Focus on Flowering and Reproduction

Flowering plants (angiosperms) emerged on our planet approximately 140 to 160 million years ago and today represent about 90% of the more than 350,000 known plant species (Paton et al., 2008). Flowers are their reproductive structures, which produce fruits containing one to many seeds. Usually flowers are both male and female, and they are often brightly colored to attract animal pollinators, but every possible variation exists from unisexual flowers to inconspicuous flowers that use wind for pollination to flowers that produce seeds without fertilization. During sexual reproduction, pollen produced in anthers, the male flower organ, is transferred to the stigma of the pistil, the female reproductive organ. In compatible conditions, the pollen then germinates and pollen tubes grow in female tissues, eventually delivering two sperm cells to an ovule for double fertilization, a process characteristic of angiosperms (Dresselhaus et al., 2016). After gamete fusion, the fertilized egg cell develops into the embryo, while the fertilized central cell forms the endosperm, the two major components of the seed.

The transition of vegetative meristems to the formation of flowers, the subsequent developmental programs that result in a range of flower morphologies, and the diverse pollination and seed development mechanisms have fascinated scientists for hundreds of years. Although the discoveries of processes such as flower induction in vegetative meristems (Sachs, 1863), photoperiodism (Garner and Allard, 1920), and the double fertilization event (Nawaschin, 1898) occurred at least a century ago, our understanding of the underlying molecular mechanisms of these processes is relatively recent, beginning, for example, with the formulation of the ABC model of flower organ development (Coen and Meyerowitz, 1991), the discovery of the flowering regulator CONSTANS (Putterill et al., 1995), and the identification of the first self-incompatibility gene (McClure et al., 1989). Since then, tremendous progress in understanding flowering and reproduction has been made; the last 10 years have seen another boost of further advances inspiring us to organize a Focus Issue representing the first issue about the topic in Plant Physiology.

In many plant species, the timing of flowering is critical for reproductive success, and thus the evolution of flowering-control systems that optimize reproductive success provide a selective advantage. For example, flowering must occur early enough in the growing season to enable proper seed development, but premature flowering when a plant is small will limit the amount of seed that can be produced. Also, in outcrossing species, synchronous flowering enables cross-pollination. In many plant species, systems have evolved to perceive the seasonal cues of changing day-length and temperature and to translate that perception into flowering. An Update by Shim et al. (2017) discusses the immense progress in understanding the molecular details of how changes in daylength lead to the induction of flowering. The daylength response system has common features in all flowering plants, indicating an ancient evolutionary origin. In contrast, vernalization systems, which evolved to enable flowering only after plants experienced exposure to the prolonged cold of winter, evolved more recently and, as discussed in the Update by Bouché et al. (2017), are molecularly distinct in different groups of plants. In Arabidopsis (Arabidopsis thaliana), many of the biochemical details of how vernalization results in competence to flower are being uncovered as illustrated in an upcoming research article (D.-H. Kim and S. Sung, unpublished data). Also, temperature fluctuations other than exposure to winter cold influence flowering; the role of this so-called ambient temperature response in petunia (Petunia hybrida) will be discussed in an upcoming research article (H.A.C.F. Leeggangers, H. Nijveen, J.N. Bigas, H.W.M. Hilhorst, and R.G.H. Immink, unpublished data).

In some species, a specific developmental state must be reached before plants can respond to seasonal cues; Hyun et al. (2017) discuss in an Update recent advances in our understanding of how such systems operate. Within a species, there is often substantial natural variation in flowering responses. In his Update, Blackman (2017) presents several examples of such variation in a range of species and discusses the possible adaptive value of such variation. In two research articles, Woods et al. (2017) and Bettgengheuser et al. (2017) explore the genetic basis of the substantial natural variation in flowering responses in the model grass Brachypodium distachyon. Finally, as discussed in an Update by McGarry et al. (2017), our knowledge of the molecular basis of how flowering is regulated has led to genetic engineering strategies to advance breeding programs and research efforts in crops such as tree species in which long generation times would otherwise greatly slow progress.

An Update by Thomson et al. (2017) revisits the ABC model of floral organ identity indicating that while it has experienced a number of modifications over the past 25 years, the model has been largely validated and essentially applies across angiosperms. Moreover, studies in recent years have yielded new insights into the specificity of the different floral organ identity factor complexes and into the elaborate downstream pathways that execute the ABC program and lead to the formation of the reproductive organs.

The genetic consequence and stereotypical cell division pattern during microsporogenesis, formation of
the diversely decorated and protective pollen coat, and the dramatically polarized pollen tube growth process are not only important for reproduction but also provide excellent model systems for genetics and cell biological studies. Advances in genetic and imaging tools have permitted detailed molecular and cell biological dissection of these complex processes in recent years (Chang et al., 2011; Quilichini et al., 2015; Cai et al., 2015; Hepler and Winship, 2015). Several articles in this Focus Issue discuss various aspects during the pathway to yield the dramatically polarized pollen tube. A research article by Liu et al. (2017) reports on the importance of repressed gibberellin acid signaling in maintaining ploidy reduction during microsporogenesis and the potential of gibberellic acid in integrating environmental stress and chromosome stability during reproductive development. An upcoming Update (C. Lambing, F.C.H. Franklin, and C.R. Wang, unpublished data) will look forward from the increasing understanding of the meiotic processes to consider how homologous chromosome recombination during meiosis might be incorporated into breeding programs in crops.

