Plant developmental biologists meet on stairways in Matera

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Summary
The third EMBO Conference on Plant Molecular Biology, which focused on ‘Plant development and environmental interactions’, was held in May 2012 in Matera, Italy. Here, we review some of the topics and themes that emerged from the various contributions; namely, steering technologies, transcriptional networks and hormonal regulation, small RNAs, cell and tissue polarity, environmental control and natural variation. We intend to provide the reader who might have missed this remarkable event with a glimpse of the recent progress made in this blossoming research field.

Key words: Plant development, Flowering, Environmental interactions, Plant biotechnology

Introduction
Multicellular organization in plants has evolved independently from that in animals, and this has led to fundamentally contrasting developmental strategies. As opposed to animals, plants get their energy from sunlight, not by ingesting other organisms, and they are sessile organisms containing cells encased in rigid cell walls. This necessitates different mechanisms for shaping the body and for coping with a changeable environment. Whereas animal development can be studied mainly at the embryo phase, studies of plant development are more complex and require knowledge of the entire life cycle of the plant and of its interactions with the environment. The rise of plant molecular research over the last few decades has fueled plant developmental research with novel techniques that can be used to tackle previously insoluble problems and has contributed to the current bloom in this field.

In May 2012, over 150 plant developmental biologists gathered in the cave city of Matera, Italy, for the EMBO Conference on ‘Plant development and environmental interactions’. The conference did not take place in a cave but scientists were welcomed and spoiled in the splendid Palazzo Viceconte, an early 17th-century mansion in the heart of the ancient city. The conference, which was expertly organized by Paolo Constantino (Sapienza University of Rome, Italy), Ida Ruberti (Consiglio Nazionale delle Ricerche, Rome, Italy) and Chiara Tonelli (University of Milan, Italy), covered all aspects of plant development, including root, shoot and leaf development, flowering and reproduction, and responses to biotic and abiotic stresses. Below, we attempt to summarize the research and ideas that were presented during this meeting, focusing on the six main themes and developments in the field that emerged: (1) the application of novel technologies; (2) insights into transcriptional networks and their hormonal regulation; (3) the importance of non-coding RNAs for different aspects of plant development; (4) new views on cell and tissue polarity; (5) environmental control; and (6) the rapidly developing field of natural variation. It was impossible to cover every aspect of the meeting and we apologize for not having mentioned the excellent work of some of our colleagues.

Steering technologies
As in all experimental science, progress in plant biology depends largely on the availability of new tools and cutting edge experimentation. This was particularly obvious at the meeting and several speakers reported the use of novel and sophisticated technologies that were implemented in their projects.

The study of dynamic growth processes in organs or in entire plants remains problematic for many plant developmental studies. For the root in particular, this has been commonly recognized as a stumbling block. The team of Philip Benfey (Duke University, Durham, USA), however, has developed a method for studying three-dimensional (3D) root growth using tomographic reconstructions of roots growing in a gel-based and transparent medium (Iyer-Pascuzzi et al., 2010). By screening different rice accessions, the Benfey group identified 99 quantitative trait loci (QTLs) that reflect 3D-root traits, thus providing proof that their system is up and running. In addition, using their imaging and analysis platform, they identified five major effect QTLs controlling central root architecture phenotypes.

In the field of microscopy, a method for generating high resolution 3D images from biological samples known as serial block-face scanning electron microscopy (SBFSEM) was used by Ykä Helariutta (University of Helsinki, Finland) to study the ultrastructure of sieve elements, which are living but enucleate phloem cells that are interconnected through sieve pores and through numerous plasmodesmata with neighboring cells. Helariutta and colleagues conducted a screen to identify mutants that were defective in sieve element differentiation based on the use of a fluorescent marker for phloem identity. Such mutants are currently being analyzed by SBFSEM to study alterations in phloem ultrastructure with special attention being given to the intercellular connections.

