms that preserved species identity. Therefore, he rejected the idea that hybridization could permanently create new species. Mendel owned a copy of Gärtner's book, *Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich*.[11] Gärtner's difficulty in explaining the reappearance of parental traits inspired Mendel to search for a mathematical explanation of inheritance. Mendel admired the scale and precision of Gärtner's experiments;[18] but differed from him by proposing that inheritance was controlled by the transmission of discrete hereditary factors (later called alleles) rather than by blending inheritance and reversion.

Gregor Mendel

Gregor Mendel (1822–1884), who is recognized as the "Father of genetics," was an Austrian monk and scientist whose pioneering experiments on pea plants laid the foundation for modern genetics. He was born on 20 July 1822 in Heinzendorf, a village in the Austrian Empire (now Hynčice in the Czech Republic), to a farming family. From an early age, Mendel showed a passion for nature and learning. Although financial difficulties frequently interrupted his education, he persevered with the support of his family and teachers. In 1843 he entered the Augustinian monastery of St. Thomas in Brünn (now Brno), where he adopted the name Gregor. The monastery was an important intellectual centre that encouraged scientific study.[19, 20]

While Mendel studied theology and philosophy to prepare for the priesthood, his interests remained deeply rooted in mathematics and the natural sciences. He attempted to obtain a high school teaching license but failed the formal examination. Recognizing his potential, the monastery sent him to the University of Vienna from 1851 to 1853. There, he studied physics, mathematics, and chemistry, gaining invaluable exposure to scientific methods that emphasized rigorous observation, experimentation, and statistical analysis. Upon returning to Brünn, Mendel worked as a substitute teacher. It was in the monastery's garden that he conducted his famous hybridization experiments on pea plants (*Pisum sativum*), ultimately discovering the fundamental laws of inheritance that changed science forever.

Between 1856 and 1863, Mendel conducted extensive experiments on the garden pea, *Pisum sativum*, in the monastery garden. He selected pea plants because they possessed several clearly contrasting traits, were easy to cultivate, had short generation times, and could either self-pollinate or be artificially cross-pollinated.[19,21] For his experiments, Mendel selected seven characters, each occurring in two alternative forms. For example, with respect to plant height, he studied tall-stemmed and dwarf-stemmed varieties. Other characters included seed shape (round *vs.* wrinkled), seed colour (yellow *vs.* green), flower colour (purple *vs.* white), pod shape (inflated *vs.* constricted), pod colour (green *vs.* yellow), and flower position (axial *vs.* terminal). For the experiments, Mendel first established true-breeding lines through repeated self-pollination. He then carried out controlled cross-pollination between plants possessing contrasting traits.

Monohybrid cross

In one set of experiments, Mendel considered only a single character existing in alternative forms. For example, when true-breeding tall plants were crossed with dwarf plants, all the offspring in the first filial (F_1) generation were tall. However, when these F_1 plants were allowed to self-pollinate, the second filial (F_2) generation produced both tall and dwarf plants in an approximate ratio of 3:1. This type of experiment is known as a monohybrid cross because only a single character is studied to trace the pattern of inheritance.

Dihybrid cross

In another set of experiments, Mendel studied the inheritance of two characters simultaneously. Such experiments are known as dihybrid crosses. [19,21] For example, Mendel crossed true-breeding tall plants having round seeds with dwarf plants producing wrinkled seeds. In the first filial (F_1) generation, all the offspring were tall plants with round seeds, indicating that tallness and round seed shape were dominant traits. When the F_1 plants were self-pollinated, the second filial (F_2) generation produced four different types of plants. These included the two parental combinations—tall plants with round seeds and dwarf plants with wrinkled seeds—as well as two new combinations, namely tall plants with wrinkled seeds and dwarf plants with round seeds. The numerical data showed that tall round, tall wrinkled, dwarf round, and dwarf wrinkled plants appeared in the ratio 9:3:3:1.

