ON THE BICENTENNIAL OF MENDEL'S BIRTH, ATTEMPTING TO RECOVER MENDEL'S INHERITANCE PRINCIPLES WITH MENDEL'S EYES

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ABSTRACT – The term "Mendel's laws" was first coined by Carl Correns, mainly referring to the law of segregation and of independent assortment in general. However, in Mendel's 1866 paper, once using Mendel's own symbol system to represent the selfing reproduction of F_1 hybrid, a sequential mathematical expression could be recovered here: Aa × Aa → (A + a)(A + a) = A/A + a/a + A/a + a/A = A + 2Aa + a → 3A + a. Clearly, the perfect square formula together with both the upstream input and the downstream output could be figured out in the sequential expression, respectively corresponding to the principles of reproductive cells formation, of fertilization, and of seeds developments, all were lectured in his second speech in 1865. Then, the expression could be unambiguously resolved into more than ten items of inheritance laws. If it is acknowledged that Mendel utilized the perfect square formula to mimic the behavior of bisexual gametes in process of sexual reproduction, the pair of symbols, A, and a, can be seen having three different senses, gametes, factors, and traits. In fact, one factor carried by one gamete with capacity to transmit one trait to offspring was eventually exemplified in his later controlled pollination experiment in Mirabilis jalapa. At last, we proposed that Mendel's speculation of function of the factor in development process had both properties of holism and of reductionism, needing to be further studied in future.

KEY WORDS: Mendelism, Mendel's gamete theory of inheritance, the principles of reproductive cell formation, the principles of fertilization, the principles of seed development

INTRODUCTION

"Mendel's Law" was first coined as a term in 1900 by Car G. Correns, one of the three rediscoverers of Mendel's hybridization experiments in *Pisum*[1)]. In March 9, 1865, Mendel had given a special lecture to "speak about (reproductive) cell formation, fertilization, and seed production in general, and in the case of hybrids in particular ... *(spracher über Zellenbildung, Befruchtung und Samenbildung überhaupt und bei den Hybriden insbesondere...)*"[2)]. In light of the two separate reports in *Neuigkeiten*, it is believed that was a deliberate time made by Mendel himself for presenting his discovery of inheritance, “Mendel’s laws”, just following the lecture concerning hybrid in evolution prior in February 9.[3)]

Here, Mendel’s “Mendel’s laws” could be deciphered from the 1866 paper by using his own symbol system to string his main discoveries together (Mendel’s 1866 paper was in German; see in both German and English that was translated by S. Müller-Wille and K. Hall, available at: http://www.bshs.org.uk/bshs-translations/mendel)[4, 5)]. As for the selfing reproduction of F_1 monohybrid, Mendel’s core presentation $A/A + a/a + A/a + a/A = A + 2Aa + a$, could be extended toward the two flanking into a sequential mathematical expression, $Aa \times Aa \rightarrow (A + a)(A + a) = A/A + a/a + A/a + a/A = A + 2Aa + a \rightarrow 3A + a$. As it is, the perfect square formula acting as a mediator appropriately links Mendel’s operational input “$Aa \times Aa$” and his resultant output “$3A + a$”, implying the rather important position of the binomial theory in the process of Mendel digging out the scientific laws of inheritance. On the other hand, the sequential link signs in the expression precisely reflect three successive processes of plant reproduction: gamete production, fertilization, and seed development. Not surprisingly, in line with Mendel’s own claims in his second lecture, they also perfectly correspond to the principle of gamete production, of fertilization, and of seed development. Here, adopting Mendel’s own symbol system in his published paper and with some of our developments, the claimed three inheritance principles were recovered as following.

PRINCIPLES OF REPRODUCTIVE CELL FORMATION

Mendel’s description of reproductive cell formation was not associated with the observation of chromosome behavior in meiosis, instead, perfectly based on the mathematical expression he obtained. The law of segregation could be recovered as $Aa \times Aa \rightarrow (A + a)(A + a)$, where in Mendel’s nomenclature *Aa* was called as “hybrid form (die Hybridform)” and the two letters in parentheses $(A + a)$ were regarded as both the two sorts of bisexual gametes and their corresponding internal factors. Originally, Mendel sentenced the segregation that “it is only possible for the differentiating elements to liberate themselves from the enforced union when the fertilizing cells are developed (*müssten wir weiter folgern, dass es den differirenden Elementen erst bei der Entwicklung der Befruchtungszellen gelinge, aus der erzwungenen Verbindung herauszutreten*)”. The law of independent assortment could be developed into $AaBb \times AaBb \rightarrow [(A + a)(B + b)]^2 \rightarrow (AB + ab + Ab + aB)^2$, and was written in the paper that “in the formation of these cells all existing elements participate in an entirely free and equal arrangement by which it is only the differentiating ones which mutually separate themselves (*Bei der Bildung dieser Zellen betheiligen sich alle vorhandenen Elemente in völlig freier und gleichmässiger Anordnung, wobei nur die differirenden sich gegenseitig ausschliessen*)”. As a conclusion, Mendel asserted that “In this way the production would be rendered possible of as many sorts of egg and pollen cells as there are combinations possible of the formative elements (*Auf diese Weise würde die Entstehung so vielerlei Keim- und Pollenzellen ermöglicht, als die bildungsfähigen Elemente Combinationen zulassen*).

