

BOOK REVIEWS

Annual Review of Plant Biology 2009. Sabeeha Merchant *et al.* (eds). Annual Review, 4139 El Camino Way, P.O. Box 10139, Palo Alto, California 94303-0139, USA. Vol. 60. 607 pp. Price not mentioned.

Glorious 60 Years! The *Annual Review* started in the year 1932, and the first volume to be published was the *Annual Review of Biochemistry*. That was the time when biochemistry began getting established as a new discipline, especially in Germany, UK and USA. In comparison, the first *Annual Review* dealing with plants started much later in the year 1950 (as I entered university as a student), a delay which is of course understandable because without basic biochemistry, one could hardly make progress in understanding plant function and behaviour. The new publication was initially given the longer title of *Annual Review of Plant Physiology*. This was because there was rather small number of people who worked with chemical or physical tools, and, by and large, the research departments in universities were then of botany. About three decades later, when recombinant DNA techniques became widely established, and the excitement of molecular biology began to touch the plant world, the name was further expanded to *Annual Review of Plant Physiology and Plant Molecular Biology*. But when finally everyone was employing the new techniques, it looked superfluous to have such a long name, and in 2002 the simple *Annual Review of Plant Biology* was born.

Simultaneously, the volume expanded and the *Annual Reviews* underwent a significant change in production style – now with coloured illustrations, since mere words were no longer adequate to comprehend the increasing complexity of articles. However, the *Annual Review of Plant Biology* has also undergone a noticeable change in the character of topics and subjects chosen. There are 24 articles. Since the complexity of the topics has increased, some aspects have to be dealt with in more detail. Now instead of simpler topics, we have generally more formidable titles, restricting the review to a more defined sub-topic. There is also now a much wider range of articles dealing with topics that are expressly applied (for example, the article on cellulosic biofuel). And reflecting the trend

towards a new integrative plant biology touching the new systematics and evolution, there are articles on plants such as *Selaginella* and *Aquilegia*, which is a matter of delight for those interested in general botany.

The core chapters

To go in a little more detail, the first article is by Jan Zeevart. The *Annual Review* editors were wise in inviting him to contribute his article in good time, since sadly Zeevart passed away soon after. James Bonner, with whom Zeevart was associated, had led one of the most dynamic plant biology groups in the world at Caltech (there is an excellent photograph of Bonner in the book and many other important facts for the younger generation of scientists). Interestingly, our own careers have some parallels. Zeevart's classic work was on flowering where by grafting experiments he demonstrated unequivocally that a powerful flowering hormone must exist. Zeevart also worked on GA induction of flowering, although his main interest continued to be in flowering – in later years he contributed also significantly to abscisic acid and its role.

Coming to the 'core' of the volume, broadly all the contents can be grouped in a few categories: 'Basic Physiology, Techniques, Taxonomy, Applied Botany or Biotechnology'. The major section of the *Annual Review* deals with basic aspects of plant biology, and touches a wide range of topics. Self-incompatibility, the subject of the first of the core chapters, was reviewed only a year earlier. However, there is a good reason for the present article by Yongbiao Xue and colleagues. Although the classical work demonstrating the existence of *S* genes was done on *Nicotiana* by Edward East at Harvard, it is the work on *Brassica* in Japan and later in USA that resulted in the first biochemical insight regarding the nature of a *S* gene product. In *Brassica*, one *S* gene product represented a ligand (from pollen) that bound to another *S* gene product, a receptor kinase (on the surface of stigma), triggering the autolytic rejection in any 'self' pollen managing to germinate and send out a tube and degrading all its important macromolecular constituents. However, worthy of note is that in many other plant families, the *S* gene in the female tissue codes for a unique RNAase that degrades

the RNA from the 'self' pollen. On the other hand, the *S* gene in the pollen (*Sp*) belongs to a class of F-box genes, the S-locus F-box (SLFs). It is through work on yeast and animals, particularly by the Nobel laureates Aaron Ciechanover, Avram Hershko and Irwin Rose, that the F-box was found to be an essential component of the proteolytic machinery. Given that an F-box protein often serves as an adaptor that binds a specific substrate protein to the SCF E3 ubiquitin ligase complex, the putative pollen *S* product SLF/SFB can be part of the SCF complex and target the S-RNAase for degradation. It is the variation in the F-box coding component that determines the self-incompatibility response. The key observation in plants, originally made in *Antirrhinum*, is now supported by extensive work on tobacco, *Petunia* and other members of Solanaceae. It now appears that in general every protein requires a dedicated special SCF to degrade it. And this subject has assumed special importance because what is common now – between different types of mechanisms of self-incompatibility – is the destruction of proteins of the pollen tubes when selfing occurs, rather than the initial trigger.

