From phenotype to genotype: celebrating 150 years of Mendelian genetics in plant breeding research

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Introduction

In the year 1866, Gregor Mendel's seminal publication "Versuche über Pflanzen-Hybriden" ("Experiments in Plant Hybridization") was published in the periodical *Verhandlungen des naturforschenden Vereines, Brünn*, Vol 4, pp 3–47 (Mendel 1866). This marked the starting point of the science of heredity which later turned into modern genetics with a variety of sub-disciplines developing throughout the life sciences, including scientific plant and animal breeding. Dealing with discrete characters, Mendel was the first to explain phenotype ratios occurring in the progeny generations following a biparental hybridization. As genes were unknown to Mendel, he hypothesized "elements" present in pollen and egg cells as causing the heritable differences between phenotypes. In the 20th century, the concept of a gene was developed, and the gene became known as the unit of inheritance, function, recombination, and mutation (Gayon 2016).

This understanding of a gene proved to be useful for plant breeding throughout many decades and contributed to significant breeding progress in major crop species. Later, new insights from molecular genetics brought considerable changes to the concept of the gene and subsequently

to plant breeding: although a more modern imagination of a gene as a coding sequence is strongly challenged by discoveries, such as split-genes, alternative splicing or the significant finding of non-coding RNA (Gayon 2016), single nucleotides within a gene became the ultimate units of interest both for selection and genetic modification. Based on advances in molecular genetics, powerful tools are currently under development for editing individual nucleotides in a gene, for selection solely based on genomic information, and for better understanding functional and regulatory genetic and epigenetic mechanisms. Apart from genomic selection, the dissection of quantitative characters through QTL analysis (Paterson et al. 1988) has particular appeal in the Mendelian context as it discloses the make-up of complex traits, each controlled by a number of individual and selectable loci behaving as Mendelian factors.

Since the rediscovery and broad recognition of Mendel at the dawn of the 20th century, different aspects on Mendel and early Mendelian genetics have been discussed across various disciplines. This includes the possible origins of Mendel's novel approach of mathematically treating biological results (Dröschner 2015) or the ongoing debate on the precision of his experiments with segregation ratios being statistically too close to the expectations (Hartl and Fairbanks 2007; Radick 2015). Molecular genetics has provided an even deeper understanding of some of the seven traits which Mendel studied in pea: the round vs wrinkled seed shape trait is due to an 800-bp insertion into the gene coding for a starch branching enzyme causing the accumulation of sugars in the wrinkled phenotype; the tall vs dwarf stem length trait is caused by a G to A nucleotide substitution in a gibberellic acid 3-oxidase 1 gene; and the yellow vs green cotyledon color originates from a 6-bp insertion to a stay-green gene prohibiting chlorophyll degradation at maturity (Reid and Ross 2011).

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This special issue of *Theoretical and Applied Genetics* presents seven papers celebrating the 150-year anniversary of Mendel's most prominent publication. The species that Mendel studied are revisited in two contributions: most importantly, the garden pea was the starting point for Smýkal et al. (2016) to analyze the development of genetics and plant breeding down to the genomic era and to "Mendelizing" continuous variation. Mendel devoted much effort to verify his results obtained from pea crosses in other species: Bicknell et al. (2016) analyze Mendel's hawkweed experiments, which failed almost completely, because Mendel could rarely obtain hybrids due to a mostly apomictic flowering biology of the species. However, the genetics of apomixis and new progress in inducible apomictic flowering might become important in seed propagated crops. A review on Solanaceae genetics by Gebhardt (2016) illustrates the importance of tomato, tobacco, petunia, and a number of other species for the development of genetics, cell biology, and modern breeding techniques throughout the 20th century; Solanaceae genetic research is continuously relevant both on a model plant level as well as on the level of human food crops. Three papers present cutting edge research in major crop species, i.e., wheat, rice, and soybean. Chen et al. (2016) describe three QTL for dwarf bunt resistance in wheat as an example of mendelizing a quantitative disease resistance; the three loci were mapped on different linkage groups, they significantly contributed to phenotypic disease resistance in different environments without pleiotropic effects on other traits, and genetic markers can be used to select for the resistance alleles. In rice, management of flowering time is important for both regional geographic adaptation and grain yield formation; Hori et al. (2016) demonstrate the integration of classical Mendelian flowering time genes and QTL analysis approaches, including the functional analysis of photoperiod genes and candidate gene cloning. In cyst nematode resistance of soybean, Kim et al. (2016) review the development of genetic, genomic, and bioinformatics tools, including genome-wide association studies for identifying, mapping, and utilizing pest resistances.

Mendel actively distributed reprints of his 1866 publication among some of his scientific peers. Moreover, although the journal of the Brno Natural History Society was not very widely known, it had a remarkable distribution among libraries and scientific institutions both in Europe and North America (Posner and Skutil 1968). Despite of all this, Mendel's paper was "rediscovered" and recognized with respect to its significance only after the year 1900. Among the many reasons for the time lag in recognition of Mendel's discoveries, the scientific discussion among his contemporaries was undoubtedly overshadowed by Charles Darwin and his theory on the evolution of species published 7 years before

Mendel's (1866) paper (Darwin 1859). Thus, Darwin's theory was the bandwagon in the second half of the 19th century for biological sciences, even though it critically lacked an acceptable explanation for the inheritance of characters which only Mendel could have provided. Bernardo (2016) reviews modern bandwagons of plant breeding research over the last 25 years: as new developments both in genotyping and phenotyping are attracting considerable attention and funding, thus generating scientific hypes, it is critically important for plant breeding to carefully monitor bandwagons and to decide about their adoption both from breeding progress and economic feasibility perspectives.

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