

## Gregor Mendel, his experiments and their statistical evaluation

JAN KALINA

*Institute of Computer Science of the Academy of Sciences of the Czech Republic, Department of Medical Informatics and Biostatistics, Pod Vodárenskou věží 2, CZ-182 07 Praha 8, Czech Republic;  
e-mail: kalina@cs.cas.cz*

KALINA J. 2014: Gregor Mendel, his experiments and their statistical evaluation. *Acta Musei Moraviae, Scientiae biologicae* (Brno) 99(1): 87–99. – Gregor Mendel (1822–1884) is now generally acknowledged as the founder of modern genetics. He was among the first to make systematic use of mathematical methods in biology, employing just the simpler rules of probability theory to work out some of the underlying laws of heredity. However, it is less well known that an element of controversy began to attach to his experimental results in the 1930's, largely as a result of the work of the eminent British statistician and biologist R.A. Fisher, who felt that Mendel's results were too close to expected values. New explanations have therefore been sought to avert suspicion that the figures may have been in some way idealised. The work in hand seeks to contribute to resolving the Mendel-Fisher controversy. An alternative statistical model for the design of Mendel's experiments is suggested, which appears to correspond to Mendel's results. At the same time, the proposed model allows a very simple interpretation.

**Keywords.** Mendel, history of genetics, Mendel-Fisher controversy, statistical analysis, binomial distribution, numerical simulation

### The life and times of Gregor Mendel

The name of Gregor Mendel (20 July 1822–6 January 1884) is inseparable from the origins of modern genetics and he was among the first biologists to make systematic use of mathematical methods. This paper describes his experiments from a mathematical point of view, reviews certain contributions on the analysis of his experiments, and proposes a new statistical model that facilitates clarification of the validity of his results. While Mendel's results are considered controversial by certain statisticians, the model proposed in this paper renders his results acceptable beyond reasonable doubt. This part of the contribution is not intended to be a detailed biography of Mendel; it concentrates upon matters that might bear upon his experiments in heredity.

The life of the “father of modern genetics” has been thoroughly described and critically analyzed by a number of authors, among them ILTIS (1924), KŘÍŽENECKÝ (1965), and OREL (2003). ILTIS (1924) has been cited as the great man's most distinguished biographer (POSNER & SKUTIL 1968), but his account has also been considered too idealized (PIEGORSCH 1990). Mendel's early years have been investigated by various researchers, as recently summarized by MATALOVÁ (2008). Recently, specialists have also contributed interesting historical papers on Mendel's life and heritage from new points of view (MATALOVÁ 2007, SEKERÁK 2007). Other works in scientific journals have recalled or popularized Mendel's life (MIKO 2008; DASTUR & TANK 2010), although without imparting any new information. Mendel's life has also been presented as narrative in several works of fiction (e.g. MAWER 1997, HENIG 2000), but the stories tend to be based on a received “legend” rather than seriously researched information.

Mendel was christened Johann Mendel; only later, when he joined the Augustinian friars, was he given the name Gregor. His parents were smallholding farmers of very limited means, part of the German-speaking population of Silesia in what is now Hynčice in the Czech Republic (then Heinzendorf bei Odrau, part of the Austro-Hungarian empire). From his earliest years, he would have been acquainted with the selective breeding of fruit trees, since his father routinely employed tree-grafting and shield budding (MATALOVÁ 2007); at the very least, he would have become acquainted with some of the unsolved practical problems associated with crossbreeding and heredity. The latent academic talents of the young Mendel came to the attention of Jan Schreiber, a priest in the local church in Dolní Vražné, who persuaded his parents to let him attend the local *gymnázium* (grammar school) from the age of eleven. The cleric was also his science teacher at the Hynčice school, and a forward-thinking pedagogue and administrator of an educational institute in Kunín (formerly Kunvald) dedicated to science and philanthropy. Mendel's deep interest in education and capacity for independent study from his earliest years have been largely attributed to Schreiber (OREL 2003).

As well as his time at the local school in Hynčice, Mendel went to a Piarist school in Lipník nad Bečvou and later studied at a highly respected secondary school in Opava that specialized in the natural sciences. This school established its own scientific museum, recognised today as the oldest museum in the Czech Lands (PLAČEK 1974). Despite the hardships of near-poverty and being away from home, he entered the academic world via the Philosophical Institute of the University of Olomouc, where his scientific horizons expanded; he graduated with excellent results (MATALOVÁ 2007).

In 1843, Mendel opted to resolve his financial problems not on the farm, but by joining the Augustinian Abbey of Saint Thomas in Brno, where he was given the name Gregor as a novitiate and ordained as a priest in 1847. The Augustinians are a mendicant order and St. Thomas, Brno is the only Augustinian monastery in the world in which the superior has the title of full Abbot (KURIAN 2012). Brno has been the traditional capital of Moravia for centuries and the abbey was founded in 1350 as the place of final rest for the Moravian margraves, or border lords (SAMEK 1993). Since 1783, it has been situated in Old Brno (Staré Brno, Altbrünn). The abbey was known as a particularly progressive scientific and humanitarian centre, suffused with Enlightenment thinking. Abbot Cyril Napp (1792–1867), a recognised specialist in breeding fruit trees (ZLÁMAL 1936), first invited Mendel to the monastery. The abbey also ran large estates, on which breeding experiments took place, some of them with sheep (FOLTÝN 2005).