Mendel's Laws of Inheritance

Based on his monohybrid and dihybrid crosses, Mendel proposed the below-mentioned laws of inheritance.[19,21]

Law of Segregation: According to Mendel, the expression of a particular character is controlled by a pair of hereditary factors, one contributed by the male parent through the pollen and the other by the female parent through the ovule. During gamete formation, the two factors controlling a character separate from each other so that each gamete receives only one factor, either of maternal origin or paternal origin, and not both. These factors do not blend or alter one another but remain unchanged through successive generations. Hence, this principle is also referred to as the *law of purity of gametes.*

Law of Dominance: When two contrasting factors controlling a character are present together in an organism, one factor may mask the expression of the other. The factor that is expressed is called the dominant factor, whereas the factor whose expression is masked is called the recessive factor.

Law of Independent Assortment: Factors controlling different characters assort independently during gamete formation, resulting in the production of new combinations of traits in the offspring. In other words, various segregation processes are independent. Thus, segregation of one pair of factors occurs independently of the segregation of other pairs of factors. This law is applicable to crosses involving more than one pair of contrasting characters, such as a dihybrid cross.

Genetic Terminology

The hereditary factors referred to by Mendel are now known as genes. The different alternative forms of a gene are called *alleles*.[19] For example, the gene controlling seed shape exists in two allelic forms: the dominant round allele (denoted by a capital letter, **R**) and the recessive wrinkled allele (denoted by a small letter, **r**). Mendel also proposed that each character is controlled by a pair of factors, meaning that an individual possesses two alleles for a particular character. When both alleles for a trait are identical (e.g., **RR** or **rr**), the condition is called *homozygous.* When the two alleles are different (e.g., **Rr**), the condition is referred to as *heterozygous.* The observable characteristics of an individual constitute its *phenotype*, whereas the genetic constitution or combination of alleles is known as the *genotype*.

Why the 3:1 Ratio and Not a 2:1 Ratio?

According to Mendel's Law of Segregation, the F1 parents in a monohybrid cross produce an equal number of gametes carrying alternative traits. For example, in a cross involving true-breeding tall and dwarf plants, the F1 progeny are heterozygous, containing both the alleles for tallness (T) and dwarfness (t). During gamete formation, these alleles segregate so that each gamete receives only one allele—either T or t. Fertilization involves the random fusion of these gametes. Because both types of gametes (T and t) are produced in equal numbers, one might initially expect an equal distribution of three zygotic combinations: (1) Pure tall (TT); (2) Pure dwarf (tt); and (3) Hybrid (Tt).

Since the T allele is completely dominant over the t allele, both TT and Tt express the tall phenotype. If these three combinations occurred in equal numbers, the resulting phenotypic ratio could be assumed as 2:1 (2 tall: 1 dwarf).

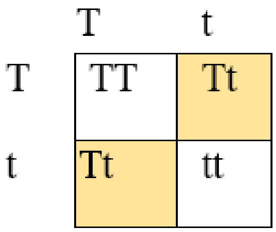
The Reality: Probability and the Punnett Square

However, Mendel's actual experiments

consistently yielded a 3:1 ratio.[19,21] This happens because the outcomes are determined by the laws of probability. In other words, the ratios are determined by the probability of events. Thus, in a monohybrid cross, there are actually *four* distinct, equally probable fertilization events, as given below:

- An ovule with T fertilized by a pollen with T, producing TT homozygote
- An ovule with T fertilized by a pollen with t, producing Tt heterozygote
- An ovule with t fertilized by a pollen with T, producing Tt heterozygote
- An ovule with t fertilized by a pollen with t, producing tt homozygote

These events can be depicted using a Punnett square (named after the British geneticist R. C. Punnett) in which the alleles carried by the male and female gametes are arranged along the top and side of the square, respectively, and the possible allele combinations resulting from fertilization are then determined (Figure 1).[19]



	T	t
T	TT	Tt
t	Tt	tt

Figure 1: Punnet square depiction of probable combinations of alleles during fertilization.