Here the possible combinations of the formative elements in equal number refer to “1*A:* 1*a*” in monohybrid experiment, as well as “1*AB*: 1*Ab*: 1*aB*: 1*ab*” in dihybrid experiment. As cited above, such symbol sorts and their ratios were already used by Mendel to reflect not only the abstract elements but also the amenable gametes. In literal, Mendel originally symbolized “*A* and *a*” to denote “two contrasting characters (*beiden Constanten Merkmale*)” or “two constant forms (*beiden Constanten Formen*)”, the former of which was dominant one (*das dominirende*), and the latter was recessive one (das recessive). Indeed, these numerical features of the microscopic gametes and the invisible elements were intelligently testified by the obtained sorts and ratios of the observable constant forms (1*A:* 1*a*) and their combinations (1*AB*: 1*Ab*: 1*aB*: 1*ab*) in his testcrosses of monohybrid and dihybrid in *Pisum* respectively. Altogether, the two letters *A* and *a* (indeed including the four combinations *AB*, *Ab*, *aB*, and *ab*) had three different implications, gametes, factors, and traits. Hartl and Orel early noticed that in Mendel's own conceptual system a pair of capital and lowercase letters *A* and *a* could represent different senses corresponding to different situations.[6)]

In Mendel's eyes, the principle of gamete formation could be simulated by using the symbols as following:

1) Law of segregation: *Aa* (♀) → (*A* + *a*); *Aa* (♂) → (*A* + *a*).
2) Law of free combination: *AaBb* (♀) → (*A* + *a*)(*B* + *b*) = (*AB* + *Ab* + *aB* + *ab*);
AaBb (♂) → (*A* + *a*)(*B* + *b*) = (*AB* + *Ab* + *aB* + *ab*).

PRINCIPLES OF FERTILIZATION

It is easy to understand, once Mendel perceived that the perfect square formula in combination mathematics, $(a + b)(a + b) = a^2 + 2ab + b^2$, could be applied to vividly mimic the uniting behavior of bisexual gametes in fertilization process of plant sexual reproduction, almost everything in his inheritance study had been achieved. Mendel's breakthrough insight that the two mathematical symbols *A* and *a* could dress up themselves as two kinds of gametes of male or female, suddenly opens a pretty broad pathway up for him to further study. On the one hand, the amenable gametes, particularly pollen grains easy to be controlled under microscope, provide Mendel an operable target on experimental platform in cellular level. In fact, Mendel succeeded in designing the alleged testcross experiments to testify his assumptions regarding the behavior of different kinds of gametes in fertilization, including the bulked pollination experiments in *Pisum* and the controlled pollination experiments in *Mirabilis jalapa* in his later life[7)]. On the other hand, through selecting various kinds of parental characters in different species and/or different varieties in his experiments, Mendel could utilize them to mark gametes then to study the behavior of markers named as factors in fertilization, as well as their functions in subsequent development process. The markers were assumedly carried by gametes.

With a lot of intelligent scientific dealing, the perfect square formula could be transformed into the expression, $(A + a)(A + a) \rightarrow A/A + a/a + A/a + a/A$, mainly to express the random uniting of bisexual gametes and the formation of primordia cells in fertilization process. Indeed, the principle of fertilization was also written in the paper by Mendel himself in a literally narrative style rather than a mathematical presentation, a similar presenting style of the principle of gamete formation mentioned above. In section of "the reproductive cells of the hybrids", Mendel asserted "It is entirely left to chance which of the two pollen kinds joins with each individual germ cell (*Es bleibt ganz dem Zufalle überlassen, welche von den beiden Pollenarten sich mit jeder einzelnen Keimzelle verbindet*)". Therefore, the random combination between male and female gametes in reproduction process was presented by means of using feather arrows in the context, just as an illustrative presentation of the perfect square formula, quite analogous to the forked line method of genetics analysis in modern genetics.