As part of his clerical duties, Mendel devoted himself to teaching as well as to self-study and it fell to him to teach physics and botany at various schools in and beyond Brno. He was an enthusiastic teacher, notable for the clarity of his lectures (RICHTER 1943). However, a new *viva voce* doctorate exam [*rigorózní zkouška*] for full teaching credentials was introduced by the government, which he failed, and he was sent to Vienna, where a new programme of scientific education had recently been made available. Under the influence of some of the leading physicists, botanists and geologists of the times, Mendel's intellectual horizons expanded. OREL (2003) notes that he

presented a thesis devoted to geology, particularly to the origin of rocks, defending the contemporaneously progressive ideas of Charles Lyell (1797–1875) who, contrary to his predecessors, held that the geological processes shaping the earth were slow, steady and still active to the present day (LYELL 1830, 1832, 1833).

Mendel returned to Brno in 1853 and took up teaching again, despite lacking full qualifications and failing the exam to become a fully-qualified teacher again in 1856, a time at which his mental health became quite unstable. Abbot Cyril Knapp, possibly the unsung hero of the birth of genetics, came to Mendel's rescue not for the first time, authorizing an extended programme of experimental hybridization at the monastery (his motives were not entirely altruistic – Australian competition was threatening the price of the Merino wool produced by the monastery sheep and the abbot was keen to improve the blood-line).

Mendel chose to demonstrate basic principles and decided on the garden pea *Pisum sativum* as his subject. He had practical reasons to do so: it has several distinct varieties, it is easy to cultivate, its pollination can be closely controlled; and it has a high proportion of successful germinations.

Mendel became abbot after Napp's death in 1867 and spent the majority of his time on administrative matters. However, an extended conflict with the government over religious obligations to pay tax (or not) adversely affected his health (VYBRAL 1968), and he finally succumbed to chronic kidney disease in 1884. No successor picked up the reins of his experiments in heredity and the new abbot, Anselm Rambousek (1824–1901), appears to have burned all his written notes (RÉDEI 2002).

### Statistical evaluation of Mendel's experiments

Mendel performed his experiments with the aim of verifying previously-formulated hypotheses and to demonstrate his theoretical knowledge to others (FISHER 1936), rather than to formulate new hypotheses (NISSANI 1994). This must be borne in mind in any statistical analysis. In terms of theoretical background, Mendel is known to have understood that two factors (genes) are responsible for the transmission of a particular trait. However, his initial analysis of the probabilities of appearance proved too mathematical for the biology specialists who read his paper (MENDEL 1866). Mendel therefore introduced a factorial design for his experiments (FISHER 1936), performed with binary traits based on the observation that in seven important characters, peas show no intermediate forms when crossed: flower colour purple or white; flower position axillary or terminal; stem length long or short; seed shape round or wrinkled; seed colour yellow or green; pod shape inflated or constricted; and pod colour yellow or green. Because the aim of his experiments was not to search for a new biological knowledge, the evaluation of the experiments did not aim to extract new information from the data, but rather to seek that which favoured his given hypotheses. Mendel used only simple probability calculations to check the correspondence between his results and their theoretical counterparts, i.e. the anticipated numbers of progeny of a particular phenotype.

Herein, we discuss the observation that Mendel's results may be too close to expected values, and overview some works analyzing this phenomenon. Some of Mendel's interpreters in the first half of the 20th century employed comparatively elementary statistical methods, including Pearson's  $\chi^2$  test and its  $p$ -value, to support the idea that Mendel had, wittingly or otherwise, manipulated his results. Under standard models, Mendel's data appear too clean and biased towards a good fit with the theoretical model under consideration. In short, the data verify the genetic hypotheses too convincingly to be convincing. As early as the first decade of the 20th century, WELDON (1902) pointed out that the results are too admirably in accord with expectations. Certain prominent statisticians of the past speculated as to whether Mendel had "cooked" his data. Prominent among these was Ronald A. Fisher (1890–1962), whose name came to be attached to the whole debate, now known generally as the Mendel-Fisher controversy (FRANKLIN 2008).

FISHER (1936) applied modern statistical methods to make a critical review of Mendel's experiments, using in particular the  $\chi^2$  tests of goodness-of-fit and their  $p$ -values, which compare observed data with values obtained under theoretical models. Fisher even used the word "falsified" of Mendel's results, (FISHER 1936), but stopped short of accusing Mendel of deliberate malpractice (FRIEDEN 1998); he actually expressed admiration for the logical and mathematical aspects of Mendel's work (BOX 1978, PIEGORSCH 1990). FISHER (1918) also expressed high respect for Mendel's understanding in the factorial design of the experiments.