Final Ratios

Because the hybrid genotype (Tt) can be formed in two different ways—through the union of a T-bearing gamete with a t-bearing gamete or vice versa—it occurs twice as frequently as either homozygous genotype (TT or tt). Consequently, the offspring exhibit the following predictable ratios: *Genotypic Ratio:* 1TT: 2Tt: 1 tt (or 1:2:1) and *Phenotypic Ratio:* 3Tall: 1Dwarf (or 3:1).

Probability rule governing dihybrid ratios

The phenotypic and genotypic ratios in a dihybrid cross can be derived by constructing a Punnett square. Alternatively, these ratios can be calculated using the probability rule known as the *multiplication rule*. [19,21]

The multiplication rule states that the *probability of two independent events occurring together is equal to the product of their individual probabilities.* For example, consider a cross between tall round plants and dwarf wrinkled plants. In the F_2 generation, the probability of obtaining tall plants, as observed in a monohybrid cross, is ¾, while the probability of obtaining round plants is also ¾. Therefore, the probability of obtaining tall round plants is: ¾ × ¾ = $^{9}/_{16.}$ Similarly, the probability of obtaining tall wrinkled plants is: ¾ × ¼ = $^{3}/_{16.}$ The probability of obtaining dwarf round plants is: ¼ × ¾ = $^{3}/_{16.}$ The probability of obtaining dwarf wrinkled plants is: ¼ × ¼ = $^{1}/_{16.}$

Thus, the phenotypic ratio for tall round, tall wrinkled, dwarf round, and dwarf wrinkled plants in the F_2 generation will be 9:3:3:1.

Genotype probabilities

The genotype probabilities can also be calculated using the same product method.[19,21] For example, consider the probability of obtaining the genotypes TT Rr and Tt Rr in the F_2 generation of a dihybrid cross, where T and t represent the alleles for tall and dwarf traits, and R and r represent the alleles for round and wrinkled traits respectively.

Probability of the TT Rr genotype: In a standard monohybrid cross, the probability of obtaining the homozygous dominant TT genotype is ¼, while the probability of obtaining the heterozygous Rr genotype is ½. Therefore, as per the multiplication rule, the combined probability of obtaining TT, Rr is: ¼ × ½ = $^{1}/_{8}$.

Table 1: Phenotypic Ratios in Mendel's F_2 Dihybrid Cross: Comparing the actual and expected number of F_2 phenotypes from a cross between plants with round-yellow seeds and wrinkled-green seeds (n=556).

Phenotypes	Actual number of F_2 phenotypes obtained	Expected number as per Mendelian dihybrid ratio	Ratio based on actual data
Round yellow	315	313 (556 x $^9/_{16}$)	9
Round green	101	104 (556 x $^3/_{16}$)	3
Wrinkled yellow	108	104 (556 x $^3/_{16}$)	3
Wrinkled green	32	35 (556 x $^1/_{16}$)	1
Total	**556**	**556**	**16**

Probability of the Tt Rr genotype: Similarly, for the heterozygous Tt, Rr genotype in the F_2 generation, the probability of obtaining the Tt genotype is ½ and that of obtaining the Rr genotype is also ½. Consequently, the combined probability of obtaining Tt, Rr: ½ × ½ = ¼.

A dihybrid cross involves different combinations of alleles. In fact, a dihybrid cross is actually two independent monohybrid crosses occurring simultaneously; hence the ratio 9:3:3:1 = (3:1) x (3:1). Therefore, analysing any single phenotype independently will yield the exact ratio of a standard monohybrid cross. For example, the actual data obtained by Mendel in his classic dihybrid cross experiment is presented in Table 1.[19]

If we isolate and consider the ratio of just a single trait, for example, seed shape (round *vs*. wrinkled), the classic 3:1 monohybrid ratio emerges as follows: Total seeds = 556

- Round seeds**:** 315 + 101 = 416
  (Expected monohybrid number: 556 x ¾ = 417)
- Wrinkled seeds: 108 + 32 = 140
  (Expected monohybrid number:556 x ¼ = 139).

Similarly, seed colour (yellow *vs*. green) also yields the same 3:1 ratio:

- Yellow seeds: 315 + 108 = 423
  (Expected monohybrid number: 556 x ¾ = 417)
- Green seeds: 101 + 32 = 133
  (Expected monohybrid number: 556 x ¼ = 139).