Jan Traas (Ecole Normale Supérieure de Lyon, France) used a dynamic 3D model that incorporates both mechanical and biochemical properties to test the hypothesis that differential cell wall stiffness accounts for morphogenesis at the shoot meristem. Simulations predicted that the walls of cells surrounding the young initiating organs should be substantially stiffer than those in the young organs themselves. However, screening the meristem surface with an atomic force microscope (Milani et al., 2011) could not corroborate the predictions as, so far, no significant difference between the central part and the leaf initiation sites could be detected. Further analyses suggested that not only wall stiffness, but also wall anisotropy, could play a substantial role in organ initiation.

Using novel techniques for measuring molecular dynamics (including binding dynamics) and protein concentrations from

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fluorescence confocal images of living cells, Rosangela Sozzani from the Benfey laboratory is studying the dynamics of the SHORTROOT/SCARECROW (SHR/SCR) pathway. Through these in vivo approaches, which are based on fluorescence correlation spectroscopy (FCS) and raster image correlation spectroscopy (RICS), it is also possible to track inter- and intracellular movements of proteins. Sozzani used these techniques to generate both local maps of SHR movement and maps of SHR-SCR oligomeric state and protein-protein complex formation in a cell type-specific manner. This work will contribute considerably to modeling the dynamics of the SHR/SCR pathway, which controls key root developmental programs (see below).

Transcriptional networks and hormonal regulation
The development of multicellular organisms relies strongly on the fine-tuned control of transcriptional networks. In plants, genetic studies, mainly in the model species *Arabidopsis*, have identified several key transcription factors that control important developmental processes. For example, in the root, one of the celebrated transcription factors is SCR, which acts together with SHR to control ground tissue patterning by regulating formative asymmetric divisions. SCR and SHR are also required for quiescent center (QC) specification and stem cell maintenance in the root, and the respective mutants show a short root phenotype that is the consequence of an early arrest of stem cell activity (Ten Hove and Heidstra, 2008). Research on the function of these transcription factors has not ceased since their identification, and several novel insights into their mechanism of action have been uncovered. However, little is known about the downstream signaling events they control. Sabrina Sabatini (Sapienza University of Rome, Italy) and her team reported on a novel feedback mechanism between SCR and hormone perception and homeostasis that might be essential for the SCR-dependent control of stem cell activity. They found that the short-rooted phenotype, but not the ground tissue defects, of *scr* mutants could be rescued by decreasing perception of the plant hormone cytokinin in the QC. Thus, SCR might function, in part, to repress cytokinin perception and/or signaling. This might be a component of a balancing mechanism because cytokinins are needed to preserve meristematic activity of the root. Also focusing on cytokinin, Ykä Helariutta’s group generated a genetic tool to directly interfere with the aperture of plasmodesmata through local callose synthesis (Vatén et al., 2011) and used this system to seal the phloem via phloem-specific callose production, thereby blocking cytokinin import into the meristem. This resulted in an immediate arrest of root elongation, showing that a continued flux of cytokinin is needed for indeterminate root growth. Sabatini’s group demonstrated further that intensified cytokinin signaling in the QC of *scr* mutants results in the induction of *ANTHRANILATE SYNTHASE beta1 (ASB1)*, which encodes a subunit of an enzyme implicated in auxin biosynthesis, thereby potentially increasing auxin levels. In other words, SCR might control stem cell activity through the tempering of cytokinin-instigated auxin biosynthesis in the QC.

Local auxin biosynthesis emerged again as non-negligible factor in other talks. Jiri Friml’s team (VIB-University Gent, Belgium) generated a computational model to understand auxin transport routes and auxin distribution patterns during early embryogenesis. The model predicted, and experiments demonstrated, that localized auxin biosynthesis in the apical cells of the embryo at the 16-cell stage is crucial for further polarization and patterning of the developing embryo. Furthermore, local conversion of the auxin precursor indole-3-butyric acid into the bioactive indole acetic acid was shown by Tom Beeckman and his group (VIB-University Gent, Belgium) to occur preferentially in the root cap. They demonstrated further that this root cap-derived auxin source contributes, at least in part, to the initiation of lateral root primordia and, thus, root architecture (De Rybel et al., 2012). From these studies, it clearly emerges that fine-tuning of the local hormonal environment by transcriptional networks is a crucial element in plant development that needs further exploration.