A number of authors have repeated Fisher's analysis of Mendel's results (e.g. RÉDEI 2002), but without contributing anything new to what may have led to bias in the results of the experiments. Other statisticians have also become involved, but the whole matter remains controversial. More seriously, there has emerged an impression among the lay public that Mendel cheated (see MAWER 1997). PIEGORSCH (1990) observes that the causes of any bias in Mendel's work remain unresolved. Other more recent authors have sought arguments in Mendel's favour. A summary of papers interpreting Mendel's experiments from the statistical point has been compiled by FAIRBANKS & RYTTING (2001).

A number of experts have spoken out against the idea that Mendel's results are falsified, e.g. GUSTAFFSON (1969) and FAIRBANKS & RYTTING (2001). NISSANI (1994) called the problem "the Mendelian paradox", because Mendel as "a man of unimpeachable integrity, finite observational powers, and a passion for science" would only very improbably commit scientific misconduct. NOVITSKI (2004a) made an overview of contributions that consider Mendel's results too close to expected results. From the psychological point of view, any individual has a tendency to classify towards verification of the facts expected or preferred, even when attempting to remain objective. A further complication of Mendel's experiments was that the number of pea plants germinating was to some extent random, excluding the possibility of fixed sample sizes.

Some of the contributions that argue for Mendel's accuracy include a paper by NOVITSKI (2004b), who calculated that the bias in one of the experiments was below the value given by FISHER (1936), a value he considered inaccurate. FAIRBANKS & RYTTING

(2001) performed other statistical analyses and came to the conclusion that the controversy cannot be resolved by means of statistics, but rather botany and historical facts and context. Moreover, Mendel's design clearly included a certain misclassification, since the practical execution of Mendel's experiments required identification of the phenotype as well as genotype of an individual seed (FAIRBANKS & RYTTING 2001). PIEGORSCH (1990) claimed to have corrected FISHER'S (1936) results for one experiment and declared FISHER'S criticism of Mendel to be unfounded. Other possible reasons for Mendel's biased results may include a subjective judgment of traits (NISSANI 1994), e.g. his own definition of a seed shape as "round" or "wrinkled".

### A statistical model to revisit Mendel's data

This section presents a new statistical model that may be used to address Mendel's experiments. Because the precise design of Mendel's experiments is not known, we propose a modification that follows PIRES & BRANCO (2010) and compare Mendel's results with randomly simulated data obtained by our own model.

We work with the results of Mendel's experiments organized in the form of 84 binomial experiments, i.e. in the same way as EDWARDS (1986) and PIRES & BRANCO (2010). As an illustration, let us describe the first of Mendel's 84 binomial experiments. In a given context, Mendel studied a given single trait and intended to verify the hypothesis that the ratio of two given phenotypes is 3:1. Statistically speaking, this will be the null hypothesis. Mendel planted  $n=7324$  pea plants. We introduce the notation  $p_0=3/4$  for the probability that a given plant has the dominant phenotype. The resulting number of plants with the dominant phenotype in the experiment was  $X=5474$ . The true but unknown probability of the given trait can be estimated by

$$\frac{X}{n} = \frac{5474}{7324} = 0.747 \quad (1)$$

We can interpret the value 5474 as the empirical counterpart of the expected value to be calculated under the null hypothesis as  $np_0 = 7324 * 3/4 = 5493$ .

We will examine the total number of 84 binomial experiments with a value of  $p_0$  equal to 1/2, 2/3, or 3/4. This corresponds to the probability of the presence of a given trait. The value of  $n$  in these experiments ranged between 19 and 8023.

The aim of Mendel's experiments was to make a decision concerning the validity of the null hypothesis. The  $\chi^2$  test can be used to perform an asymptotic test on the parameter of the binomial distribution. Figure 1 shows the  $p$ -values computed with the  $\chi^2$  test for the 84 experiments. Because the null hypothesis was true in all 84 situations, the histogram should correspond to uniform distribution which seems, however, fairly improbable. This is the core of the Mendel-Fisher controversy.

The exact design of Mendel's experiments is not known. PIRES & BRANCO (2010) proposed a new model for Mendel's experiments assuming that "Mendel would decide to repeat some experiments and report only the best results of both." This is speculation not

supported by historical evidence, but Mendel's results do not seem to contradict it. On the other hand, his results appear to be closer to such an assumption than to the assumption than each experiment was performed only once.

PIRES & BRANCO (2010) considered the criterion in the following form. If the  $p$ -value of the  $\chi^2$  test is lower than a fixed given threshold  $c$ , the experiment is repeated. Otherwise the test is not repeated. The criterion for repeating the experiment may be expressed as  $G(X) \geq 1-c$ , where  $G$  is the distribution function of  $\chi^2_1$  distribution. Here,  $X$  is assumed to be the realization of a random variable following the binomial distribution  $Bi(n, p)$ . The intention is to test the null hypothesis  $H_0 : p = p_0$  for a known value  $p_0$ . We formulate the criterion of PIRES & BRANCO (2010) in a form of a condition on  $X$ , which denotes the number of successful trials in the experiment.

