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on the garden pea

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The life sciences owe a lot to green peas. And perhaps even to the bishop of St Thomas Abbey in Brno – now the Czech Republic. It was there, in the 1850s, that Gregor Johann Mendel (1822-1884) decided to undertake studies on heredity using mice. The bishop, however, disagreed with research involving animal sex, so his friar turned to the more innocent garden pea. Mendel spent the best part of a decade cross-breeding peas, while considering seven different phenotypic traits that seemed – to him – to be inherited independently: stem length, pod shape, pod colour, seed shape, flower colour, flower location and plant height. Little did he know that the results he so painstakingly jotted down, and which were published in 1866, would bring about a small revolution in the world of biology – although only in the first quarter of the 20th century. And now, 150 years on, science has not only acquired a far finer knowledge in the field of molecular biology but it also has the technology to take a closer look at the genes – and their mutations – that Mendel used to lay down the basis of heredity and its mechanisms. Despite this, however, the products of only four genes have been characterised to date: two enzymes (SBE1 and gibberellin 3beta-hydroxylase), an Myb transcription factor and a biochemical regulator (protein stay-green).



"The Green Pea Family", by Corinne Taunay Courtesy of the artist

Mendel was not the first to wonder how features were passed down generations nor to use the garden pea (Pisum sativum) to find out. 70 years before, a certain Knight had also cross-bred green peas to understand the inheritance of the colour of the pea flower. In those days, it was thought that a progeny's traits were the direct result of a blending of its parents'. We know now that things are more Fortunately, complicated. Mendel chose characteristics that were - happily and perhaps coincidentally - more or less independent, which is why he managed to elaborate a theory which later became so prevalent.

Over the course of seven years (1856-1863) Mendel cultivated and studied 29,000 pea plants, and his

famous article – "Experiments on Plant Hybridization" – was published ten years later. Surprisingly, Mendel's contemporary, Charles Darwin (1809-1882), was unaware of his paper. Yet, years later, Mendel's laws of inheritance and Darwin's theory of natural selection would give rise to one of the most revolutionary theories of biology: evolutionary biology. In a way, this is perhaps to be expected, since the actual words "gene" and "mutation" were only coined in the very beginning of the 20th century – thus giving a different light altogether to the notion of inheritance and its mechanisms.

Mendel's theory is based on mutations. But: which exactly? It hasn't been such a straightforward task to identify them; in order to study the exact genes and mutations Mendel used, scientists have had to track down the precise cultivars that were available back then. Luckily, many of them had been exploited for hundreds of years for agricultural purposes already. The "wrinkled pea", for instance, was distributed throughout Europe because of its sweetness. Surprisingly though, and despite modern technology, only four of the seven traits Mendel examined have been characterised: flower colour, stem length, pod colour and seed shape.

The shape of a pea's seed is due to a structural enzyme known as the starch branching enzyme – or SBE1. A mutation in SBE1 brings about changes in starch synthesis and metabolism, and causes differences in seed development. In wrinkled seeds,

SBE1 activity is reduced, reducing in turn starch content. This probably leads to the accumulation of sucrose in immature seeds, which have high water content because of increased osmotic pressure. The end result is a change in the seed's shape. Though very little is known on the molecular level, it is now clear that a change of osmotic pressure caused by a decrease in starch content has a direct role in seed development.

The length of the pea's flower stem is the doings of a structural enzyme known as gibberellin 3betahydroxylase, which controls gibberellin (GA) metabolism. Gibberellins are plant hormones which regulate growth and various developmental processes, such as stem elongation, germination, flowering and leaf senescence for instance. Gibberellin 3beta-hydroxylase converts one form of gibberellin (GA20) to its bioactive form (GA1) – which has a direct effect on controlling the length between the plant's nodes.

The seeds of peas are green, and the colour of mature seeds and senescing seeds usually fades to a yellow as carotenoid is revealed while chlorophyll is being degraded. One particular protein, however, keeps the seeds and leaves green, and is known as the "stay-green protein" (SGR). The exact function of SGR is not known in detail. It is highly conserved in plants, where it is involved in the degradation of chlorophyll-protein complexes, perhaps during plant senescence, following translational or post-translational regulation of chlorophyll-degrading enzymes.

Mendel noted that coloured seed coats were always associated with coloured purple flowers, as well as pigmentation in the leaf axils, whereas colourless seed coats were always associated with white flowers and no pigmentation in the leaf axils suggesting that it was the doings of one same gene. The product of this gene turned out to be a Myb (myeloblastosis) transcription factor - a basic helixloop-helix protein A - which determines the accumulation of anthocyanin pigmentation throughout the plant - particularly in its flowers. Purple, for instance, is caused by the accumulation of anthocyanin pigments, derived from phenylalanine. Historically, white peas were first mentioned in the "Ruralia commoda", a text on agriculture dating back to the 13th and 14th centuries, and written by an Italian judge, Pietro de Crescenzi (c.1230-1320).

Little is known about the other three traits used by Mendel: pod colour, pod shape and the positioning Despite this. Mendel of flowers. would. undoubtedly, be very intrigued by what cytology, biochemistry, molecular biology and bioinformatics has managed to unveil with regards to his work. He would have been very surprised, too, to realise that what he had judged to be transmitted intact from parent to offspring - and in an independent manner - can actually be subject to disruption and linkage. Though Mendel may have been lucky in choosing the different traits, there is little doubt that he must have taken great care in his choice in the first place. And modern technology, rather than weakening a model of inheritance that was outlined over 150 years ago, has actually added to it and refined it.

Cross-references to UniProt

Basic helix-loop-helix protein A, *Pisum sativum* (Garden pea) : E3SXU4 Gibberellin 3-beta-dioxygenase 1, *Pisum sativum* (Garden pea) : O24648 Starch branching enzyme I, *Pisum sativum* (Garden pea) : Q41058 Protein STAY-GREEN, chloroplastic, *Pisum sativum* (Garden pea) : A7VLV1

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