Annals of Botany **108**: 585–587, 2011
doi:10.1093/aob/mcr217, available online at www.aob.oxfordjournals.org

PREFACE: PART OF A SPECIAL ISSUE ON SEXUAL PLANT REPRODUCTION

SEXUAL PLANT REPRODUCTION

Flowering plants are the most successful group of land plants, containing over 90 % of species and dominating almost every terrestrial ecosystem. This evolutionary success is due, in part, to their sophisticated reproductive biology centred on the eponymous flower, where female gametophytes are hidden and protected by the sporophyte carpel/pistil, animals are the principal transport vectors of the sperm-containing male gametophytes (pollen), and fertilization no longer requires water on account of the pollen tube. This combination of reproductive traits has permitted the evolution of an extraordinary array of mating and pollination systems that we are only just beginning to understand.

At a time of unprecedented human population expansion and biodiversity loss, research on plant reproduction, with its potential to help increase crop yields and deliver food security, and to guide effective conservation strategies, has never been more important. This Special Issue collates a diverse set of reviews and papers that span the breadth of current research on the reproductive biology of angiosperms, from the evolutionary development of the flower, the genetics and cell biology of pollen–pistil recognition and fertilization, to the emerging discipline of ecological and evolutionary systems biology.

The issue begins with two papers describing the utility of two basal angiosperms for evolutionary developmental (‘evo-devo’) studies aimed at understanding the origin of the flower and the evolution of reproductive processes in the earliest angiosperms. Vialette-Guiraud *et al.* (2011) review the merits of the fast-growing *Cabomba* (Nymphaeales, grown internationally in aquaria) as a model for studies of flower evolutionary development, while Prychid *et al.* (2011) show the amenability of the unusual water lily relative *Trithuria* (sole genus of Hydatellaceae) as a model for studies of pollen–stigma interactions and pollen tube growth in an ancient angiosperm. Next Whitney *et al.* (2011) consider why so many angiosperm petals have conical epidermal cells. They review recent studies aimed at elucidating the role of conical epidermal cells in petal function and the fitness benefits they afford. They highlight the effects of this cell type on petal colour, scent production, wettability, petal reflexing and pollinator grip on the flower, concluding that the fitness benefits they afford plants vary according to type of pollinator and habitat. The interaction between stamen development and winter dormancy in *Prunus armeniaca* is the subject of the following paper by Julian *et al.* (2011). Winter dormancy of flower buds occurs in the majority of temperate trees, many of which, like *P. armeniaca* are important fruit crops, yet little is known about developmental processes associated with the onset and break of bud dormancy. Here, they show that dormancy interrupts stamen development before meiosis and the production of microspores, while breakage of dormancy follows a clear sequence of physiological events.

The following eight review papers cover aspects of the pollen–pistil interaction and self-incompatibility (SI) in diverse groups of plants, both monocots and eudicots, showcasing the molecular diversity of these key reproductive processes across angiosperms. Few researchers have done more to shed light on the complex cellular and molecular interactions that occur during pollen germination and pollen tube growth on, and in, the pistil than Elizabeth Lord. This work, carried out ostensibly on lily (*Lilium longiflorum*), is the subject of the first review by Chae and Lord (2011), who describe the identification and characterization of two key small cysteine-rich proteins, SCA (stigma/style cysteine-rich adhesion) and chemocyanin, that respectively play pivotal roles in pollen tube adhesion and directional growth of pollen tubes in lily. Interestingly, despite being identified in a monocot these proteins are conserved in *Arabidopsis* (a eudicot) where they appear to perform similar roles in pollen–pistil interactions.

Papers by Meng *et al.* (2011) and McClure *et al.* (2011) then review current understanding of molecular and cellular regulation of RNase-based gametophytic SI (GSI), focusing largely on species from the Solanaceae but also extrapolating from molecular data on RNase-mediated GSI in the Rosaceae and Plantaginaceae. In this SI system incompatibility results from cytotoxic degradation of pollen RNAs by pistil-secreted S-RNases, but the precise mechanism by which *S*-specificity is achieved through ‘interaction’ between S-RNases and the pollen *S*-determinant, an *S*-locus F-box protein (SLF/SFB), is still unclear. From their studies in *Petunia inflata*, Meng *et al.* (2011) provide evidence for their intuitive protein-degradation model, where compatibility arises by specific degradation of non-self S-RNases in the pollen tube mediated by SLF. Meanwhile, McClure *et al.* (2011) articulate an alternative model, involving non-S proteins, most notably HT, as well as SLF, where compatibility is explained not by degradation of a non-self-S-RNase but rather by its compartmentalization within the pollen tube away from cytoplasmic RNAs. From the Solanceae we then move to the Papaveraceae where the genetic basis of GSI is identical but the molecular mechanism is different. The poppy GSI system is mediated through interaction between pistil PrsS (a protein ligand) and pollen PrpS (a receptor), which activates a Ca^{2+}-dependent signalling network that culminates in inhibition of pollen tube growth. This novel mechanism was elucidated in the lab of Noni Franklin-Tong and this review by Poulter *et al.* (2011) summarizes their most recent findings on how components of the pollen Ca^{2+} signalling system interact with and affect the actin cytoskeleton. The even more intriguing GSI system of the grasses, involving not one but two incompatibility loci (*S* and *Z*) is the subject of the next review by Klaas *et al.* (2011), which summarizes recent progress mapping the *S* and *Z* loci in perennial rye grass (*Lolium perenne*) before speculating on possible physiological mechanisms for pollen rejection.