*Algorithm 1:* The experiment is performed once with  $n$  plants. Let  $X$  denote the realization of the random variable with binomial distribution  $Bi(n, p)$  where the intention is to test the null hypothesis  $H_0 : p = p_0$  for the known value  $p_0$ . Let  $\chi^2$  denote the test statistic of Pearson's  $\chi^2$  test of independence. The experiment is performed once more, if and only if

$$\chi^2 \geq G^{-1}(1-c) \tag{2}$$

where  $G^{-1}$  is the inverse of the function  $G$ .

We now use the formula for the  $\chi^2$  test statistic in the form

$$\chi^2 = \frac{(2X-n)^2}{n} \tag{3}$$

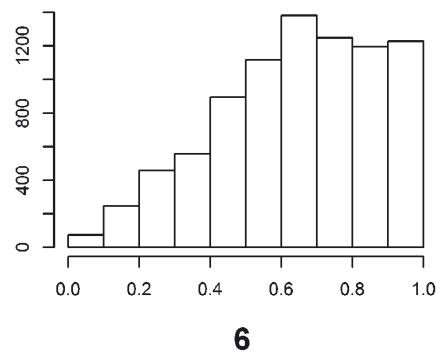
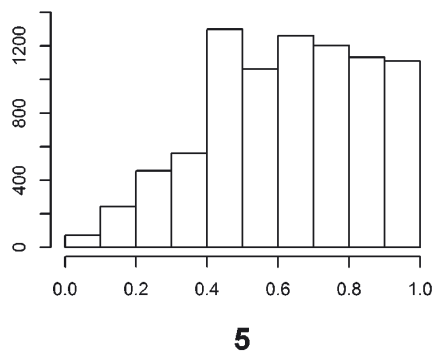
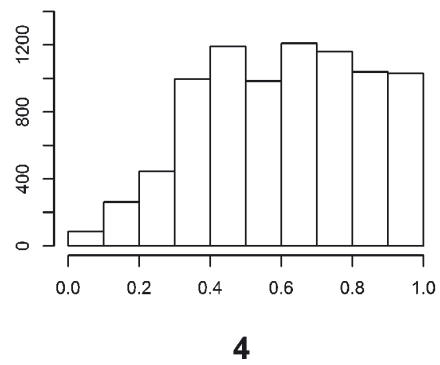
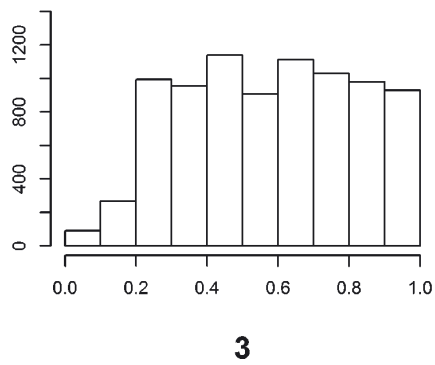
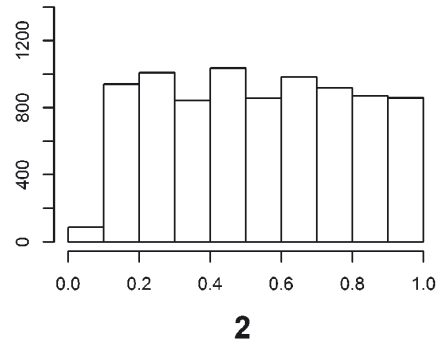
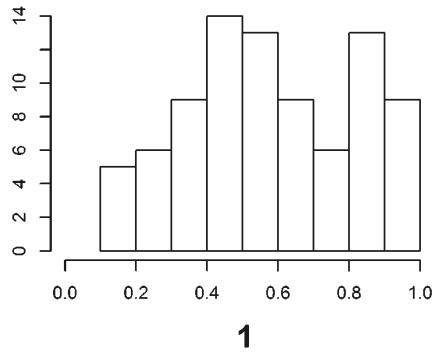
to derive an alternative formulation of the PIRES & BRANCO (2010) model.

*Theorem 1.* Under the assumptions of Algorithm 1, the following conditions are equivalent:

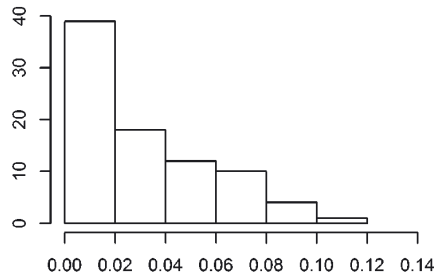
- i.  $\chi^2 \geq G^{-1}(1-c)$
- ii.  $p < c$  where  $p$  is the  $p$ -value of the  $\chi^2$  test
- iii.  $np_0 - (np_0(1-p_0)G^{-1}(1-c))^{1/2} \leq X \leq np_0 + (np_0(1-p_0)G^{-1}(1-c))^{1/2}$  (4)