Mendel knew that the prerequisite for establishment of the perfect square formula is one term in the first binominal only uniting with one term in the second binominals, which could perfectly correspond to one to one relationship between male gamete and female gamete in fertilization. He stated that "according to the rules of probability it will always occur on the average of many cases that each pollen form *A* and *a* unites equally often with each germ form *A* and *a*; one of the two pollen cells *A* will therefore come together with a germ cell *A*, the other with a germ cell *a* in fertilization, and in the same manner a pollen cell *a* will be joined with a germ cell *A*, and the other with *a* (*Indessen wird es nach den Regeln der Wahrscheinlichkeit im Durchschnitte vieler Fälle immer geschehen, dass sich jede Pollenform A und a gleich oft mit jeder Keimzellform A und a vereinigt; es wird daher eine von den beiden Pollenzellen A mit einer Keimzelle A, die andere mit einer Keimzelle a bei der Befruchtung zusammentreffen, und eben so eine Pollenzelle a mit einer Keimzelle A, die andere mit a verbunden werden*)". And also, he was aware of that the resultant data of his bulked pollinations of hybridization experiments in *Pisum* had an average property, that is, the so-called "on the average" in the sentence above. However, Mendel only referenced "the opinion of renowned physiologists, for the purpose of propagation one pollen cell and one egg cell unite in Phanerogams into a single cell (*der Ansicht berühmter Physiologen vereinigen sich bei den Phanerogamen zu dem Zwecke der Fortpflanzung je eine Keim- und Pollenzelle zu einer einzigen Zelle*)". Consequently, Mendel's neglect of this deficiencies in his bulked pollinations in *Psium*, shortage of explicit numerical relationship between bisexual gametes in fertilization, led him to do the single and double pollen grains pollination experiments in *M. jalapa* in his later life, even taking the risk of his eyes illness.[7, 8)]

In order to disprove Darwin's opinion regarding three pollen grains required for a fertilization event, which could completely break into pieces the rightness of the perfect square formula in plant reproduction that he discovered and the physiologist's opinion in fertilization that he referenced, Mendel had to initiate the controlled pollination experiments in *M. jalapa*. At last, according to the content of Mendel's letters to Nägeli preserved, his experimental results of single pollen grain pollination, together with the designed pedigree frameworks of both the single and the two pollen grain experiments, essentially exemplified that in one fertilization one factor carried by one pollen cell could unite with another factor carried by one ovule cell. Furthermore, retrospectively, in contrast with the bulked pollination experiment in *Pisum* and the other plant materials, in the controlled pollination experiments in *M. jalapa* Mendel could easily manipulate a hereditary factor by merely taking a gamete as its carrier to transmit a trait to offspring. Here Mendel's accurately positioning a factor in a gamete was suggested to be coined as the Gamete Theory of Inheritance, just aiming to mimic the nomenclature of Sutton-Boveri's Chromosome Theory of Inheritance then make it easy to place Mendel's discovery in the historical line of origin and development of genetics.[7, 8)]

Additionally, when Mendel investigated the reproduction or fertilization in *Pisum,* the ovist and spermist visions of generation that almost dominated the scientific thinking of eighteenth-century even by the early years of nineteenth century, still did not realized that both sexes contributed equally to the offspring 9). Mendel might catch the insight of parental equal contributions in plant cross once noticing the consistent results in reciprocal crosses. And, the testified one-to-one relationship between bisexual gametes in *M. jalapa* also told Mendel that the parental factor and maternal factor coming together in primordial cells might have equal contributions to offspring. Sure, how about the functions of the two factors in one zygotic cell indeed relates to the principle of seed development as introduced below. Comprehensively summarizing Mendel's principle of fertilization, it could be simulated by using the symbols with no knowledge of chromosomes in meiosis, just as following:

1) Law of random fertilization:

$$(A + a)(A + a) \rightarrow A/A + a/a + A/a + a/A$$

2) One factor in pollen cell uniting one factor in egg cell (also named "Equal contribution of parents"):
$1A \times 1A \rightarrow 1A/A$; $1A \times 1a \rightarrow 1a/A$; $1a \times 1A \rightarrow 1A/a$; $1a \times 1a \rightarrow 1a/a$

