Article:

Radick, GM (2015) Beyond the "Mendel-Fisher controversy". Science, 350 (6257). 159 - 160 (2). ISSN 0036-8075

https://doi.org/10.1126/science.aab3846

Beyond the "Mendel-Fisher controversy"

Worries about fraudulent data should give way to broader critiques of Mendel's legacy

By Gregory Radick

One hundred and fifty years ago, Gregor Mendel delivered his lectures on "Experiments on Plant Hybrids," going on to publish them in 1866 (1). Around the world, celebrations of the monk whose work with pea varieties made him the father of genetics are underway. Mendel has alas also acquired another, less auspicious title, as "the father of scientific misconduct," owing to suspicions that he faked some of his data (2). The suspicions have turned out to be groundless (3, 4). Along the way, however, they not only damaged Mendel's reputation unfairly but, as a look at the history of the controversy shows, sent critical discussion of his data down a sidetrack.

The Mendel-Fisher controversy, as it is known, takes its name from a 1936 paper by the Cambridge statistician and theoretical geneticist Ronald Fisher (5). But the discovery that Mendel's data conform improbably closely to the predictions of his theory – that his data are "too good to be true" – was due not to Fisher but to a scientist from the previous generation, the Oxford biologist W. F. R. Weldon (1860-1906). "About pleasanter things, I have heard of and read a paper by one Mendel on the results of crossing peas, which I think you would like to read," Weldon wrote to the mathematician Karl Pearson in October 1900, only a few months after Mendel's paper had been rediscovered (6). Over the next year, Weldon grew skeptical. The more he learned about different pea varieties and their pedigrees, the more convinced he became that Mendel's "laws" had no validity beyond the artificially purified races Mendel worked with, and that the binary categories he used to classify pea characters – green/yellow for seed color, round/wrinkled for seed shape, and so on – obscured a far more variable reality.

While preparing a paper setting out his concerns, Weldon checked the "probable error" of Mendel's results, using a standard formula to calculate expected deviations from the theoretically predicted values, given the number of observations made. For example, Mendel had reported that, in the offspring of the hybrid pea plants, out of 7,324 seeds, 5,474 had the dominant character of roundedness – a figure extremely near to the predicted 75% for a sample of that size. Most of Mendel's other data sets showed similarly remarkable agreement with his theory. "He is either a black liar, or a wonderful man," judged Weldon, in a letter to Pearson in November 1901 (7). In his published paper, Weldon stressed the improbable nature of Mendel's results. Run Mendel's experiments again at the same scale, Weldon reckoned, and the chance of getting worse results is 16 to 1 (8).

For Weldon, the data problem was of interest as a symptom of a much deeper problem: the binary categories Mendel had used, and the oversimplified theory of dominance he had erected on their basis. In the book-length manuscript where Weldon discussed the 1866 paper most fully, he did not even mention his previous analysis of probable error (9). What he dwelt on, at length, was the mounting evidence against anything like Mendel's view of dominance as something an inherited character possesses independently of its developmental context. The effect of the same bit of chromosome on a body can be different depending on the hereditary background and the wider environmental conditions. The manifest character can be dominant, or recessive, or neither.

Weldon was at work on the manuscript in 1904 to 1905, while in full battle mode with Pearson and other allies against the growing corps of “Mendelians,” led by William Bateson. At Weldon’s death in 1906, the manuscript was still unfinished and unpublished. It is thus no wonder that his larger critique was ignored and the importance of context generally paid no more than lip service (10). (Bateson late in life cheerfully admitted that “scientific Calvinism” struck him as a fair summary of Mendelism’s message (11).)

Even so, the more statistically minded of the Mendelians took heed of Weldon’s data analysis (12). One was the young Fisher, who, in a talk on heredity in 1911, spoke about the 16-to-1 odds that Weldon first calculated (13). When asked in the mid-1930s to contribute to a new journal in the history of science, Fisher made the problem his own. However, he drew a very different lesson from the Mendel case than Weldon had.

Re-analyzing Mendel’s data statistically, Fisher, too, found that they are improbably good. But what that showed, Fisher argued, was what a great thinker Mendel was. Relatively soon after the crossing experiments were begun, Mendel must have worked out his theory in the abstract. From that moment, Mendel knew how his data ought to look. Mendel’s program of experiments thus became, in Fisher’s words, “a carefully planned demonstration of his conclusions.” For Fisher, the data’s shortcomings were thus largely to Mendel’s credit. Such blame as Fisher was willing to consider he meted out to a well-meaning but misguided underling, who, Fisher surmised, must have quietly got rid of whatever plants threatened to mess up the master’s ratios. “Mendel was deceived by some assistant who knew too well what was expected” (5).

Although, like Weldon, Fisher expressed himself more pungently in private correspondence, his paper was intended to settle rather than spark controversy. There was no “Mendel-Fisher controversy” for decades, even as Fisher succeeded in raising the profile of the need for statistical evaluations of goodness of fit in genetics and other areas of research. Only towards the end of the 1960s did Fisher come to be understood as having levelled an accusation of fraud. Quite why that happened, and why the accusation then became so widely known, are matters for ongoing historical inquiry. What is plain is that Fisher’s analysis had a far greater prominence in the publications near the centenary of Mendel’s paper (1965 to 1966) than in those around the 1950 Golden Jubilee of genetics (14). In 1950 genetics was under immense political pressure due to the influence of Mendelism-rejecting Trofim Lysenko in the Soviet Union. Unsurprisingly, Western geneticists chose not to emphasize concerns about Mendel’s data. Only from the mid-1960s, when Lysenkoist biology was in terminal decline, did those concerns begin to be aired.

But now the Cold War is long gone, and the consensus view after half a century of debate is more or less where it was at the start: Mendel’s data are indeed improbably good, but that in itself is not evidence of fraud, nor is there any other evidence for suggest fraud (3). So should we let the matter drop? That would be a missed opportunity. Undoubtedly Mendel suffered from unconscious bias, counting as yellow what ought to have counted as green when it supported his theory (4). But stopping there would leave untouched the question of whether Mendel was right to work with just the two categories in the first place, and the connections between those categories and the absence of the developmental context from the traditional Mendelian picture – a picture that remains central to education in genetics. It has proved very hard to “unthink” determinist Mendelism, even as genetics in the 21st century goes ever further in disclosing the importance of variability, interaction, complexity and even ancestry (15). If the time is ripe for retiring the problem of Mendel's data, it is also ripe for rediscovering, and engaging with, Weldon's critique of Mendelian concepts.

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Illustration with caption

A plate of peas. In this photographic plate from Weldon's 1902 article (8), images 1 to 6 and 7 to 12 show a color scale from green to yellow in the seeds of two hybrid pea varieties (with the seed coats removed). Images 13 to 18 show color variation in cotyledons of the same seed, and 19 to 24 show differences between the color of a seed's coat and its cotyledons (though Weldon was not happy with the colors as published). Another, black-and-white plate displayed degrees in the development of wrinkles. Weldon’s point was that inherited characters are diverse in way that a Mendelian perspective, indifferent to developmental context, neither acknowledges nor accounts for.