**Table 1.** An equivalent formulation of the PIRES & BRANCO (2010) criterion.

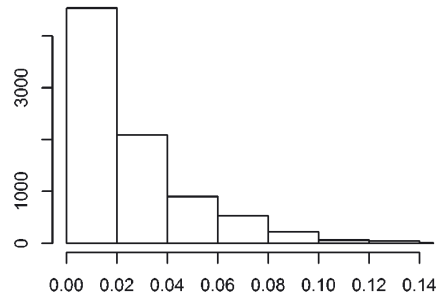
Value of $p_0$	Criterion (4) for repeating the experiment
$p_0 = 1/2$	$n/2 - 0.641\sqrt{n} \leq X \leq n/2 + 0.641\sqrt{n}$
$p_0 = 2/3$	$2n/3 - 0.604\sqrt{n} \leq X \leq 2n/3 + 0.604\sqrt{n}$
$p_0 = 3/4$	$3n/4 - 0.555\sqrt{n} \leq X \leq 3n/4 + 0.555\sqrt{n}$



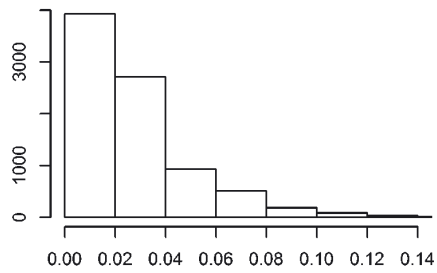
**Figs 1–6.** Statistical analysis of Mendel's 84 binomial experiments. 1 –  $p$ -values computed for Mendel's data by  $\chi^2$  test. 2–6 – Averaged results from 100 numerical simulations according to Algorithm 1 with  $c=0.1$  (Fig. 2),  $c=0.2$  (Fig. 3),  $c=0.3$  (Fig. 4),  $c=0.4$  (Fig. 5),  $c=0.5$  (Fig. 6).



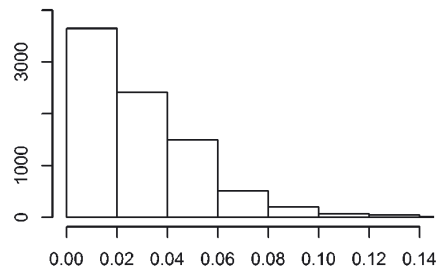
**7**



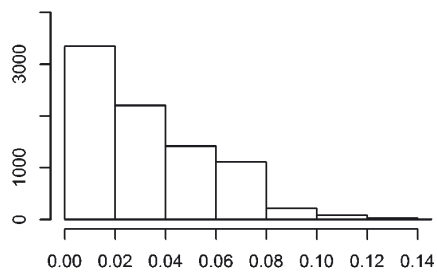
**8**



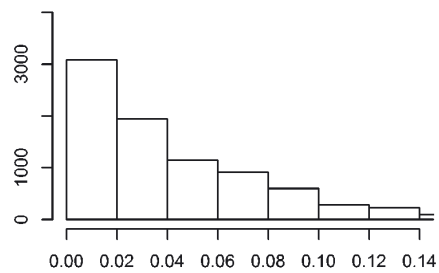
**9**



**10**



**11**



**12**

**Figs 7–12.** Statistical analysis of Mendel's 84 binomial experiments. 7 – Classification error (6) computed for Mendel's data. 8–12 – Averaged results from 100 numerical simulation according to Algorithm 2 with  $k=0.02$  (Fig. 8),  $k=0.04$  (Fig. 9),  $k=0.06$  (Fig. 10),  $k=0.08$  (Fig. 11),  $k=0.10$  (Fig. 12).



Table 1 evaluates the criterion (4) for particular choices of  $p_0$ . Value  $c$  is replaced by 0.201, which is the most suitable constant suggested by PIRES & BRANCO (2010).

A numerical simulation was performed according to Algorithm 1 with different values of threshold  $c$ . We simulated a binomial random variable for each of Mendel's 84 experiments. The  $i$ -th variable for  $i = 1, \dots, 84$  was generated from the binomial distribution  $Bi(n_i, p_i)$  where  $n_i$  is the total number of plants in Mendel's  $i$ -th experiment and  $p_i$  is the assumed (expected) probability of a given trait in the same experiment. We repeated the numerical simulation 100 times and the computed averages are shown in Figs. 2–6. These may be interpreted as approximations to the real  $p$ -values computed for Mendel's data by the  $\chi^2$  test.

The extreme cases  $c=0$  and  $c=1$  are not shown. For  $c=0$ , each experiment is performed only once and the  $p$ -values correspond to uniform distribution. For  $c=1$ , each experiment is performed twice; in this case, the distribution of the  $p$  values corresponds to a maximum of two independent uniformly distributed random variables. Thus, the choice  $c=1$  corresponds to a linearly increasing trend in the entire interval between 0 and 1.

PIRES & BRANCO (2010) found the value  $c=0.201$  to yield optimal correspondence with Mendel's results. In other words, the histogram of simulated data in Fig. 3 should correspond best to the histogram of real data in Fig. 1. Nevertheless, we do not see this correspondence as very convincing.