PRINCIPLES OF SEED DEVELOPMENT
Laws of development of qualitative characters

The mathematical equation that Mendel solely presented in his 1866 paper was $A/A + a/a + A/a + a/A = A + 2Aa + a$. The three items in right side of the equation was also used by Mendel to represent the three discernible characters in the offspring of hybrid. The two constant forms, *A* and *a*, were respectively named as the dominant one and the recessive one as introduced above, meanwhile, the symbols of *A* and *Aa* were also termed as "parental character (*Stamm-Character*)" and "hybrid character (*Hybriden-Merkmales*)" respectively in the paper. If staring at the figure of the segregation of F_2 seed traits in the pods of a selfed F_1 pea plant in plate that was firstly made by A. D. Darbishire[10)], Figure 1, and imaging the uniform appearance of seed traits in the pods produced from a selfed plant of constant form, it is easy to understand Mendel could explicitly distinguish the separable/variable dominance from the constant dominance in his eyes. In the original text, Mendel stated that "The dominating trait can have a *double meaning* here, namely that of parental characteristic or that of hybrid trait. In which of the two meanings it appears in each individual case can only be decided by the next generation. As a parental trait, the same must devolve without alteration to all descendants, as a hybrid trait on the other hand it must observe the same behavior as in the first generation (*Das dominirende Merkmal kann hier eine doppelte Bedeutung haben, nämlich die des Stamm-Characters oder des Hybriden-Merkmales. In welcher von beiden Bedeutungen dasselbe in jedem einzelnen Falle vorkommt, darüber kann nur die nächste Generation entscheiden. Als Stamm-Merkmal muss dasselbe unverändert auf sämmtliche Nachkommen übergehen, als Hybriden-Merkmal hingegen ein gleiches Verhalten wie in der ersten Generation beobachten*)".

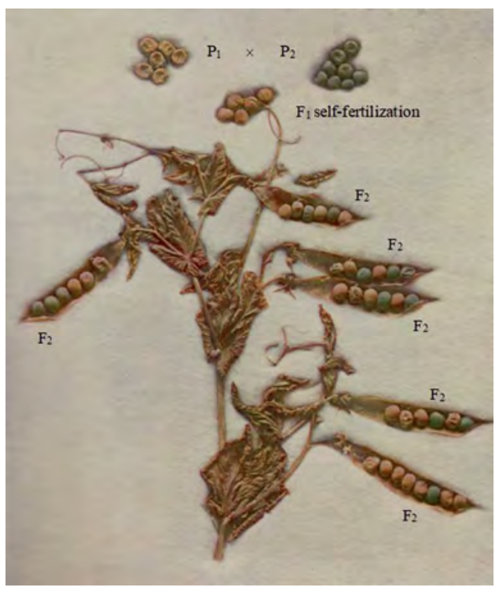

Fig. 1. The observable segregation of F_2 seed traits in the pods of a selfed F_1 pea plant. Seed color (yellow versus green) and shape (round versus wrinkled) segregate independently. Mendel may have distinguished the segregation appearance in both seed traits from the corresponding constant transmission in the pods of a selfed homozygote plant (adopted from VAN DIJK et al, 2022).

After seeing Mendel's unique usage of the three symbols, *A*, *Aa*, and *a* to express the three distinguishable characters in the 1866 paper, we should no longer criticize that Mendel had not adopted the modern usage of *AA* and *Aa* to respectively represent homozygous and heterozygous genotypes[6, 11]. As far as the genotypes of offspring of F_1 hybrid is concerned, they were denoted by Mendel himself with the four fractions in the left side of the equation, *A*/*A*, *a*/*a*, *A*/*a*, and *a*/*A*. All four fractions were derived from the illustrative simulation of the random fertilization, so the two letters in fractions represent the composition of two factors in one primordia cell. Mendel termed *A*/*A* and *a*/*a* as "constant-union (*constant Vereinigung*)" while *A*/*a* and *a*/*A* as "hybrid-union (*hybrider Vereinigung*)", respectively corresponding to homozygous and heterozygous genotypes in modern genetics. It is worth to note here Mendel's two fraction forms designed to represent the modern heterozygous genotypes imply he also noticed the phenotypic difference of offspring from the reciprocal crosses. Thus, the published equation could perfectly reflect relationships between the four genotypes and the three phenotypes, consistent with the sharp insight that the equation "summarizes the expected genetic constitutions of the progeny of hybrid on the left and gives their physical and breeding characteristics on the right"[6].

