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Meeting Report

Flowering plants return to the sea...

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From 18 to 22 June this year, around 120 fans of floral biology met at Hyères-les-Palmiers on the French Côte d'Azur for the latest in a series of two-yearly workshops on 'Molecular Mechanisms Controlling Flower Development'. These international meetings usually take place somewhere on the Mediterranean coast, and Hyères provided an idyllic setting in which to meet up with colleagues and discuss science on the beach as well as in the lecture hall or poster room. One flowering plant that really did return to the sea, *Posidonia oceanica*, was to be found growing in the shallow coastal waters surrounding the conference venue, and many delegates could be seen splashing about and (no doubt) thoroughly investigating this marine monocot between scientific sessions.

The workshop, of which details can be found at: <http://www.ens-lyon.fr/RDP/FlowerWorkshop2019/>, was divided into seven oral sessions and formatted so that a maximum number of speakers could present their data in 20 min highlighted talks, 15 min standard talks, or 4 min 'flash posters'. In all, 74 oral presentations were made, involving nearly two-thirds of delegates, who came mostly from Europe, but also from as far afield as China, Japan, Vietnam, Mexico, and Washington State. It is impossible in a short review to cover all the subjects addressed at the meeting, so the following is a personal view of some of the highlights and novel themes to emerge.

The workshop got underway with its traditional starting topic of 'Flowering', namely the complex and interconnecting networks used by flowering plants to initiate their reproductive phase in response to numerous environmental and endogenous cues. Much of what is known about flowering comes from the model plant *Arabidopsis thaliana*, which is a typical annual species that flowers once in its life cycle, promptly sets seed, and dies. It has been known for several years that multiple cues for flowering in *Arabidopsis* converge on the FLOWERING TIME (FT) protein, which moves from its site of synthesis in the leaves to the shoot apex where flower production is initiated. However, two recent research trends were evident from this year's workshop. First, several mobile signals other than FT are coming to the fore, including a potentially large list of metabolites that can promote flowering, as highlighted in

a talk by Reyes Benlloch (IBMCP, Valencia, Spain). Secondly, several research groups are now focusing on alternative models with contrasting life cycles and flowering requirements. For example, the work of George Coupland's laboratory (MPI-Cologne, Germany) demonstrates that endogenous cues that depend on the age of the plant are of particular importance to flowering in perennial Brassicaceae (Hyun *et al.*, 2019). Indeed, although the workshop included a devoted 'evo-devo' session, the prominent presence of new and emerging models (Fig. 1) in all seven scientific sessions meant that evolutionary considerations were discussed throughout the meeting.

Many species require vernalization: cold treatment as a necessary prelude to flowering. However, the need for vernalization can cause unwanted delays in plant breeding programs, which is why Richard Immink's group (Wageningen University, The Netherlands) recently made a screen of some 9000 chemical structures to find a compound that could bypass the vernalization requirement (Fiers *et al.*, 2017). Two compounds were found to have the desired effect in *Arabidopsis*, one of which might prove of practical use in crop species. Interestingly, this compound did not appear to act via any of the known dedicated components of the vernalization pathway, but instead induced FT by a novel mechanism, possibly involving the production of hydrogen peroxide.

After deciding to flower, a plant must then determine how its flowers should be arranged, and so the workshop turned its attention to the subject of inflorescence architecture. The enlargement of model species from *Arabidopsis* was clearly apparent in this theme too, with several impressive talks featuring cereals, legumes, Solanaceae, and Asteraceae. One particularly interesting model for inflorescence architecture is cultivated rice, which has undergone the domestication process twice from distinct wild species in Asia and Africa. These domestication events appear to have resulted in parallel changes to the rice panicle, and a collaboration involving Stefan Jouannic and Helene Adam (IRD-Montpellier, France) and Ngang Giang Khong (Agricultural Genetic Institute, Hanoi, Vietnam) is taking a multidisciplinary approach to discover whether similar genetic targets and developmental processes were