In the light of expression (4), the interpretation of Algorithm 1 appears quite complicated, considering the fact that Pearson's  $\chi^2$  test came into use only in 1900, i.e. after Mendel's death. At that time, the principles of statistical hypothesis testing had not been formulated either.

We propose an alternative algorithm with a clearer interpretation. It is based on the quantity

$$\frac{|X - np_0|}{n} \quad (5)$$

This is the difference between  $X$  and the expected value of  $X$  divided by the number of observations.

The quantity in (5) can be also interpreted as a classification error obtained under the null hypothesis. To illustrate this, let us consider the first of the 84 Mendel's binomial experiments with  $X = 5474$  and  $n = 7324$  and  $p_0 = 3/4$ . The quantity (5) compares the value  $X$  with  $np_0 = 5493$  and is equal to 0.0026. It can be stated that  $X - np_0 = 19$  is the number of plants differing in their real trait from the trait which is expected under the null hypothesis. Thus, under the null hypothesis 5493 out of 7324 plants are expected to be classified with the dominant phenotype. However, the reality deviates from this expected result by a classification error equal to 19 plants.

Our criterion based on (5) may be described in the following way. If this ratio exceeds a fixed given threshold  $k$ , the experiment is repeated. Otherwise the test is not repeated. The criterion corresponds to comparing observed counts with their theoretical

counterpart computed under the null hypothesis and standardising them by the number of observations.

*Algorithm 2:* We assume that the number of plants with the phenotype under consideration follows the binomial distribution  $Bi(n, p_0)$ . The experiment is performed once with  $n$  plants, and let the resulting number of plants with the phenotype under consideration be denoted by  $X$ . The experiment is performed once more, if and only if

$$\frac{|X - np_0|}{n} \geq k \quad (6)$$

It is now trivial to formulate Algorithm 2 in an equivalent (and more practical) way.

*Algorithm 2 (equivalent formulation):* We assume that the number of plants with the phenotype under consideration follows the binomial distribution  $Bi(n, p_0)$ . The experiment is performed once with  $n$  plants and let the resulting number of plants with the phenotype under consideration be denoted by  $X$ . The experiment is performed once more, if and only if

$$n(p_0 - k) \leq X \leq n(p_0 + k) \quad (7)$$

The true values of the quantities (6) computed for Mendel's 84 experiments are shown in Fig. 7. Further, we performed a numerical simulation to study the performance of Algorithm 2 on Mendel's data. As above, we generated random variables following a binomial distribution for each of Mendel's 84 experiments. Each simulation was repeated 100 times and the results were averaged. Figures 8–12 show the histograms of 84 averaged values obtained by Algorithm 2 using various values of the constant  $k$ . A very small value for  $k$ , which corresponds to performing each experiment twice, seems unrealistic. On the other hand, a very large value for  $k$  in Algorithm 2 requires each experiment to be performed only once. The optimal  $k$  seems to lie between these two extremes.

Based on Figs. 7–12, we may subjectively select the value  $k = 0.04$  to yield the best correspondence between the real values of (6) and the simulated values. In other words, Fig. 9 corresponds to Fig. 7 better than any other histogram for other values of  $k$ .

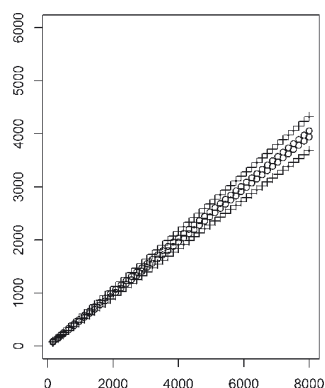
The expression (7) is simple and intuitive, contrary to expression (4). Thus, we may suggest that we have proposed a fairly simple model that appears to fit to Mendel's results well. Table 2 illustrates particular values of the lower and upper limits obtained from (7) for a wide range of values of  $n$ .

Let us compare the limits given by Algorithms 1 and 2. The optimal values of the thresholds for (4) and (7) are shown in Figures 13–15 for various values of  $n$ , particularly for  $p_0 = 1/2$  (Fig. 13),  $p_0 = 2/3$  (Fig. 14), and  $p_0 = 3/4$  (Fig. 15). It follows from (7) that Algorithm 2 requires  $X$  to lie between limits that are obtained as a linear function of  $n$ . The graphs show the limits (4) obtained by Algorithm 1 to be close to linear. The limits obtained by Algorithm 2 appear to be substantially farther apart than those obtained by Algorithm 1.

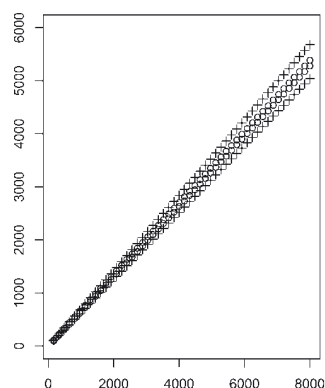
This brings us to the proposal that Mendel may have repeated an experiment for a second time more often than assumed by PIRES & BRANCO (2010). Moreover, if Mendel performed his experiments according to Algorithm 2, it would be possible to state that he did not falsify the results. Assuming Algorithm 2 further, it would be possible to say that the design of the experiments was responsible for the bias in Mendel's results, compared to a situation in which each experiment was performed only once.