No doubt, the published equation might be the core expression of "the principle of seeds development" that Mendel orally presented in 1865. The development process should refer to not only the formation of seed, but also the subsequent vegetable growth as well as following reproductive growth. Mendel explained the equation as "The differentiating feature (here we translated "Merkmale" as "feature" in common sense, just distinguished from the genetics concept of "trait" or "character". Please see the similar treatment in Zhang's paper in Genetics, 2017) [3] of two plants can, in the end, only depend upon differences in the constitution and grouping of the elements that stand in vital interaction in their foundation cells (*Die unterscheidenden Merkmale zweier Pflanzen können zuletzt doch nur auf Differenzen in der Beschaffenheit und Gruppirung der Elemente beruhen, welche in den Grundzellen derselben in lebendiger Wechselwirkung stehen*)". Here besides "the constitution of the elements" (the generally known genotype), two else things of "the grouping of the elements" and the "vital interaction in their foundation cells" were also put forward by Mendel as the causes for phenotype in parallel. The mutual interactions between many factors in group that are responsible for the same one character might not only include the intra-factor-pair (interallelic) and also inter-factor-pairs (non-allelic) interactions in modern genetics. In Mendel's hybridization experiments, the former could be the complete dominance that produces 3*A*:1*a* in the two seeds characters in *Pisum* (1*A*:2*Aa*:1*a* → 3*A*:1*a*), or the incomplete dominance only producing 1*A*:2*Aa*:1*a* in the study of flower colors in *M. jalapa*, and so on; the latter could be the cumulative interactions between multiple factor-pairs in development of quantitative characters as introduced below.

Furthermore, Mendel also stated that "This development occurs according to a constant law, which is grounded in the material constitution and the arrangement of the elements that attained a viable union in the cell (*Diese Entwicklung erfolgt nach einem constanten Gesetze, welches in der materiellen Beschaffenheit und Anordnung der Elemente begründet ist, die in der Zelle zur lebensfähigen Vereinigung gelangten*)". Here it is worth pointing out that "the arrangement of the elements" might refer to the linear arrangement of factors in chromosome that was later discovered by T. H. Morgan, but also, very likely referred to "the position effect" as demonstrated in the designed fraction form of his four genotypes. It is clearly introduced by Mendel as that "in the form of fractions, with the pollen cells above, and the germ cells below the line (*in Bruchform angesetzt werden, und* *zwar für die Pollenzellen über, für die Keimzellen unter dem Striche*)". Mendel had taken the bipaternal origin of the two factors in one somatic cell into account, implying the common phenomenon in animal reproduction such as difference between mule (horse × donkey) and hinny (donkey × horse) might ever attract his attention in the daily life. Trying to figure out whether it is the maternal influence in genetics or parental imprint in epigenetics that is responsible for mule different from hinny makes no sense in reality. The words "arrangement" in writing and the "fraction forms" in demonstrating jointly exemplified that not only factors themselves, but also the certain mechanisms that could link the factors with their parental origin in time and/or their intracellular distribution in space, now called as epigenetic mechanism or spatiotemporal influence, were all considered by Mendel as the possible causes for the corresponding character development in his genetics thoughts. On the other hand, Sekerák interpreted the expression "arrangement of elements (*Anordnung der Elemente*)" as "Mendel's discovery of inherited information" [12, 13)], which was also evidenced by Mendel's usage of "expressed (*ausgesprochen*)" to describe the functional run of factors (*Anlage*) in his 9th letter to Nägeli.[8)]

At first sight, here is no position set aside by Mendel for environment, a pretty important aspect that is generally regarded as cause for character or phenotype in his equation expression as well as in his interpretative words. This is the reason why Mendel was usually regarded as holding a view that "environmental changes do not cause inherited changes" [14)]. In fact, the equation was the resultant expression of a mathematical running, thus no position for environmental effect to set. Then, aiming to explain the equation, Mendel had smartly taken a unique methodology of "the difference principle", interpreting it as "the difference between two plants" was due to "the difference between two genotypes". C. K. Waters stated that "The difference principle is easily applied to experimental contexts because geneticists deliberately simplified the causal situation by standardizing environmental conditions......"[15)]. That is, by uniformizing environmental conditions, Mendel erased the environmental effect for the phenotypic difference. R. C. Lewontin ever pointed out that "Given the genotype, the phenotype corresponding to it was unambiguously defined, at least under the condition of Mendel's experimental garden" [16)]. Maybe, Mendel had read Darwin's deep conviction in *the Origin of Species* that the inheritance of environmental effects played a central role in generating variability. So, in the contextual part that Fairbanks and Rytting considered as a direct response to Darwin[17)], Mendel argued that "If the changes in conditions of vegetation were the only cause of variability......This, however, is not the case, as we know ......(Wäre die Aenderung in den Vegetations-Bedingungen die alleinige Ursache der Variabilität,......Das ist bekanntlich nicht der Fall......)". The sentences demonstrate that Mendel considered that there isn't without environmental cause for variability. But, He did think that the environmental effect was not "the only cause of variability". After a comprehensive reading through the paper, it could be figured out that Mendel explicitly viewed both the internal factors and the external environment jointly responsible for the organism variability, especially the environment effect in the case of quantitative character as introduced below. This is nearly 45 years earlier than W. Johannsen's distinction between genotype and phenotype [18)].

