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FLOWERING NEWSLETTER

My favourite flowering image

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Abstract

I selected my favourite image from a paper by Professor Friedrich Laibach, the founder of *Arabidopsis* research. His paper from 1951 is the first paper dealing with natural variation for flowering time in this species, a topic many scientists including myself, have followed up and has resulted in large steps forward in our understanding of flowering time regulation. How this topic came to be of interest in my laboratory in Wageningen is described in this short overview.

Key words: *Arabidopsis*, flowering time, flowering time mutants, natural variation.

A short paper dealing with my favourite image of flowering would be expected to contain a historical perspective related to my research on flowering time genetics. Because our contribution to this field was based mainly on tables and figures representing leaf counts and days to flowering, no exciting picture from my own research can serve as a favourite image. Therefore, I chose a drawing that appeared in a little known paper by Laibach (1951), the founder of *Arabidopsis* research. In 1951, he summarized his observations on flowering time variation with some intriguing observations about the large amount of natural variation for this trait, which later became an important research topic in my laboratory as well. Laibach promoted research on *Arabidopsis* because he noticed the large phenotypic variation in nature before he started working on induced mutants (Laibach, 1943). He also recommended that this natural variation should be studied using genetics for which *Arabidopsis* was very well suited. This early research on flowering time genetics in Germany was followed up later by Napp-Zinn at the University of Cologne, who had already identified genetically important genes such as *FRIGIDA* and *FLC* (not then known by these names) (Napp-Zinn, 1957), that later on appeared to be the crucial major genes that explain flowering time variation in nature and also helped us to understand the mechanisms of vernalization.

The Laibach (1951) paper contains some interesting observations that have not really been followed up. One is his picture of a bolting *Arabidopsis* in a test tube that does not show any sign of a flower. I also very much liked the flower reversion brought about by transferring a flowering late accession from natural long days (LD) to natural short days (SD), which I have chosen as my favourite image (Fig. 1). I have not seen such flower reversions in *Arabidopsis*. I included this intriguing picture in the first general review on *Arabidopsis* flowering time in the *Arabidopsis* book chapter written together with Jose M. Martinez Zapater, George Coupland, and Caroline Dean (Martinez-Zapater *et al.*, 1995). This image can be seen as recognition that Laibach founded the field of flowering time research in *Arabidopsis*.

Natural flowering time variation was the main research interest of my PhD supervisor Jaap van der Veen, who started working on natural variants (van der Veen, 1965). Later, he focused on induced late-flowering mutants, having in mind to go back to natural variation assuming that the same genes identified with mutants would show variation in nature. When I joined his laboratory in 1976, I took over most of van der Veen's ongoing projects except his work on flowering time mutants for which he had built up a good collection in the Landsberg *erecta* background. This mutant collection included alleles of *CO* and *GI* that had been described earlier by Rédei (1962), *fca*, and *ft* without

Fig. 1. Reversion to the vegetative phase in accession St in natural short days after starting flowering under natural summer conditions in Germany (Fig. 10 in Laibach, 1951).

realizing that one of them was a mutant impairing the magic florigen. Van der Veen intercrossed these mutants and used F_2 progenies to give students experience with quantitative genetics. When doing mutagenesis and mapping experiments I collected additional late-flowering mutants and also mapped them on the emerging genetic map. In those days, mapping was done exclusively using morphological markers within one (in our case the L*er*) accession, which made phenotyping easier because all the modifiers that one sees segregating in almost all the between-accession crosses often used for mapping, including the progeny of L*er*×Col crosses, do not segregate.

After van der Veen's retirement in 1987, I joined his project and together we wrote up what we knew about flowering time mutants, resulting in a paper in *Molecular and General Genetics*, which would later become frequently cited (Koornneef *et al.*, 1991). This appeared at a key moment because *Arabidopsis* had been rediscovered and several new groups started working on *Arabidopsis* mutants and also on natural variants. This renewed interest in flowering allowed us to obtain EU funding together with George Coupland, Caroline Dean, and Jose Martinez-Zapater, which also allowed me to start molecular biology in my group in Wageningen. This ultimately resulted in the isolation of the *FWA* gene by Wim Soppe; *fwa* was the first epi-mutant with a flowering time phenotype to be cloned (Soppe *et al.*, 2000). Natural variation in flowering time soon became a major topic in my laboratory using the Cape Verde Island accession Cvi. This was not because of flowering time, as Cvi flowers almost at the same time as L*er* and Col, but because its large seeds intrigued me. However, I knew from George Coupland, who had sent me the Cvi seeds, that this accession was less sensitive to day-length than most others. The flowering time phenotype became obvious when we saw a strong segregation for flowering time in the F_2 and later generation progenies of the cross L*er*×Cvi. This variation became the topic of our first successful QTL cloning effort, identifying that Cvi had a special dominant *CRY2* allele (El-Assal *et al.*, 2001). This confirmed van der Veen's idea, that induced mutants (*cry2* was known as *fha* in our collection) identified genes that also show variation in nature. Later on this was also seen for *ft* (Schwarz *et al.*, 2009). However, for some loci where mutants have a strong effect, such as *CO* and *FCA*, and probably also *GI*, no obvious natural variation has been identified thus far.

The reason why little time was spent on early flowering mutants was that van der Veen, as well as I, carefully looked for normal looking mutants and avoided the sick and very pleiotropic mutants which is how most early mutants appear. Mutants that were late because they did not grow were also discarded which made it important to check the number of leaves, as well as flowering time itself. The fact that one of the early accessions, L*er*, was used in LD conditions also meant that the window in which to look for even earlier genotypes was limited.

The work on the flowering time mutants was very satisfying because it led to the dissection of a very complicated pathway, many details of which are now known, and which showed that even quantitative mutants were extremely useful for this dissection. This is partly because of the redundancy of the various pathways which we realized in the double mutant analyses that van der Veen had performed with this students. These data were incorporated in the *Molecular and General Genetics* paper, suggesting that this could give clues to the various pathways. Although the pathways mentioned in this paper were not exactly right and were incomplete it helped the flowering time researcher to think of different pathways from the beginning, which was also suggested by the variation in environmental factors that influence flowering. Flowering time is one of the most successful pathways where genetics, with molecular biology, has solved many of the basic questions that plant physiologists have been asking for many years, and where biochemical and chemical approaches had little success because the crucial molecules and processes were different from the standard small molecule approach of those days.

Because of the huge developments in the field, being a partner in the early studies on the genetics of flowering time genetics, which I follow now at some more distance, has been, and will be, a pleasure.

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