The article by Gareth Jenkins on 'Signal transduction in responses to UV-B radiation', focuses on a likely new photoreceptor controlling photomorphogenesis. Although BL effects (covering also the UV-A region) are well known through discoveries such as those of phototropin and the CRY photoreceptors, little is understood of the shorter wavelength effects of the UV-B region (in the range 280–320 nm), which is rather harmful. Animals, including humans escape the harmful effects of such high-energy UV radiation, because we can move away from light. However, plants, stationary as they are, must withstand such radiation. Jenkins, through his own groundbreaking recent work as also through a review of older literature, has provided evidence for the existence of a unique gene and its product UVR8, which may act like a photoreceptor. The molecule does not have a typical chromophore, but has as many as 14 tyrosine residues.

Another chapter of great fundamental significance is by Stacey Harmer on 'Endogenous rhythm'. After the advent of the recombinant DNA techniques in the late 1970s and early 1980s, there has

been rapid progress in understanding the mechanism of circadian rhythm with the first clock genes isolated from *Drosophila* and *Neurospora*. A rhythm turned out to be the result of a feedback loop, wherein the product of a critical clock gene inhibited its own synthesis, resulting in the familiar diurnal periodicity in respect of many physiological phenomena. However, with more intensive work in higher organisms, it has been found that there are multiple feedback loops. This now appears to be the case also in plants, and in addition to the well established CCA, LHY and TOC-1 proteins, these loops have been found in recent years to accommodate several other players.

'Phloem transport', a topic of continuing mystery, has been reviewed by Robert Turgeon and Shmuel Wolf. Turgeon is one of the leaders in the field. In recent years several studies have shown high quantity of raffinose family oligosaccharides in companion cells in the phloem in minor veins. Turgeon and his group provided evidence for 'a polymer trap' model, where these high molecular weight sugars would prevent the 'original' lower molecular weight sugars that are the first products of photosynthesis – to go back into the leaf cell, where they are first made. Export of the newly made photoassimilate is thus 'vectorized' and

assured. However, many kinds of nutrients and regulatory molecules move up or down through the phloem and there is yet a lot to be learnt as to how directional movement of many kinds of molecules is controlled.

Another article of great fundamental interest is of Damon Lisch on 'Epigenetic regulation transposable elements in plants'. In most of the higher genomes, genuine coding sequences constitute only a small fraction of the genome and the vast majority of the genome is made up of repeat elements and transposons (in humans, a large fraction of the genome is made up just of one such element repeated hundreds and thousands of times). The nature and function of transposons is enigmatic. But the focus of this article is on the epigenetic regulation of activity of transposons themselves, which is brought about by the methylation of their DNA. Indeed epigenetic silencing is a subject of wider interest since it is related to the formation of heterochromatin, wherein hundreds of ordinary genes and chromosome arms, even entire chromosomes, can be silenced by methylation of histones as also DNA – transposons have been shown to be involved in it in several cases. However, this is an area where far more clarity is required. In recent past, what we have achieved are the sequences of a model genome for a particular species. With the ability of sequencing multiple genomes in short times, with newer technologies, much activity is expected in the future in unravelling the relationship between structural genes and transposons, and also how the environment can influence transposon activity. This volume includes an excellent article by Blake Myers and his colleagues on the new sequencing technologies which will play an important part in understanding the role of transposons and genomic alterations in evolution and in the life of a plant.

Signalling

In the area of signalling, there is an article of special interest by John Walker and colleagues on '14-3-3 and FHA domains mediate phosphoprotein interactions'. The 14-3-3 proteins, which were first discovered in animals in the brain in the middle of the sixties, were later found in plants by Robert Ferl in the early 1990s and have been the subject of research in

many laboratories of the world. These proteins interact with more familiar phosphoproteins. Phosphorylation is often the first step in targeting another protein and it is the 14-3-3 protein (the name comes from the order of elution in a column fractionation) that augments and serves as a recognition module for a variety of other interacting protein substrates. Typically, 14-3-3 binds to the phosphorylated region. The article also reviews information about FHA module, another modulator of the activity of target proteins.