As for the modern gene concept, its synonymous words such as "anlage (*Anlage*)", "factors (*Factoren*)", "element (*Elemente*)" scatter in context of the paper, whose property of material entities was expressed everywhere. But, in sharp contrast with the publically accepted genetics determinism, Mendel never said in the paper that one factor could solely determine one character or trait. Throughout the paper, Mendel repeated no less than six times to express a kind of multiple one-to-one correspondence relationships between gametes, factors, and characters. One version said that "*pea-hybrids form germ-and pollen cells which according to their constitution correspond in equal number to all the constant forms that emerge from the combination of the traits that were united by fertilization* (*dass die Erbsen-Hybriden Keim- und Pollenzellen bilden, welche ihrer Beschaffenheit nach in gleicher Anzahl allen constanten Formen entsprechen, welche aus der Combinirung der durch Befruchtung vereinigten Merkmale hervorgehen*)" (Mendel's emphasis)[6]. These corresponding relationships with the numerical equation between the three counterparts were already evidenced by his testcrosses experiments in *Pisum* and the later controlled pollination experiments in *M. jalapa*. When introducing his thinking about the function of a factor, Mendel stated "both (bisexual gametes) are equipped with the disposition to animate completely identical individuals (*beide mit der Anlage ausgerüstet sind, völlig gleiche Individuen zu beleben*)". Here the German verb "beleben" can indeed be translated as "animate", or "vivify", or "vitalize", or "invigorate", rather than many translators' word "create"[19–21], for Mendel did not regard his factor as "Creator" or "God". On the other hand, Mendel also used the difference principle to explain the factor function as difference-maker, which was recognized by K. Nasmyth and expressed as "*A-a*" and "*B-b*" and so on[22]. In a letter to Nägeli, Mendel stated that "the anlage for the functional development of either the pistil alone or of the anthers alone, must have been expressed in the organization of the primordial cells from which the plants developed, and that this difference in the primordial cells could possibly be due to the ovules as well as the pollen cells being different as regards the sex anlage (*die Anlage für die functionsfähige Entwicklung entweder blos des Stempels, oder nur der Staubgefässe schon in der Organisation der Grundzellen ausgesprochen sein musste, aus welchen die Pflanzen hervorgegangen sind, und dass dieser Unterschied in den Grundzeiten möglicherweise davon herrühren könnte, dass die Eichen sowohl, als auch die Pollenzellen in Bezug auf die geschlechtliche Anlage verschieden waren*)"[8]. In short, Mendel did think that the factor corresponding to the character is an invigorator or an animator, and a difference-maker, but not a determinant or creator. Further, Mendel always held the idea of alleles in pair just like the now-known homologous chromosomes in pair, similar to his dealing with quantitative traits as below. This may be induced by his daily observation in cross experiments between paternal and maternal parent in pair, also see Kalmus's insight of Aristotelian contrariety[23] and Matalova's another explanation in this aspect.[24]

Comprehensively, the expression of Mendel's developmental genetics could be represented as "genotype" + "environment" → "phenotype". In his language system, the "environment" frequently mentioned in the paper refers to "natural living conditions". The "genotype" was introduced in an inclusive style, that is "the constitution of factors" together with their "grouping in pairs" with "interactions" in and between "factor pairs", and the "arrangement in cellular space" and the "parental imprint in history" that could be regarded as epigenetic influence in now days. To some extent, Mendel's gene concept originally made its sense by itself, because many senses generally recognized as its exceptions such as "the effects of other genes, epigenetic modifications, the interplay of development and environment, chance"[25], and so on, had already been coined into the rudimental concept by Mendel himself. What Mendel simply presented in the equation of genotype and phenotype could be modified as the formula: $A/A + a/a + A/a + a/A = \mathrm{A} + 2\mathrm{Aa} + \mathrm{a} \rightarrow 3\mathrm{A} + \mathrm{a}$, where according to modern genetics notation, italicized and regular letters are separately applied to denote factors and its corresponding characters, further respectively distinguishing genotype from phenotype.