Several articles in this Issue provide additional understanding on anther differentiation and pollen maturation, in particular pollen coat formation. ZLi et al. (2017) furthered the characterization of a receptor-like kinase (EMS1)-controlled pathway on anther cell fate, in particular the tapetal cells that play a crucial role in pollen coat formation and thus pollen maturation and viability. Two articles, W.L. Li et al. (2017) and Suzuki et al. (2017), independently demonstrated the importance of a β-(1,3)-galactosyltransferase, which synthesizes arabinogalactan and pectin in the cell wall during pollen coat formation in Arabidopsis. These works also implicate the importance of arabinogalactan-protein in the construction of the pollen coat. Two other articles, Xu et al. (2017) and Chen et al. (2017), focus on crop plants and identified, respectively, an acyl transferase from rice (Oryza sativa) and an oxidoreductase from maize (Zea mays) as playing important roles in anther cuticle and wall formation and pollen viability. The importance of tapetal degeneration to pollen maturation is further underscored in two studies (Cui et al., 2017; Gao et al., 2017); they provide insight on the involvement by Cys and Asp proteases in tapetal cell death during the late stage of pollen development. Interestingly, the Asp proteases described by Gao et al. (2017) have signatures for glycosylphosphatidylinositol modification, a feature associated with an increasing number of proteins with critical roles in reproduction (Cheung et al., 2014).

The polarized pollen tube growth process has been extensively studied for decades, and the basic cellular framework, involving a dynamic actin cytoskeleton, an active and tip-focused vesicular trafficking system, and numerous regulatory factors, has been well established (Cheung and Wu, 2008); mechanistic elaborations will undoubtedly continue. Here, the Update by Michard et al. (2017) examines the huge repertoire of ion channels, transporters, and pumps expressed in pollen and consider how they might together orchestrate a dynamic environment of ion homeostasis compatible to supporting apical growth. It also highlights many remaining challenges, including how known and yet to be identified sensors for ionic changes mediate the growth response and which regulatory mechanisms coordinate transporter activities.

The Update by Bedinger et al. (2017) documents the impressive progress on the molecular characterization of S-locus-mediated self-incompatibility, a set of highly diverse genetic systems that prevent growth of pollen on a noncompatible pistil. Interesting is how related systems also govern incompatibility between different species. Much less is known about how the pollen tube navigates its way toward and inside the ovule. The first molecule secreted by the female gametophyte for pollen tube attraction was discovered about 10 years ago in maize (Marón et al., 2005). Since then the synergid cells neighboring the egg cell have been shown to generate and secrete multiple peptides and especially small Cys-rich proteins including the pollen tube attractant LURE (Okuda et al., 2009; Takeuchi and Higashiyama, 2012). A recent breakthrough has been the identification of two LRR-RLK receptor complexes involved in interaction with LURE1 in Arabidopsis. The two leading scientists of this discovery, Higashiyama and Wang, discuss in this issue the identification of different receptor complexes, the role of the central cell in LURE1 expression, and mechanisms to prevent multiple pollen tube visitation to the female gametophyte (Higashiyama and Yang, 2017). Another player in pollen tube guidance is the AMOR arabinogalactan sugar chain containing a bioactive terminal disaccharide enabling pollen tubes to respond to LURE peptides. The Higashiyama group (Jiao et al., 2017) now reports a structural activity study of the AMOR factor.

In contrast to male gametophyte development, the formation of the female counterpart, the embryo sac, is less studied. Tekleyohans et al. (2017) provide an Update on female gametophyte patterning along its micropylar-chalazal axis. A lateral inhibition model is proposed suggesting that the two female gametes control the development and cell fate of accessory cells. In doing so the egg cell plays the major role. Thus, specific attention is dedicated to the precursor cell of the embryo. As outlined in Tekleyohans et al. (2017), differentiation of the egg cell was recently shown to be promoted by a family of plant-specific transcriptional regulators in Marchantia, which provides the advantage of having only a single copy of these genes. Now Resentini et al. (2017) report that expression of the egg-cell-specific ECI gene family is regulated by the transcriptional regulator SUPPRESSOR OF FRIGIDA4 and chromatin modification in Arabidopsis.

After gamete fusion, the fertilized egg cell develops into the embryo and the central cell generates the endosperm. By comparing eudicot and monocot model plants, Zhao et al. (2017) provide an Update on recent advances and open questions on gene regulatory
networks during zygote development, parental influences on early embryogenesis, zygotic genome activation, and cell fate determination. Gehring and Satyaki (2017) discuss recent advances of imprinting research, which is especially linked to endosperm development. An important role of imprinted genes is postulated for plant speciation. That mating between different species can result in hybrid vigor is well known to breeders, but hybridization also happens in nature and in fact is frequent in plants and animals. Finally, Goulet et al. (2017) discuss how new advancements in genomic and genetic tools are revolutionizing our ability to investigate how and why hybridization contributes to biological diversity.

We are grateful to all authors for their thoughtful and exciting manuscripts and thank the numerous reviewers for critical assessment of the papers. Additional manuscripts will appear in the next issue of *Plant Physiology* that will be linked to this Focus Issue. We hope you enjoy reading the issue and share our vision that tremendous progress has been made in the field during recent years with more discoveries to be expected in the near future.

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**LITERATURE CITED**


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