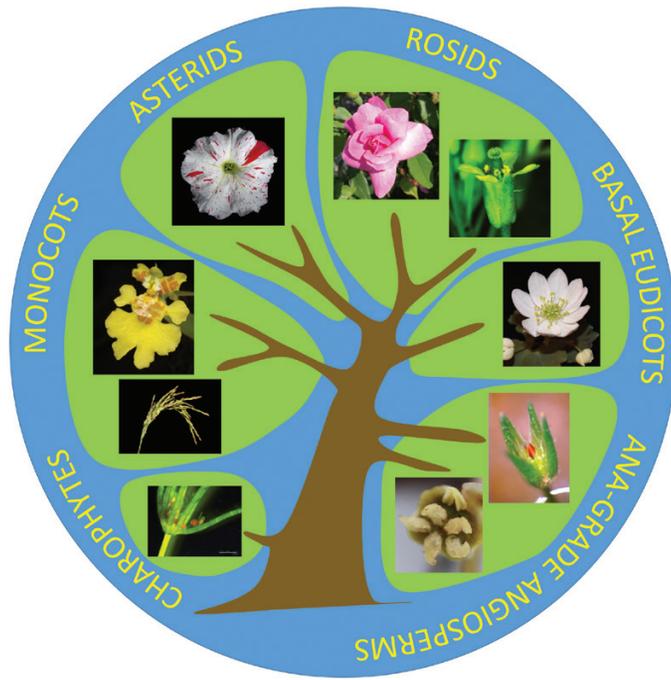


Fig. 1. Some of the many plant models featured in 'Molecular Mechanisms Controlling Flower Development, 2019'. Clockwise from bottom left: *Chara braunii* (image: G. Theißen), *Oryza sativa* (Asian cultivated rice; image: H. Adam), *Erycina pusilla* (image: B. Gravendeel), *Petunia hybrida* (image: M. Vandenbussche), *Rosa chinensis* 'Old Blush' (image: M. Bendahmane), *Arabidopsis thaliana* (image: C. Scutt), *Thalictrum thalictroides* (image: V. Di Stilio), *Trithuria submersa* (image: C. Scutt), and *Amborella trichopoda* (image: C. Scutt). The ANA grade comprises the three most basally diverging extant angiosperm lineages of Amborellales (containing only *A. trichopoda*), Nymphaeales (water lilies and their allies, including *T. submersa*), and Austrobaileyales.

affected in these two events. Working on another cereal crop, Scot Boden (John Innes Centre, Norwich, UK) has revealed a previously unsuspected role for an amino acid transporter in wheat spikelet formation, suggesting that small metabolites may influence inflorescence architecture as they do flowering. Inflorescences in Asteraceae are showy, flower-like platforms consisting of many small flowers that develop in both left- and right-turning spirals, often defined by pairs of quite large Fibonacci numbers (Elomaa *et al.*, 2018). Using a combination of reporter lines, imagery, and modeling, Teng Zhang (Helsinki University, Finland) elegantly showed how growth and hormone dynamics contribute to generate these patterns in the inflorescence meristem of *Gerbera hybrida*.

Moving on from inflorescence architecture, a major part of the workshop was devoted to a detailed discussion of flower and fruit development. Several talks and associated posters addressed the central question of how quaternary complexes of MADS-box transcription factors, also known as floral quartets, act on specific subsets of direct target genes to control floral patterning and organ identity. Three major ideas came to the fore, all of which may be involved in this process. Kerstin Kaufmann (Humboldt University, Berlin, Germany) emphasized the importance of the width of the minor DNA groove in the CARG box motifs to which MADS proteins are known to bind, and which can vary between motifs. Cezary Smaczniak

from the same research group talked about the role of complexes formed between MADS proteins and numerous other classes of transcription factors and chromatin remodeling enzymes, which can also affect the specificity and the positive or negative transcriptional effects of the complexes formed. Chloe Zubieta (CEA-Grenoble, France) has been addressing the specificity of MADS complexes mainly using a structural biology approach. Her work indicates that differential flexibility occurs within quaternary MADS complexes of different compositions. As these complexes are hypothesized to bind simultaneously and cooperatively to two CARG boxes, the spacing between adjacent motifs may also be a determining factor in the specificity of the interaction.

An interesting presentation in a further session of the workshop, given by Günter Theißen (Friedrich Schiller University, Jena, Germany), returned to the subject of quaternary MADS complexes, but took an evo-devo approach that might also provide insights into their mechanism of action. By analysing homologs of classic MIKC-class MADS proteins from early-diverging land plants and their charophyte green algal relatives (Nishiyama *et al.*, 2018), he showed that quaternary binding behavior evolved following the duplication of an exonic segment of an ancestral MIKC-class gene in a common ancestor of land plants. It seems therefore that earlier MADS complexes bound only as dimers to single CARG boxes, and so any influence of motif spacing on the specificity and cooperativity of the DNA-protein interaction would presumably have been a later mechanistic addition.