1) Gene corresponding to Character:
   Gene ↔ Character: $A \leftrightarrow \mathrm{A}$, $B \leftrightarrow \mathrm{B}$, $C \leftrightarrow \mathrm{C}$...;

Gene ∈ {*A*, *B*, *C*...}; Character ∈ {A, B, C...}

2) Alleles corresponding to Traits:
Allele ↔ Trait: *A* ↔ A, *a* ↔ a;
Allele ∈ {*a* | *A*, *a*}; Trait ∈ {a | A, a}

3) Allele pair corresponding to Trait pair:
Allele pair ↔ Trait pair: a (*A*, *a*) ↔ a (A, a);
Allele pair ∈ {*a* | (*A*, *a*)}; Trait ∈ {a | (A, a)}

4) Allele difference determining Trait difference:
Allele difference → Trait difference: *a* (*A* – *a*) → a (A – a)
Allele difference ∈ {*a* | (*A* – *a*)}; Trait difference ∈ {a | (A – a)}

5) Genotype plus Environment determining Phenotype:
A/*A* + *a*/*a* + *A*/*a* + *a*/*A* + environment → A + 2Aa + a

6) Genotype difference determining Phenotype differences:

(*A*/*A* - *A*/*a*); (*A*/*A* - *a*/*A*); (*A*/*A* - *a*/*a*); (*A*/*A* - *A*/*A*) → (A/A – A/a); (A/A – a/A); (A/A – a/a); (A/A – A/A)
(*A*/*a* - *A*/*A*); (*A*/*a* - *a*/*A*); (*A*/*a* - *a*/*a*); (*A*/*a* - *A*/*a*) → (A/a – A/A); (A/a – a/A); (A/a – a/a); (A/a – A/a)
(*a*/*A* - *A*/*A*); (*a*/*A* - *A*/*a*); (*a*/*A* - *a*/*a*); (*a*/*A* - *a*/*A*) → (a/A – A/A); (a/A – A/a); (a/A – a/a); (a/A – a/A)
(*a*/*a* - *A*/*A*); (*a*/*a* - *a*/*A*); (*a*/*a* - *A*/*a*); (*a*/*a* - *a*/*a*) → (a/a – A/A); (a/a – a/A); (a/a – A/a); (a/a – a/a)

7) Law of complete dominance: *A*/*A* + *a*/*a* + *A*/*a* + *a*/*A* = 3A + a

8) Law of incomplete dominance (co-dominance): *A*/*A* + *a*/*a* + *A*/*a* + *a*/*A* = A + 2Aa + a

Laws of development of quantitative characters

As a skillful horticultural breeder, Mendel had succeeded in dividing pairs of contrasting characters into qualitative characters and quantitative characters, the former could be sharply defined while the latter could be described only by "more and less" in numbers[3)]. In interspecific cross in common bean (*Phaseolus*), Mendel observed that "the white flowers and seed–coat color only appeared once among 31 plants of the first generation (namely F_2 generation) (*dass nämlich die weisse Blüthen- und Hülsenfarbe unter 31 Pflanzen der ersten Generation nur einmal vorkam*)". And speculated that "This coloring appears only once in the series, and could therefore also only be developed once in the average in each 16, and with three color characters only once even in 64 plants (*Diese Färbung ist in der Reihe nur einmal enthalten, und könnte daher auch nur im Durchschnitte unter je 16, bei drei Farbenmerkmalen sogar nur unter 64 Pflanzen einmal entwickelt werden*)". He also applied his understanding of multiple factors for quantitative characters to flowering time and peduncles length in *Pisum*, believing the essential consistence of factors between qualitative and quantitative characters. Mendel's interpretation of multiple factors for the quantitative characters, Figure 2, was forties years earlier than William Bateson and G. U. Yule's multiple-gene hypothesis, which was initially based on Hermann Nilsson-Ehle's experimental results in study of wheat grain color in 1909. Furthermore, Mendel also detected the quantitative characters quite sensitive to environment, such as the degree of soil fertility to the length of stem, and the effect of temperature as well as the seeds' depth in the earth on the flowering time, and so on. It is worthy to report here, according to a series of figures in a preserved page of Mendel's notes R. A. Fisher identified it as the expected ratio of 9: 3: 4 in Mendel's study of flower color in *Phaseolus*, just reflecting the recessive epistasis of non-allele interactions in modern genetics. According to the mathematical expression Mendel presented in the context, he did always not hold the idea of multiple alleles, quite different from Olby's otherwise interpretation as evidence for Mendel as non Mendelian.[11)]

In addition, Mendel also reported the phenomenon of hybrid vigor (*Ueppigkeit*) and of pleiotropy (one cause for multiple effects) that he observed in the hybridization experiments. The former was exemplified by the longer of the two parental stems in stem