The remaining three papers in this section focus on species with sporophytic SI (SSI) where the S phenotype of the pollen is determined by the *S* genotype of its parent plant, thereby giving pollen and pistil a diploid S phenotype, which allows for complex patterns of dominance interactions between *S* haplotypes in pollen and pistil. This makes for more complex genetics than in GSI, where pollen genotype determines pollen phenotype and dominance interactions are impossible (pollen) or futile (pistil) because they would lead to breakdown of SI. So far the molecular machinery responsible for SSI has only been elucidated in the Brassicaceae, even though SSI has been extensively studied in the Asteraceae and Convolvulaceae and in its heteromorphic form in the Primulaceae. Here Allen *et al.* (2011) provide evidence for a novel molecular mechanism of SSI in the Asteraceae and review progress in identifying candidate *S*-proteins and other proteins regulating pollen–pistil interactions in *Senecio*, their chosen model Asteraceae. Next, Tedder *et al.* (2011) describe their recent investigations into SSI in *Arabis alpina* in the Brassicaceae. In members of this family, notably *Brassica* sp. and *Arabidopsis lyrata*, SSI is regulated at a molecular level by the stigma-specific S-receptor kinase, SRK, and the pollen-specific cysteine-rich protein, SCR. Tedder *et al.* (2011) identify 15 putative *SRK* alleles in *A. alpina* and find variation in the strength of SI within and between populations, thus providing an ideal new model for future molecular studies of natural variation in SSI. The SSI system of the Brassicaceae and Asteraceae is regulated by numerous *S* haplotypes (over 70 have been identified in *Brassica oleracea*), whereas in the SSI system operating in the Primulaceae, and other families with heteromorphic SSI, just two *S* haplotypes showing complete dominance (*S* and *s*) are involved. 'Heteromorphic' refers to the fact that the two possible *S* genotypes (*Ss* and *ss*) produce two distinct flower phenotypes ('pin' and 'thrum') associated with each S phenotype. This association between flower form and compatibility was first noted in primroses (*Primula vulgaris*) by Darwin, who described crosses between long-styled ('pin') flowers and short styled ('thrum') flowers as 'legitimate' (i.e. compatible) while self pollinations and crosses between the same flower types were 'illegitimate' (i.e. incompatible). The lab of Phil Gilmartin has been mapping the *S* and *s* loci in *P. vulgaris* for many years, and the review by Li *et al.* (2011) summarizes their progress to date and describes exciting recent work that has identified the first candidate *S* locus-linked genes.

The penultimate review in this section by Dresselhaus *et al.* (2011) discusses the virtues of maize as a cereal model for studying all aspects of pollen–pistil interactions, from early compatibility/incompatibility determination, to pollen tube guidance and fertilization. In their review they lament the fact that despite the importance of grasses in agriculture too little is known about the molecular basis of these reproductive processes that impact so critically (e.g. through intra- and interspecific incompatibility phenomena) on practical aspects of cereal breeding. Proof that maize can function as such a model is provided from their own studies of molecular signalling events involved in pollen tube guidance to the ovule. This latter theme is the subject of the last paper in this section, which focuses on signalling events between pollen tube and ovule prior to fertilization. Kanaoka *et al.* (2011) describe studies of these events in *Torenia fournieri*, which is unusual among angiosperms in partially extruding its embryo sac (female gametophyte) from the ovule, thereby making *in vitro* studies of fertilization highly tractable. Studies have shown that pollen tubes are attracted to the ovule/embryo sac in response to small cysteine-rich proteins (CRPs) secreted by the synergids. Here Kanaoka *et al.* (2011) report the identification and characterization of a CRP from *T. concolor*, and provide initial evidence that species-specific CRPs impose species specificity on pollen-tube attraction.

The remaining three papers of this issue highlight ecological aspects of plant reproductive biology research. In the first paper, Lay *et al.* (2011) explore the relationship between plant–pollinator interactions and plant–herbivore interactions over space and time in *Erysimum capitatum* (Brassicaceae) – a plant with a generalist relationship with pollinators and herbivores. They show that pollinators and herbivores both select on floral traits – each preferring plants with more flowers – and herbivore activity sometimes negatively impacts on pollinator visitation. Compensatory reproductive mechanisms are proposed to mediate these interactions and allow *E. capitatum* to succeed in a complex selective environment. In the following paper, Yakimowski *et al.* (2011) investigate theoretical predictions about investment in male vs. female flowers in dioecious and monoecious plants. To do this they have measured the relative size and daily number of male and female flowers in dioecious and monoecious populations of insect-pollinated *Sagittaria latifolia* (Alismataceae). They show that for both dioecious and monoecious populations male flowers are larger and more numerous than female flowers, but female floral displays are larger on a daily basis as a consequence of greater synchrony in female flower opening. These differences, they suggest, are shaped by sexual selection for more effective pollen dispersal.