What helped Mendel formulate the laws of heredity?

As mentioned earlier, several early hybridization experiments were remarkable and contributed greatly to the understanding of the mechanisms of heredity. Mendel learned hybridization techniques and gained important insights from these studies. Thomas Andrew Knight, John Goss, and Carl Friedrich von Gärtner all conducted independent experiments using the genus *Pisum* (garden pea), the same plant used by Mendel.[11,13,14,17] By selecting plants with two distinct seed colours to track inheritance patterns, they observed that the F1 generation exhibited only one of the two parental colours. However, crosses involving these F1 plants produced offspring displaying both parental colours. This crucial observation indicated that traits do not blend and that one colour is dominant over the other. Gärtner also noted that hybrids frequently showed a stronger expression of one of the parent's traits over the other. Mendel was also significantly influenced by the work of Kölreuter, who conducted more than 500 extensive plant hybridization experiments using *Nicotiana* (tobacco) species. Through elaborate hybridization experiments, Charles Naudin concluded that traits are determined by specific "essences"—a concept that foreshadowed Mendel's own postulation of discrete hereditary "factors."[15] He came remarkably close to modern genetic theory by suggesting that these essences segregate without influencing one another during gamete formation, postulating this as the concept of "disjunction."

Despite these breakthroughs, Mendel's predecessors were ultimately unable to arrive at definitive, logical conclusions regarding the mechanisms of heredity. Their interpretations were often constrained by a preconceived belief in the "fixity of species" or influenced by *Naturphilosophie*. They largely maintained that hybrids are inherently unstable and possess a natural tendency to revert to parental forms—viewing this reversion as a biological mechanism designed to prevent the formation of new, permanent species through hybridization.[15]

Mendel's experience in plant breeding

Being an experienced plant breeder who had studied the hybridization experiments of his predecessors, including Kölreuter and Gärtner, Mendel was well aware of the techniques required for controlled crossing. To ensure the true-breeding nature of his subjects, he tested each pea strain by selfing the plants and growing their progeny for two years;[19] this confirmed that the plants remained identical with respect to selected traits generation after generation. In this manner, he established and maintained several true-breeding strains of pea plants, routinely repeating his experiments to verify his results and confirm trait consistency.

Departure from conventional ideas and concepts

In a significant departure from his predecessors, Mendel applied a rigorous mathematical treatment to his biological data, deriving distinct statistical ratios and providing robust explanations for them. He firmly rejected the prevailing theory of blending inheritance, postulating instead that discrete units—which he termed "factors"—were responsible for the expression of traits. Above all, his scientific insights remained unhampered by contemporary doctrines and dogmas such as the fixity of species or the theory of special creation.

Mathematical approaches to interpreting results

During his university education in Vienna, Mendel's scientific temperament was greatly influenced by two eminent professors, Christian Doppler and Franz Unger.[20] Doppler adopted a highly practical and innovative teaching approach, demonstrating experiments to students and encouraging them to conduct their own investigations. Mendel also attended Doppler's course on higher mathematics. From Unger, Mendel learned plant anatomy and physiology. Unger's interests were broad and included cell biology, plant anatomy and physiology, and palaeontology. He believed in evolution and proposed that all plants could be traced back to an "original plant," even before Charles Darwin formulated his evolutionary theory. Unger was convinced that cells were the fundamental units of life. He observed relationships in size and structure among plants and collected data on a large scale. The mathematical training and experimental approach to problem-solving that Mendel acquired from Doppler, together with Unger's studies on plant characteristics, had a decisive influence on Mendel's later research in plant hybridization and numerical data analysis. This ultimately led him to apply extensive statistical analyses to his findings—a methodology that was revolutionary and highly unusual among biologists of his time.

Mendel's ratios – Too perfect or biased?