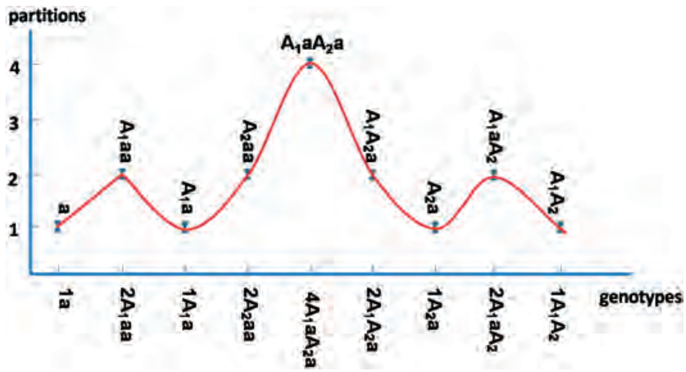

Fig. 2. The curve line made from Mendel presented data of multiple genes inheritance in quantitative character.

length usually exceeded by the hybrid in *Pisum,* while the latter was supported by the white color of the seed–coat constantly conjoined (constant ... verbunden) with the white color of flower in *Pisum*, as well as in *Phaseolus*.

1) Multiple Genes corresponding to one Character:

Gene ↔ Character: A ↔ A, B ↔ B, C ↔ C...;

Gene ∈ {A_1, A_2, A_3......A_n; B_1, B_2, B_3......B_n; C_1, C_2, C_3......C_n ......}; Character ∈ {A; B; C......}

2) Alleles corresponding to Traits:

Allele ↔ Trait: A_1 ↔ A_1, A_2 ↔ A_2, A_3 ↔ A_3......a ↔ a;

Allele ∈ {a | A_1, A_2, A_3... A_n, a}; Trait difference ∈ {a | A_1, A_2, A_3... A_n, a }

3) Allele pair ↔ Trait pair: $a(A_1, a)$ ↔ a(A_1, a); $a(A_2, a)$ ↔ a(A_2, a); $a(A_3, a)$ ↔ a(A_3, a) ......;

Allele pair ∈ {a | (A_1, a); (A_2 , a); (A_3, a)......}; Trait pair ∈ {a | (A_1, a); (A_2, a); (A_3, a)......}

4) Allele difference determining Trait differences:

Allele difference → Trait difference: (A_1- a) → (A_1 - a); (A_2- a) → (A_2 - a); (A_3 - a) → (A_3 - a) ......;

Allele difference ∈ {a | (A_1 - a); (A_2 - a); (A_3 - a)...... (A_n - a)}

Trait difference ∈ {a | (A_1 - a); (A_2 - a); (A_3 - a)...... (A_n - a)}

5) Polygeny plus environment determining quantitative traits:

$(A_1 + a)^2 (A_2 + a)^2$ (......) + Environment → 1 $\mathrm{A_1A_2}$ 2 $\mathrm{A_1aA_2}$ 1 $\mathrm{A_2a}$

2 $\mathrm{A_1A_2a}$ 4 $\mathrm{A_1aA_2a}$ 2 $\mathrm{A_2aa}$

1 $\mathrm{A_1a}$ 2 $\mathrm{A_1aa}$ 1 aa

CONCLUSIONS

On the bicentennial of Mendel's birth, we do our best to draw a gross picture that might have been seen in Mendel's eyes and to recover the comprehensive insight of his genetics thoughts from the picture. Maybe, Mendel was enlightened by the mathematical expression of the perfect square formula when he did his study. He had a sudden brain wave and realized that the two symbols could perfectly act the bisexual gametes, then the mathematically modeled sequential expression containing the formula itself could vividly mimic the behaviors of bisexual gametes in the process of plant reproduction. The entity property of bisexual gametes together with the continuity linking them to foundation cells in sexual reproduction inspired Mendel thinking that, a reproductive cell might carry a material factor that could transmit a corresponding character from parents to offspring. After his repeated verification experiments in lots of plant materials, the perfect square formula in "Mendel's black box" together with the upstream input and the downstream output[13] were respectively lectured as the principles of reproductive cells formation, of fertilization, and of seeds developments in his second speech in 1865. Maybe due to the irresistible power of his times as previously introduced[7], Mendel had to integrate his two speeches into one paper published and presented his findings of inheritance in a modified style, where he repeatedly stress the corresponding relationships between characters, gametes, and factors. Mendel's knowledge regarding the function of his factors in development process were a kind of pure speculation that was yielded by standing before and looking at the fertilized zygote cell as a whole, thus possessing both property of holism and of reductionism. This study shed some valuable lights on Mendel's developmental genetics, unfortunately, almost thoroughly ignored in the general Mendelian genetics. No doubt, it is worthy for us to further study in future.

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