Many other presentations in the meeting focused on the precise roles of MADS-box factors in different systems. These included both well-developed core eudicot models such as *Petunia*, tomato, and *Cardamine*, and basal eudicots in which some methods of functional genetic analysis are becoming available, as explained by Verónica Di Stilio (Washington University, Seattle, USA), who has used virus-induced gene silencing and horticultural mutants to uncover processes of neo- and subfunctionalization in the evolution of MADS-box genes in the ranunculid *Thalictrum thalictroides* (Galimba *et al.*, 2018). Among the talks featuring core eudicot models, Michiel Vandenbussche (ENS-Lyon, France) gave a thorough analysis of the *SEPALLATA* (*SEP*) and *APETALA1* (*API*) MADS-box subfamilies in *Petunia*, showing that the roles of these genes in organ identity and floral meristem determination have evolved along substantially different lines in the asterids compared with the rosids (Morel *et al.*, 2017). A further impressive feat of functional genetics was presented by Vojtech Hudzieczek (Institute of Biophysics, Brno, Czech Republic), who has developed gene editing in the dioecious angiosperm *Silene latifolia* and used this to demonstrate a role in male fertility for a Y chromosome-linked *AP3*-class MADS-box gene. This technical breakthrough might pave the way to solving long-standing questions on the mechanism of sex determination in *Silene*. A further talk in this section by Silvia Moschin (Padua University, Italy) explored the presence and expression of MADS-box floral homeotic genes in the basal angiosperm *Trithuria submersa*, a novel experimental system for which functional genetic methods have yet to be developed.

Numerous speakers focused on developmental processes within specific floral organs that rely on classes of regulators other than MADS-box proteins. These included an analysis by Stefan de Folter (LANGEBIO-Irapuato, Mexico) of cross-talk between the basic helix–loop–helix transcription factor SPATULA and hormone signaling in the Arabidopsis gynoecium (Reyes-Olalde et al., 2017), and a transcriptomics-based analysis of the evolution of multiple families of transcriptional regulators in the gynoecium by Annette Becker (Justus-Liebig University, Giessen, Germany). Maura Cardarelli's laboratory (Sapienza University, Rome, Italy) provided two interesting talks on Arabidopsis stamen development, one of which showed how this process is coordinated by alternative transcripts of the transcription factor gene *AUXIN RESPONSE FACTOR8*, while the other, given by Davide Marzi, demonstrated a developmental effect of light quality. Again moving away from classical models, Barbara Gravendeel (Leiden University, The Netherlands) gave a fascinating talk on specialized floral organs that facilitate pollen transfer in orchids. Protein–protein interaction and gene expression data suggest that several transcription factors whose orthologs function in the development of the dehiscence zone in Arabidopsis may contribute to the formation of these unique floral structures in Orchidaceae (Dirks-Mulder et al., 2017, 2019). At a higher level of regulation, flower development is ultimately coordinated by the master transcriptional regulator LEAFY (LFY), and Leonie Verhage (CEA-Grenoble, France) delved way back in evolutionary time to show how LFY's DNA-binding behavior became more uniform before the radiation of extant vascular plants. Bifunctional LFY proteins, possessing an alternative binding behavior, are still present in some bryophyte (*sensu lato*) and green algal lineages.

Aspects of flower development revealed through genomic-scale approaches were particularly featured in the workshop. For example, a pair of talks by Jeremy Just and Lea Francois (both of ENS-Lyon, France), respectively, detailed the production of a high-quality assembly of the rose genome (Raymond et al., 2018) and the use of this resource to identify the gene behind the double-flowered phenotype in modern rose cultivars (Francois et al., 2018): an *miR172*-resistant variant of an *AP2*-family transcription factor. François Parcy (CEA-Grenoble) presented novel methods to combine large *in vivo* and *in vitro* data sets with the objective of determining the rules that govern transcription factor binding to DNA, using the master regulator LFY as an example.

Another fascinating session of the workshop looked at functional aspects of the reproductive system in flowering plants. Lucia Colombo (Milan University, Italy) focused on a female-expressed histone deacetylase in Arabidopsis that is required for pollen tube guidance, while Thomas Dresselhaus (Regensburg University, Germany) gave a wide-ranging presentation on the multiple defense-related pathways that operate along the pollen tube's journey from the stigma to the micropyle in both grasses and Arabidopsis (Zhou and Dresselhaus, 2019). From the same university, Stefanie Sprünck provided evidence for the widespread conservation of multiple mechanisms that regulate fertilization, even between Arabidopsis and the probable sister to all other living flowering plants, *Amborella trichopoda*. This work

involved the impressive characterization of the egg apparatus transcriptome in *Amborella* (Flores-Tornero et al., 2019). Finally in this section, Daphné Autran (IRD-Montpellier, France) described sophisticated imaging, modeling, and experimental approaches to investigate spatial relationships in the Arabidopsis ovule during megaspore mother cell formation.

The effect of music on plants remains controversial, but its effect on plant scientists was clearly apparent at the workshop. This year's event coincided with the annual *Fête de la Musique* in France, and a Balkan sextet of immense talent travelled from the town of Sète to help us close the meeting in style. Delegates made their way home the following day, safe in the knowledge that the next Flower Development Workshop will be organized by Cristina Ferrandiz, Paco Madueño, and colleagues in Spain in 2021. Hope to see you there!

Keywords: Angiosperms, flowers, flowering, flower development, flowering plants, inflorescence architecture, plant evo-devo, sexual plant reproduction

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