**Table 2.** Lower and upper limits of Algorithm 2 obtained from (7) for  $p = 1/2$  and the optimal value  $c = 0.04$ .

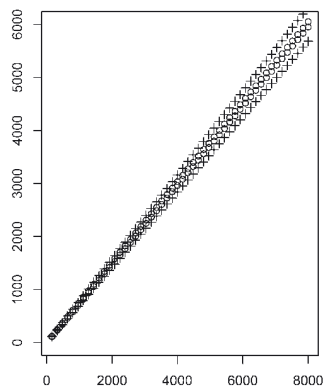
$n$	30	100	300	1000	8000
$n(p - c)$	14	46	138	460	3680
$n(p + c)$	16	54	162	540	4320



**13**



**14**



**15**

**Figs 13–15.** Comparison of Algorithms 1 and 2 for explaining the results of Mendel's binomial experiments. Lower and upper limits of the criterion for repeating the experiment for various values of the number of plants  $n$  in the first experiment. The circles denote the lower and upper limits of interval (4) for  $X$  obtained according to Algorithm 1 for  $c = 0.201$ . The plus signs denote the lower and upper limits of the interval (7) for  $X$  obtained according to Algorithm 2 for  $k = 0.04$ . Three situations for  $p_0 = 1/2$  (Fig. 13),  $p_0 = 2/3$  (Fig. 14),  $p_0 = 3/4$  (Fig. 15).

### Conclusions

Mendel's experimental work in genetics demonstrated that he was a scientist of exceptionally high intelligence and insight. His results became one of cornerstones of modern biological theory. Mendel had a fervent passion for scientific experiments and his thoroughness, inductive thinking, and technical competence were carried over into his experimental research in genetics, beekeeping, and meteorology. At the same time, events revealed that he was patient, stubborn, and goal-directed, even intransigent. He had to be well aware of the phenomenal importance of his results, although it was the early 20th century before his work found wider currency, for some time largely misinterpreted. The underlying mechanisms had to await the momentous work of WATSON & CRICK(1953) and CRICK (1990)

Mendel's work has been subject to a number of controversies, some of them far from over. While Mendel may be considered a founder of mathematical biology, his work led to intense debate from the statistical point of view. Some of the ongoing discussions concern not only his background in probability, but also his education and social commitment in the role of the abbot. Recent analyses have shown possible statistical, biological, philosophical (SEKERÁK 2007), and historical reasons for Mendel's results being so close to expected values and they consistently make no accusations of intentional falsification.

While Mendel's fascination extends to specialists in various disciplines, this paper aims to interpret his results from a particular statistical point of view. We assume that Mendel repeated an experiment if a simple quantity exceeded a given threshold. Such a quantity may be interpreted as a classification error. We search for arguments in favour of this model by investigating Mendel's binomial experiments with various probabilities (1/2, 2/3, 3/4) that a given plant has a given dominant phenotype. The model described as Algorithm 2 is validated by means of a numerical simulation. The criterion for repeating the experiment is illustrated in Figs 13–15.

While PIRES & BRANCO (2010) proposed a statistical model allowing us to hope that "the controversy is finally over", we have shown a numerical simulation that fits Mendel's data even more reliably and seems to offer a more realistic explanation of his results. We hope, therefore to have contributed to rehabilitating Mendel's legacy by a new interpretation of his results from another statistical point of view.

### Acknowledgements

This paper was supported by the Neuron Fund for Support of Science. The author is grateful to Anthony Long, Svinošice, for suggestions valuable to the improvement of this contribution.

### References

- BOX J.F. 1978: *R.A. Fisher: The life of a scientist*. Wiley, New York.  
CRICK F. 1990: *What mad pursuit: A personal view of scientific discovery*. Basic Books, New York.  
DASTUR A.E., TANK P.D. 2010: Gregor Johann Mendel: The father of modern genetics. *Journal of Prenatal Diagnosis & Therapy* 1: 3–4.