Hormonal crosstalk is also controlled by transcriptional networks. This was illustrated by the work of Jan Lohmann (Heidelberg University, Germany), who dug into another famous veteran network, namely the WUSCHEL/CLAVATA pathway, which controls stem cell fate in the shoot apical meristem (Lenhard and Laux, 2003). Using ChIP-on-chip experiments, Lohmann and colleagues identified the basic helix-loop-helix transcription factor HECATE (HEC1) as a direct and negative target of WUSCHEL. In the organizing center of the shoot apical meristem, i.e. the region where WUSCHEL is operating, HECATE function has to be inhibited, as illustrated by the loss of stem cell activity when HEC1 is driven by the *WUS* promoter. Notably, when HEC1 was expressed above the organizing center, namely in the stem cell area, using the *CLV3* promoter, massive stem cell proliferation was observed. Remarkably, this all seems to happen in the absence of altered *CLV3* expression or *WUS* upregulation, indicating that HEC1 is able to uncouple stem cell behavior from the WUS/CLV system. Constitutive overexpression of HEC1, again accompanied by stem cell over-proliferation, resulted in ‘pin-shaped’ inflorescences, which led the Lohmann group to investigate the link with auxin because such phenotypes are the hallmark of reduced polar auxin transport. They showed that auxin modulates HEC1 expression, which in turn controls expression of the PIN1 and PIN3 auxin transporters. Furthermore, a meta-analysis of HEC1-overexpression lines suggested a role for HEC1 in inhibiting the cytokinin response by direct regulation of cytokinin-inducible response regulators. The identification of HEC1 as a novel stem cell-promoting factor acting partially independently from the WUS/CLV system and interfering with auxin transport and the cytokinin response illustrates the complexity of stem cell regulation in plants.

Upstream of transcriptional regulation, cells communicate with their neighborhood typically through ligand-receptor interactions that lead to the induction of signal transduction cascades. The numerous receptor-like kinases and putative signaling peptides present in plant genomes suggest a considerable role for signal transduction cascades during developmental processes (De Smet et al., 2009). However, to date, this has been investigated in detail in only a few cases, of which the above-mentioned WUS/CLV signaling cascade is an example. Two processes that rely on correct cell-to-cell communication in the plant’s life cycle are pollination and fertilization. Work from Ueli Grossniklaus’ laboratory (University of Zürich, Switzerland) showed that the female, more specifically the synergid cells, controls one of the last steps in fertilization, namely pollen tube rupture and release of the male gametes, collectively referred to as pollen tube reception. These conclusions are based on genetic studies of female gametophytic mutants that show defective pollen tube reception and are therefore semi-sterile. The elucidation of the complete signal transduction cascade between the synergid cell and the pollen tube is far from being completed, but genes studied so far potentially code for crucial, plasma membrane-localized elements in the male-female communication system. One gene, *FERONIA*, encodes a receptor-like kinase (Escobar-Restrepo et al., 2007), and another, *NORTIA,*
encodes a seven-transmembrane-domain protein with similarity to a powdery mildew resistance locus (MLO) (Kessler et al., 2010). Given that FERONIA not only seems to control pollen tube reception but also modulates infection by powdery mildew hyphae, Grossniklaus speculated on the intriguing idea that angiosperms have been hitchhiking ancient defense mechanisms against pathogens for their gametophytic interaction mechanisms (Kessler et al., 2010). Their recent work has also shown that glycosylation of these membrane proteins might play an important role in the recognition process between the male and female components. Besides pollen tubes, another example of tip-growing filamentous cells is root hairs. Liam Dolan (University of Oxford, UK) presented evolutionary insights into transcriptional regulation of root hair growth. In the moss Physcomitrella patents of root hair growth. In the moss, mutants UK) presented evolutionary insights into transcriptional regulation filamentous cells is root hairs. Liam Dolan (University of Oxford, UK) presented evolutionary insights into transcriptional regulation of root hair growth. In the moss Physcomitrella, mutants defective in the RHD SIX-LIKE transcription factors RSL1 and RSL2 show fewer rhizoids (structures similar to root hairs) whereas gain-of-function mutants show the opposite phenotype (Jang et al., 2010). The Arabidopsis homolog RSL4 is expressed in the root below the root hair zone but the protein is ‘carried on’ by differentiating cells, and RSL4 protein stability controls the duration and thus extent of root hair elongation. These intriguing observations point towards an ancient mechanism for controlling growth of filamentous cells.