The final paper of the Special Issue (Shimizu *et al.*, 2011) reviews recent experiments that have applied the emerging discipline of ecological and evolutionary systems biology (which seeks to understand gene functions under natural field conditions) to study two key aspects of plant reproductive biology: flowering time and the evolution of self-compatibility (SC). To investigate control of flowering time, they analysed the expression of *FLC* (a key regulator of flowering) in *Arabidopsis halleri* in naturally fluctuating environments. These expression data, when combined with modelling, showed that in the 6 weeks preceding flowering, *FLC* acts as a quantitative tracer of temperature to modulate flowering. Shimizu *et al.* (2011) then show the merits of using a systems biology approach to study the evolution of SC in *Arabidopsis thaliana*. Both examples stress the importance of next-generation DNA sequencing in making this new, systems biology approach to plant reproductive biology possible. It is therefore fitting to end with a paper that looks to the future for plant reproductive biology research – a future made bright by technological advances in DNA sequencing and analysis that will offer hope for understanding the basis of natural variation among reproductive traits and its relationship with phenotypic plasticity.

Simon J. Hiscock
E-mail: Simon.Hiscock@bristol.ac.uk

LITERATURE CITED

Allen AM, Thorogood CJ, Hegarty MJ, Lexer C, Hiscock SJ. 2011. Pollen–pistil interactions and self-incompatibility in the Asteraceae: new insights from studies of *Senecio squalidus* (Oxford ragwort). *Annals of Botany* **108**: 687–698.

Chae K, Lord EM. 2011. Pollen tube growth and guidance: roles of small, secreted proteins. *Annals of Botany* **108**: 627–636.

Dresselhaus T, Lausser A, Márton ML. 2011. Using maize as a model to study pollen tube growth and guidance, cross-incompatibility and sperm delivery in grasses. *Annals of Botany* **108**: 727–737.

Julian C, Rodrigo J, Herrero M. 2011. Stamen development and winter dormancy in apricot (*Prunus armeniaca*). *Annals of Botany* **108**: 617–625.

Kanaoka MM, Kawano N, Matsubara Y, Susaki D, Okuda S, Sasaki N, Higashiyama T. 2011. Identification and characterization of TcCRP1, a pollen tube attractant from *Torenia concolor*. *Annals of Botany* **108**: 739–747.

Klaas M, Yang B, Bosch M, Thorogood D, Manzanares C, Armstead IP, Franklin FCH, Barth S. 2011. Progress towards elucidating the mechanisms of self-incompatibility in the grasses: further insights from studies in *Lolium*. *Annals of Botany* **108**: 677–685.

Lay CR, Linhart YB, Diggle PK. 2011. The good, the bad and the flexible: plant interactions with pollinators and herbivores over space and time are moderated by plant compensatory responses. *Annals of Botany* **108**: 749–763.

Li J, Webster MA, Smith M, Gilmartin PM. 2011. Floral heteromorphy in *Primula vulgaris*: progress towards isolation and characterization of the *S* locus. *Annals of Botany* **108**: 715–726.

McClure B, Cruz-García F, Romero C. 2011. Compatibility and incompatibility in S-RNase-based systems. *Annals of Botany* **108**: 647–658.

Meng X, Sun P, Kao T-h. 2011. S-RNase-based self-incompatibility in *Petunia inflata*. *Annals of Botany* **108**: 637–646.

Poulter NS, Bosch M, Franklin-Tong VE. 2011. Proteins implicated in mediating self-incompatibility-induced alterations to the actin cytoskeleton of *Papaver* pollen. *Annals of Botany* **108**: 659–675.

Prychid CJ, Sokoloff DD, Remizowa MV, Tuckett RE, Yadav SR, Rudall PJ. 2011. Unique stigmatic hairs and pollen-tube growth within the stigmatic cell wall in the early-divergent angiosperm family Hydatellaceae. *Annals of Botany* **108**: 599–608.

Shimizu KK, Kudoh H, Kobayashi MJ. 2011. Plant sexual reproduction during climate change: gene function *in natura* studied by ecological and evolutionary systems biology. *Annals of Botany* **108**: 777–787.

Tedder A, Ansell SW, Lao X, Vogel JC, Mable BK. 2011. Sporophytic self-incompatibility genes and mating system variation in *Arabis alpina*. *Annals of Botany* **108**: 699–713.

Vialette-Guiraud ACM, Alaux M, Legeai F, Finet C, Chambrier P, Brown SC, Chauvet A, Magdalena C, Rudall PJ, Scutt CP. 2011. *Cabomba* as a model for studies of early angiosperm evolution. *Annals of Botany* **108**: 589–598.

Whitney HM, Bennett KMV, Dorling M, Sandbach L, Prince D, Chittka L, Glover BJ. 2011. Why do so many petals have conical epidermal cells? *Annals of Botany* **108**: 609–616.

Yakimowski SB, Glaettli M, Barrett SCH. 2011. Floral dimorphism in plant populations with combined versus separate sexes. *Annals of Botany* **108**: 765–776.