Gregor Mendel, his experiments and their statistical evaluation

- EDWARDS A.W.F. 1986: Are Mendel's results really too close? *Biological Reviews* **61**: 295–312.
- FAIRBANKS D.J., RYTTING B. 2001: Mendelian controversies: A botanical and historical review. *American Journal of Botany* **88(5)**: 737–752.
- FISHER R.A. 1918: The correlation between relatives on the supposition of Mendelian inheritance. *Transactions of the Royal Society of Edinburgh* **52**: 399–433.
- FISHER R.A. 1936: Has Mendel's work been rediscovered? *Annals of Science* **1**: 115–137.
- FOLTÝN D. et al. 2005: *Encyklopedie moravských a slezských klášterů*. Libri, Praha. (In Czech.)
- FRANKLIN A., EDWARDS A.W.F., FAIRBANKS D.J., HARTL D.L., SEIDENFELD T. 2008: *Ending the Mendel-Fisher Controversy*. University of Pittsburgh Press, Pittsburgh.
- FRIEDEN B.R. 1998: *An unexpected union? Physics and Fisher information*. Cambridge University Press, New York.
- GUSTAFFSON A. 1969: The life of Gregor Johann Mendel—Tragic or not? *Hereditas* **62**: 239–258.
- HENIG R.M. 2000: *The monk in the garden: The lost and found genius of Gregor Mendel, the father of genetics*. Houghton Mifflin Harcourt, Boston.
- ILTIS H. 1924: *Johann Gregor Mendel, Leben, Werk und Wirkung*. Springer, Berlin.
- KŘÍŽENECKÝ J. 1965: *Gregor Johann Mendel 1822–1884. Text und Quellen zu seinem Wirken und Leben*. Deutsche Akademie der Naturforscher Leopoldina, Halle.
- KURIAN G. 2012: *The encyclopedia of Christian civilization*. Wiley, New York.
- LYELL C. 1830, 1832, 1833: *Principles of geology* 1, 2, 3. John Murray, London.
- MALÝ R. 2002: *Církevní dějiny*. Matice cyrilometodějská, Olomouc. (In Czech.)
- MATALOVÁ A. 2007: Mendelovo rodiště na kulturní mapě Evropy třetího tisíciletí. *Informační listy*, Genetická společnost Gregora Mendela, No. 32, 14–19. (In Czech.)
- MATALOVÁ A. 2008: Primary sources to Johann Gregor Mendel's early years. *Folia Mendeliana* **42–43**: 7–11.
- MAWER S. 1997: *Mendel's dwarf*. Transworld, Ealing.
- MENDEL G. 1866: Versuche über Pflanzen-Hybriden. *Verhandlungen des Naturforschenden Vereines in Brünn* **4**: 3–47. (First English translation in 1901, *Journal of the Royal Horticultural Society* **26**: 1–32.)
- MIKO I. 2008: Gregor Mendel and the principles of inheritance. *Nature Education* **1** (1).
- NISSANI M. 1994: Psychological, historical, and ethical reflections on the Mendelian paradox. *Perspectives in Biology and Medicine* **37**: 182–196.
- NOVITSKI E. 2004a: On Fisher's criticism of Mendel's results with the garden pea. *Genetics* **166**: 1133–1136.
- NOVITSKI C.E. 2004b: Revision of Fisher's analysis of Mendel's garden pea experiments. *Genetics* **166**: 1139–1140.
- OŘEL V. 2003: *Gregor Mendel and beginnings of genetics*. Academia, Prague. (In Czech.)
- PIEGORSCH W.W. 1990: Fisher's contributions to genetics and heredity, with special emphasis on the Gregor Mendel controversy. *Biometrics* **46**: 915–924.
- PIRES A.M., BRANCO J.A. 2010: A statistical model to explain the Mendel-Fisher controversy. *Statistical Science* **25(4)**: 545–565.
- PLAČEK V. 1974: *Slezské muzeum Opava 1814–1974*. Slezské muzeum v Opavě, Opava. (In Czech.)
- POSNER E., SKUTIL J. 1968: The great neglect: The fate of Mendel's classic paper between 1865 and 1900. *Medical History* **12(2)**: 122–136.
- RÉDEI G.P. 2002: Vignettes of the history of genetics. In Kang M.S. (Ed.): *Quantitative Genetics, Genomics, and Plant Breeding*. CABI Publishing, Oxford, pp. 1–20.
- RICHTER O. 1943: Johann Gregor Mendel wie er wirklich war: Neue Beiträge zur Biographie des berühmten Biologen aus Brüns Archiven. *Verhandlungen des Naturforschenden Vereines in Brünn* **74(2)**: 2–262.
- SAMEK B. 1993: *Klášter augustiniánů v Brně*. Památkový ústav, Brno. (In Czech.)
- SEKERÁK J. 2007: *Problém filosofické interpretace přírodovědného textu: G.J. Mendel*. Doctoral thesis, Masaryk University, Brno. (In Czech.)
- VYBRAL V. 1968: Der Streit Mendels mit der Staatsverwaltung über die Beitragspflicht des Klosters zum Religionsfonde. *Folia Mendeliana* **6**: 231–237.
- WATSON J.D., CRICK F.H.C. 1953: A structure for deoxyribose nucleic acid. *Nature* **171**: 737–738.
- WEILING F. 1986: Das Wiener Universitätsstudium 1851–1853 des Entdeckers der Vererbungsregeln Johann Gregor Mendel. *Folia Mendeliana* **21**: 9–40.
- WELDON W.F.R. 1902: Mendel's laws of alternative inheritance in peas. *Biometrika* **1(2)**: 228–254.
- ZLÁMAL B. 1936: *Ke kulturnímu významu starobrněnského opata P. Cyrila Nappa (1792–1867)*. Velké Meziříčí. (In Czech.)