Tolerance to stress

To turn to another broad area of current interest, the biology of stress tolerance, there are five articles on various aspects in this volume. An article of interest is one by Thomas Boller and Georg Felix on 'A renaissance of elicitors'. Following the development of recombinant DNA techniques, we have witnessed many exciting discoveries such as signals and signalling mechanisms, receptor kinases, protein degradation mechanisms, and so on, that bear on mechanisms of tolerance to stress. Yet, until around 2000, little was known about pathogen-associated molecular patterns that served as elicitors (most of the earlier attention was on chitins in fungi or peptidoglycan from bacteria). But around the turn of the century, the bacterial flagellin protein was recognized to be a major elicitor in plants by the Boller laboratory, leading to the activation of leucine-rich repeat receptor kinases coded by the *R* (resistance) genes. These kinases are cytoplasmic proteins with a nuclear binding site in front of a series of LRRs. This review gives the reader a broad perspective of microbe associated molecular patterns, the recognition of which plays a key role in innate immunity. The article ends finally with a brief consideration of the way the host tackles the invasion.

The article by Ken Shirashu focuses on the HSP90-SGT1 chaperone complex and how it helps in the correct folding and functioning of the more well-known NB and LRR-containing (NLR) immune sensors, which are vital to mount a defence to pathogens and whose role came to light by the work of groups such as those of Fred Ausubel, Jeff Dangl, Jonathan Jones, Brian Staskawicz and others.



Dawdle (*ddl*) phenotypes. Plants carrying a *ddl* T-DNA allele have many developmental defects (97). Wild type (WT), *ddl-1* complemented with genomic *DDL*, and *ddl* plants (left to right) show the defective phenotype of the *ddl* mutant.

Continuing the theme of stress biology, Ruiz-Ferrer and Oliver Voinnet have an article on 'Roles of plant small RNAs in biotic stress responses'. After the discovery of a role of small RNAs in *Caenorhabditis* and tomato, research on small RNA has become one of the most important areas of plant biology, and small RNAs are involved in every aspect of cellular metabolism from regulation of protein synthesis to chromatin remodelling. However, these authors focus their attention on stress response triggered by viruses, fungi and bacteria. Owing to the development of better experimental and computational methods, an ever-increasing number of small noncoding RNAs are being uncovered in different plants.

A review of interest to investigators of the areas of both photosynthesis and stress is by Krishna Niyogi and colleagues. To my knowledge, this is one among the few that deals with the response of the plant to excess light in totality, that is, from photoperception by dedicated photoreceptors to the various types of responses. Much attention has been paid, however, to the events inside the chloroplast, which is the special research area of the senior-most author. With the basic photosynthetic machinery unravelled, it is time now to turn to aspects such as how this machinery copes up with stress and with changing climate such research is of great interest.

Another article of interest from the viewpoint of both stress and the broader area of Developmental Biology is entitled 'Jasmonate passes muster: a receptor and targets for the defense hormone'. Evidence for a role of this hormone in defence was first found by Clarence Ryan, with whom the author (John Browse) was associated for sometime. Jasmonate, besides being the principal defence hormone of the plant, has also a role in ensuring pollen fertility. This article reviews the recent work relating not only to the biosynthesis of this hormone and its mechanism of action, but also touches upon its receptor, its 3D structure and many other related aspects.

Continuing with the theme of metabolism and basic plant biology is an article on 'Photorespiratory metabolism: genes, mutants, energetics, and redox signaling' by Christine Foyer and colleagues. More than a quarter century ago, a little after photorespiration was discovered, the first article was published in this series by William Ogren who was a pioneer in the

subject. However, at that point, the major focus all articles on the subject was on the basic pathway and its likely advantage to plants because of the recapture in C4 plants of some of the carbon dioxide released. The present article has, however, a fundamentally different perspective. The photo-respiratory pathway is a major source of H₂O₂ in photosynthetic cells. And through pyridine nucleotide interactions, photorespiration makes a key contribution to cellular redox homeostasis whereby the reducing power cells is stored as pools of reluctant and antioxidant compounds such as ascorbate (vitamin C) and the tripeptide, thiol glutathione. Multiple signalling pathways are thus affected, including those that govern plant hormonal, environmental and defence responses, as also programmed cell death.