Mendel was extra cautious about the ratios. His observed results exhibit a remarkably close fit to the expected values (Table 1). Sir Ronald A. Fisher, a renowned British statistician and geneticist, examined Mendel’s data across all reported experiments using a Chi-Square goodness-of-fit test.[19] He discovered that the observed results were extraordinarily close to the expected Mendelian ratios, meaning the deviations between the observed numbers and the theoretical expectations were improbably small. Consequently, Fisher suggested that the data may have been systematically adjusted—either consciously or unconsciously—to better fit the expected ratios. However, this controversial finding does not imply that Mendel was dishonest. Modern historians and statisticians offer a few key possibilities for this "too-good-to-be-true" data.

Confirmation Bias: Mendel may have been exceptionally careful while recording results and may have unconsciously favoured observations that agreed with his expectations. For example, he might have stopped counting once the ratios appeared sufficiently close to the predicted values or classified ambiguous traits (such as slightly wrinkled versus round seeds) in a manner consistent with his hypothesis.

Assistant hypothesis: Fisher himself proposed that assistants involved in tending the thousands of pea plants may have omitted doubtful observations or unintentionally adjusted counts to satisfy Mendel’s expectations, especially if they were aware of the anticipated results.

Selective Reporting: The published data may represent only a selected portion of the many experiments Mendel conducted, while experiments showing larger natural statistical deviations may not have been included in the final report.

Between 1854 and 1856, Mendel cultivated and tested thousands of pea plants, operating under the principle that a larger sample size of independent measurements would effectively rule out random phenomena. Although he began his investigations with 34 varieties of garden peas, he eventually narrowed his selection to 22 varieties with highly consistent characteristics. However, in his final paper, he reported the results of only seven monohybrid crosses, one dihybrid cross, and one trihybrid cross.[19] This selective reporting of only the crosses that best fit his expectations has drawn criticism from modern commentators, as it can make the data appear biased towards his hypotheses.

Why Mendel’s ratios remain undistorted by linkage?

The garden pea (*Pisum sativum*) is a diploid organism with seven homologous pairs of chromosomes (2n = 14 chromosomes). For the hybridization studies, Mendel selected only seven pairs of alleles representing different traits. Earlier it was believed that these selected alleles were located on seven different chromosomes. However, in 1975, a Swedish geneticist named Stig Blixt published a famous paper in *Nature* mapping out exactly which chromosomes held the genes for Mendel's seven traits.[22,23] The actual distribution looks like this:

- *Chromosome 1:* Seed coat/flower colour (*A*) and Cotyledon colour (*I*)
- *Chromosome 4:* Stem length (*LE*), Pod form (*V*), and Flower positio (*FA*)
- *Chromosome 5:* Pod colour (*GP*)
- *Chromosome 7:* Seed shape (*R*)

Mendel postulated the law of independent assortment based on the results of his dihybrid crosses. A limitation of dihybrid and trihybrid crosses is that when two genes are located very close together on the same chromosome, they tend to be inherited as a single unit, a phenomenon known as *linkage*. In such cases, the genes do not assort independently, resulting in deviations from the expected Mendelian ratios. However, Mendel did not encounter major difficulties due to linkage. This was because, compared with his monohybrid crosses, he performed relatively few crosses involving more than one pair of contrasting traits and published the results of only one dihybrid and one trihybrid cross among them.[19] By a fortunate coincidence, the traits he studied together were either located on different chromosomes or were positioned far apart on Chromosome 1 and Chromosome 4, allowing them to assort almost independently. Because of this wide separation, frequent genetic recombination occurred during meiosis, producing nearly 50% recombination frequency.[24] Since 50% is the maximum possible recombination frequency, such alleles behave as though they assort independently, yielding the classic 9:3:3:1 dihybrid phenotypic ratio without revealing genetic linkage. However, in the case of Chromosome 1, the genes controlling seed coat colour and cotyledon colour are relatively close together, therefore showing a recombination frequency of about 30% rather than 50%. Mendel, however, never published the results of a dihybrid cross involving these two traits together. As a result, linkage never showed up in his experimental data.

