Mendel of Mathematics

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Last July (July 22 or 20 [5, 6, 10]), biologists celebrated the 200th birthday of one of the 19th century's most influential scientists: the singular discoverer of the fundamental rules of heredity, Gregor Mendel (1822–1884). Arguably, though not normally viewed as such, Mendel is among the 19th century's most influential mathematicians as well.

Mendel's story has been a staple of the education of generations of students. In the standard retelling in the biology curriculum, a student learns that Mendel, an Augustinian friar at the St. Thomas Abbey in Brünn, Moravia (Brno in the Czech Republic), conducted hybridization experiments from 1856 to 1863 with the garden pea plant, *Pisum sativum*. Considering each of seven traits, Mendel examined thousands of plants over multiple generations, at times crossing plants of different types, at other times allowing the plants to self-fertilize. In careful experiments requiring precise gardening, characteristic ratios of variant types recurred across the traits. From these ratios, Mendel proposed a model of heredity whose main principles have come to be known as "Mendel's laws." The law of segregation states that an individual offspring inherits one hereditary factor from the mother and one from the father, and that for each parent, the factor transmitted to the offspring is chosen at random among the two such factors present in the parent. The law of independent assortment states that hereditary factors that underlie different traits are inherited independently of one another.

A hint of the connection of Mendel and mathematics will emerge when the student is assigned homework problems that involve numerical counts from Mendel's crosses—perhaps of round and wrinkled peas, perhaps of yellow and green peas, perhaps of round yellow and wrinkled green peas. The student will compute probabilities (employing the binomial theorem—but perhaps implicitly, rather than stated as such) and will apply statistics to test if the data fit Mendel's laws. The student learns that despite the indispensable position Mendel's laws occupy in the modern understanding of the entire field of genetics, Mendel went unrecognized by his contemporaries: in 1865, he reported his findings in two meetings of the Natural Science Society in Brünn, in whose proceedings he published his paper [9], and only in 1900 was the paper "rediscovered" by three separate researchers and quickly popularized by a fourth, launching genetics as a new branch of science, with Mendel recognized as its founding figure. The consequences of this delay will be noted, as an adequate theory of heredity was greatly needed in Mendel's time: the lack of such a theory presented a significant gap for the theory of evolution by natural selection introduced by Charles Darwin in 1859, and the effort to integrate Mendel's work with Darwin's was central to early 20th-century biology.

The biology instructor may reflect on some of the reasons for Mendel's success, and on lessons of Mendel's story for modern scientists. First, a careful choice of study organism can be central to the discovery of general principles. Second, experimental replication and consideration of sufficient sample sizes are critical for obtaining reliable findings. Third, success often emerges from sustained painstaking, tedious effort.

At this point, the biology curriculum's historical interlude about Mendel ends, perhaps leaving unstated a fourth, critical factor in Mendel's achievement. In particular, Mendel was "of mathematics."

Mendel was born to a poor farming family and was acquainted with plants and gardening from an early age. He showed academic promise and was sent away to school, and he entered the abbey in 1843 as a way both to make ends meet and to continue studying. During his early studies at the Olmütz Philosophical Institute from 1840–1843, he was attracted to mathematics and physics. At the University of Vienna from 1851–1853, alongside courses in botany, chemistry, paleontology, and zoology, Mendel studied mathematics and physics with Christian Doppler, of the Doppler effect, and Andreas von Ettingshausen, whose 1826 book *Combinatorial Analysis*, according to D. Knuth,

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originated the notation $\binom{n}{k}$ for binomial coefficients [7] and was the "*first text to discuss combinatorial generation methods in a perspicuous way*" [8]. In Mendel's work on plant hybridization, it would be a combinatorial style of reasoning that he would put to such effective use.

Mendel's 1866 paper details numerous quantitative experiments with the seven traits, reporting the numbers of plants of different types. His mathematical pattern recognition from his initial experiments must have led him to his conceptual model, inspiring predictions of still further ratios and subsequent experiments to test the model. He identifies 2.96:1, 3.01:1, 3.15:1, 2.95:1, 2.82:1, 3.14:1, and 2.84:1 in experiments with the seven traits as variants of the 3:1 ratio that his model predicts. One of the more complicated experiments produces nine classes, numbering 38, 35, 28, 30, 65, 68, 60, 67, and 138 plants, respectively, and Mendel writes "*If one compares the number of forms that occur in each of these divisions, the average ratios 1:2:4 are unmistakable*" [1]. In another section, he predicts a ratio that takes the form 2^n-1:2:2^n-1. A mathematical mind noticed empirical ratios, abstracted general principles, devised experiments to test if the consequences of those principles were observed, and assessed the agreement of the experiments with the principles.

Compare Mendel with his contemporary, Charles Darwin (1809–1882). Like Mendel, Darwin also worked by iteratively using observations to formulate general principles and designing experiments to test those principles; modern readers celebrate his reasoning as inventive and inspired [11]. Unlike Mendel, however, Darwin did not use mathematics. Indeed, in Darwin's autobiography, he wrote

> *I attempted mathematics, and even went during the summer of 1828 with a private tutor (a very dull man) to Barmouth, but I got on very slowly. The work was repugnant to me, chiefly from my not being able to see any meaning in the early steps in algebra. This impatience was very foolish, and in after years I have deeply regretted that I did not proceed far enough at least to understand something of the great leading principles of mathematics; for men thus endowed seem to have an extra sense* [2].

The non-mathematical Darwin conducted plant breeding experiments with many species. In one self-fertilization experiment with snapdragons, his counts of two types of plants are close to Mendel's predicted ratio of 3:1; the numbers are noted, but the numerical ratio is not analyzed [4]. It would be unfair to criticize Darwin for this omission, as Darwin is believed not to have known about Mendel's paper and he had a different working hypothesis for the nature of heredity, but the example illustrates one of the reasons commonly given for the field's failure to appreciate Mendel's work before 1900: that its members did not generally share Mendel's inclination toward mathematics [13].

The story of Mendel's discovery, "*one of the triumphs of the human mind*" [14], is an opportunity to describe to biology students the importance of mathematics as a tool to see in biology what cannot otherwise be seen. It is also a chance to describe to mathematics students the potential of mathematical thinking, using even elementary ideas, to transform a biological field. This dynamic of a mathematical mind approaching a biological problem, uncovering fundamental biological discoveries—and sometimes even inspiring new mathematics—has replayed many times throughout the history of the interface of mathematics and biology [3]. Although mathematical contributions do sometimes continue to go unrecognized until biology catches up [12], few examples of this unfortunate phenomenon are as dramatic as Mendel's story, as many areas of biology—with genetics being a principal example—now have a strong mathematical tradition. Biologists celebrate Mendel's achievement. Mathematicians should too.

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