Genomics

A few articles in this volume are broadly concerned with the genomes and related aspects. 'Bias in plant gene content following different sorts of duplication: tandem, whole-genome, segmental, or by transposition' has been authored by Michael Freeling, one of the world experts in the area. Many may come across somewhat unfamiliar terms – yet with the explosion in new technologies and rapid advances in science, new terminology becomes inevitable. However, the main focus of the article is on the origin of new genes, especially by polyploidy. Edward B. Lewis, while working with Thomas Morgan in Caltech, had earlier proposed that many of the new genes will arise by duplication. This idea was further developed by Marcus Rhoades and later by Susumu Ohno in his classical book *Evolution by Gene Duplication* (1970). However, often a bias follows and the extra gene provides the material for newer changes and correction – the old function is lost by deletion. Freeling has popularized the term 'fractionation' (gene loss involving one or the other homologue) and the article addresses how 'bias' operates in such fractionation.

A second important contribution is by Dan Kliebenstein on the subject of quantitative trait loci (QTLs). Although QTLs have a long history, the topic has assumed new importance not only because many agriculturally important traits are influenced by QTLs, but also because they are important for understanding the

molecular basis of evolution. The microarrays have opened up the possibility of evaluating variations in entire genomes and the author devotes considerable attention to these aspects which are of interest both from fundamental and applied viewpoints, one good example being QTLs affecting flowering time behaviour. The key players in respect of control of flowering time are well known now, but much less is known about the identity of genes where polymorphism exists, e.g. variations that generate a latitudinal cline controlling photoperiod sensitivity. Although Kliebenstein's personal engagement has been largely with resistance of plant host to *Botrytis cinerea* and variations in glucosinolate biosynthesis in *Arabidopsis*, he has addressed the entire subject in a general way emphasizing key concepts and is a valuable chapter for the general reader.

Thirdly, there is an article by Tatjana Kleine *et al.* on 'DNA transfer from organelles to the nucleus: the idiosyncratic genetics'. It is valuable, since the authors have given the first detailed insight (following sequencing of the *Arabidopsis* genome and the use of microarray analysis) into the evolutionary aspects of the origin of modern-day eukaryotic cells. Apart from the now commonly known stipulation – of great interest, i.e. of the transfer of a large number of genes from organelles to nucleus (about 20% of the genes in the nucleus may be derived from organelles), the article focuses on the logic and nature of genes transferred and those still retained in the organelles. The new microarray technique has enabled comprehensive analysis of genomes. However, transfer has occurred also between chloroplast and mitochondria. An important issue is also the origin of new genetic information by the creation of new exons.

Ecology, evolution and systematics

Of special interest from the viewpoint of the broad discipline of plant biology is the article by Elena Kramer on *Aquilegia* belonging to the family Ranunculaceae, which is now being developed as a new model for the study of plant development, ecology and evolution. The genus was the subject of extensive studies by Verne Grant, the famous American evolutionary biologist. Kramer has taken

advantage of his pioneering work and also of investigators such as Heinz Saedler and Elliott Meyerowitz on genes controlling flower development. She has thus launched a pathbreaking study of the area of the evolution of floral morphogenesis and this naturally includes molecular biology of differentiation of special organs and shapes, making good use of the extensive studies on speciation by Verne Grant.

Another article of phylogenetic and evolutionary interest is that by Jo Ann Banks on *Selaginella*, which is a pteridophyte and a genus of great interest representing not merely the evolution of the terrestrial habit from primitive bryophytes, but also evolution of heterospory. Work on its genome sequence was completed recently. *Selaginella* appears also to be the plant which in Indian ancient texts is known as 'Sanjeevani' – the review cites a reference in which studies have been carried out in collaboration with Syed Hasnain (formerly of the Centre for DNA Finger Printing and Diagnostics, Hyderabad) claiming extraordinary beneficial properties of extracts of *Selaginella*. The article is a good example of the type of investigations that will come in the next decade at the interface of molecular biology and evolution. Although *Selaginella* is a rather small plant, its relatives (lycopods) were plants that almost reached a height of 30 m in the Carboniferous era, and advances in genomics are expected to shed light on this remarkable group of plants, which is largely extant now.