Non-Mendelian patterns of inheritance

The pairs of alleles for the traits Mendel selected exhibited complete dominance, which is precisely why he obtained such clear, predictable ratios for his monohybrid and dihybrid crosses. However, many other types of dominance relationships exist between alleles.[19,25-27] These include *incomplete dominance,* where the heterozygous phenotype appears intermediate between the phenotypes of individuals homozygous for either allele.[19] In *codominance,* both phenotypes of the two homozygotes are simultaneously expressed, a classic example being human ABO blood group alleles.[25] Furthermore, some traits are controlled by more than two alleles. In such cases, a population's gene pool may contain *multiple alleles* for a specific trait, although an individual possesses only a single pair of alleles for that trait.[26] Similarly, quantitative traits such as weight and skin colour are determined by a complex set of multiple genes acting additively, which is known as *polygenic inheritance.*[27] Gene expression is also influenced by several other genetic mechanisms. For instance, an allele at one locus may block or mask the phenotypic expression of an allele at another gene locus, a process known as *epistasis.*[26] In other instances, mutant alleles of two entirely different genes may produce identical phenotypes. Additionally, *sex-linked alleles* show distinct inheritance patterns because they are carried on sex chromosomes.[19] Collectively, these diverse patterns are referred to as *non-Mendelian inheritance*, as they deviate from typical Mendelian phenotypic ratios.

Publication and neglect

Mendel presented his findings in 1865 to the Natural History Society of Brünn and published them in 1866 in a paper titled *Experiments on Plant Hybridization* (*Versuche über Pflanzen-Hybriden*).[28] However, his work attracted little attention at the time because most biologists favoured blending theories of inheritance and failed to appreciate the importance of mathematical analysis in biology.[20] As a result, Mendel remained largely outside the mainstream scientific community. Even the distinguished plant physiologist Carl Wilhelm von Nägeli, with whom Mendel maintained extensive correspondence between 1866 and 1873, failed to recognize the significance of his discoveries. Although Nägeli possessed the expertise to understand the work, he dismissed Mendel's conclusions as "only empirical".[20] Historians have further noted that Nägeli fundamentally believed Mendel's conclusions to be incorrect and regarded him more as an amateur investigator than as a professional scientist. [11,29]

In 1868, Mendel was elected abbot of the St. Thomas Monastery, and the administrative responsibilities associated with this position greatly reduced his scientific activities. Nevertheless, he continued to pursue his scientific interests through detailed studies in meteorology and bee breeding many more years. He died on January 6, 1884, in Brünn. Before his death, Mendel reportedly told one of the novices: "My scientific work has brought me a great deal of satisfaction, and I am convinced that it will be appreciated before long by the whole world."[21] Indeed, sixteen years later, his work received worldwide recognition.

The Rediscovery of Mendel's Findings

In 1900, Hugo de Vries, Carl Correns, and Erich von Tschermak, each working independently in different European countries, published the results of their experiments that agreed with Mendel's findings. Their publications drew attention to Mendel's original paper and rightly attributed the priority of discovery to him. Since then, the patterns of trait expression and the ratios described by Mendel have been validated in numerous instances and are widely used in pedigree analysis. They form the foundation of transmission genetics, implying the statistical principles governing the inheritance of genes from one generation to the next. Consequently, the hereditary transmission involving dominant-recessive alleles, Mendelian ratios, and laws is universally known as Mendelian genetics.[21]

Conclusion

When Mendel published his paper on inheritance, no one knew of the existence of chromosomes or genes. The mechanism of heredity was a black box to him.[20] Despite this, by focusing entirely on data representing the plant phenotypes of parental, F1 and F2 generations, he correctly concluded that each trait is controlled by two unit factors—one inherited from each parent. His experiments are widely appreciated for their brilliant planning, careful observations, rigorous numerical analysis of data to derive ratios, and insightful interpretation of results. They were explicitly designed to answer specific questions regarding how offspring characteristics relate to those of their parents. The principles of heredity he proposed were later seamlessly integrated into the chromosome theory of inheritance and modern genetics.

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Conflicts of interest

There are no conflicts of interest.

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