The article by Pamela and Douglas Soltis on 'The role of hybridization in plant speciation' highlights the role of polyploidy in the evolution of angiosperms. Following the work of George Stebbins, Jens Clausen, and Verne Grant in USA, polyploidy became a major focus of biosystematics research. Since the majority of angiosperms are polyploids, it has become important to know the precise mechanism (whether a group is homoploid, autopolyploid or allopolyploid), its prevalence and role in evolution. With the sequencing of several genomes, research on polyploidy has acquired a new level of sophistication. In recent years, polyploidy has attracted a lot of interest also of molecular biologists, since there is often a strong dosage effect and many genes are silenced by chromatin remodelling (*Arabidopsis* itself appears to be a polyploid).

Miscellaneous – applied aspects and techniques

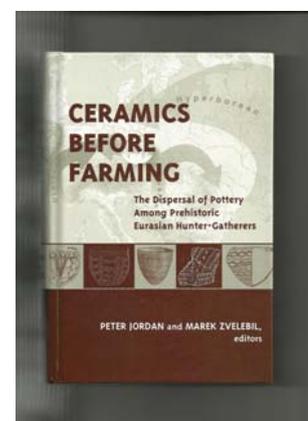
Certain other articles pertain to applied or biochemical aspects. The American plant biologist, Christopher Somerville is well known for his role in promoting research on *Arabidopsis*. However, Somerville has had strong interest as much in applied as fundamental aspects of plant biology and here, along with Andrew Carroll, he reviews the subject of cellulosic biofuels (a few years earlier he had reviewed the area of cellulose synthesis) which is of great topical interest these days. There is another article by James Kirby and Jay Kearling on the biosynthesis of isoprenoids, a group which includes such important molecules like menthol, taxol, carotenoids, vitamin A and artemisinin acid (effective against malaria). A third article is by Peggy Lemaux on 'Genetically engineered plants and foods: a scientist's analysis of the issues (Part II)'. Presently, there is a lot of controversy in regard to genetic engineering. There are those who are convinced about its great benefits to man and there are those who are not. And, surprisingly, even in advanced countries in the West, not everyone has accepted the idea of genetic engineering. We have the example of Germany, scientifically one of the leading countries (DNA was first isolated here), where genetically engineered crops have not been accepted. My own knowledge is limited on these issues, but Lemaux has a well-researched, readable article (contained in this volume in Part II). She is in favour of the new technologies; yet, she clearly states that many issues still need to be addressed (one example is her concern on the use of the new technology for obtaining pharmaceutical or industrial proteins).

There is not sufficient space to discuss even briefly all articles. However, mention can be made of a review by Stacey Simon and others on the 'New shortread technologies for transcriptional analyses', which differ from conventional capillary-based sequencing. The new 'next generation sequencing' has departed from the Sanger sequencing chemistry. In 2000, Sydney Brenner introduced the MPSS technique, in which sequencing was performed on templates formed as beads or spots of DNA. In the last 5 years, many other improvements and new technologies have been introduced, especially by Roche, Illumina, Applied Biosystems, and

Helicos Biosciences (here, true single-molecule sequencing is done). However, the tremendous depth of analysis available now also points to challenges in future in the integration of data. There is also an article by Achim Walter and colleagues on 'Environmental effects on spatial and temporal patterns of leaf and root growth'.

S. C. MAHESHWARI

*School of Life Sciences,
Jaipur National University,
Jagatpura,
Jaipur 302 025, India
e-mail: satish_maheshwari@hotmail.com*



Ceramics Before Farming. The Dispersal of Pottery Among Prehistoric Eurasian Hunter-Gatherers. P. Jordan and M. Zvelebil (eds). Left Coast Press, Walnut Creek, CA, USA, 2009. 589 pp. Price: US\$ 99.00.

Archaeologists have been traditionally viewing ceramic production and use to be the product of agriculturally based societies and equating it with Neolithic revolution. However, researches done in the last few decades have shown that pottery emerged in various parts of the world towards the end of the prehistoric period. In northern Eurasia, it has been shown that the tradition of using pottery long predated the introduction of agriculture. This began initially in east and northeast Asia and progressed westwards across Siberia. This volume is an attempt to understand the origins of pottery in the region. The authors appear to have succeeded remarkably in this endeavour.

This 'synthetic overview' volume has had a long incubation period. It began