Small RNAs in plant development

The plant field has made seminal contributions that initiated the whole field of small RNAs (sRNAs), and the role of sRNAs in various aspects of plant development is still being studied intensively. Through the local silencing of key developmental regulatory genes, sRNAs can act as driving factors for crucial morphogenetic events. They can move across a few cell layers and might work in a non-cell autonomous and concentration-dependent manner, thereby having a role largely analogical to morphogens. The power of sRNA action on plant development was nicely illustrated by Marja Timmermans (Cold Spring Harbor Laboratory, USA). Most leaves are not radially symmetric but have distinct upper and lower sides; the upper side is specialized for capturing the sunlight whereas the lower surface accounts for gas exchange. On the lower side, miR166 accumulates and thereby limits the expression of its targets, HD-ZIPIII transcripts, to the upper side, whereas trans-acting short-interfering RNAs (ta-siRNAs) restrict the expression of ARF3 and ARF4 transcription factors to the lower side (Kidner and Timmermans, 2010). Intriguingly, the Timmermans group could show that these sRNAs generate opposing gradients by mobility from the lower and upper epidermis, thereby specifying a sharp boundary between the two sides. Decreasing the level of one sRNA coincides with a sharp increase in the level of the opposing one, and results in an uneven border between upper and lower leaf sides and decreased robustness in leaf development. Furthermore, the presence of a START domain in the HD-ZIPIII family suggest that, alongside sRNA-dependent control, these transcription factors might be activated by binding to lipophilic ligands. An ongoing yeast-1-hybrid screen of a library of 22,000 diverse compounds promises to identify potential ligands and tackle this possibility.

Besides upper/lower polarity, leaves come in all kinds of shapes and forms. For example, different species display a huge variability ranging from smooth to strongly incised leaf margins. Arabidopsis presents only modest serrations at its margins whereas its relative Cardamine hirsuta forms compound leaves with distinct leaflets (Hay and Tsiantis, 2010). Miltos Tsiantis (University of Oxford, UK) and his group identified miR164A as an important sRNA that controls C. hirsuta leaflet number by repressing expression of CUP-SHAPED COTYLEDON (CUC2) gene, a member of the NAC transcription factor family. CUC2 in turn influences auxin transport by promoting convergence points of expression of PIN1 (Petrasek et al., 2006; Bilsborough et al, 2011) at the leaf margin. In these convergence spots, auxin maxima are generated which then repress CUC2 expression. This feedback loop generates a pattern of auxin maxima interspersed with CUC2 expression along the leaf margin and the entire system relies on PIN1-dependent auxin transport (Bilsborough et al., 2011). Not surprisingly, Tsiantis stumbled upon a Cardamine pin1 mutant in a screen for reduced leaf number mutants in this species, confirming the role of PIN1-dependent auxin maxima in promoting leaflet formation.

The relevance of sRNA mobility was a central theme during the talk of Ykä Helariutta who demonstrated the importance of plasmodesmata for the movement of miR165/166 from the endodermis to the inner stele (Vatén et al., 2011). This movement results in a graded occurrence of the HD-ZIPIII targets that is crucial for proper xylem patterning. Moreover, this inward movement of miRNA is part of a bidirectional cell signaling mechanism; activation of MIR165/166 transcription is provoked by SHR, which moves from the stele to the endodermis (Fig. 1). George Coupland (Max Planck Institute for Plant Breeding Research, Cologne, Germany) reported on the importance of miR156 in vernalization, a process that accelerates flowering in response to chilling. This work was performed in Arabis alpina, a perennial relative of A. thaliana in which young axillary meristems...
remain vegetative during flowering (Wang et al., 2011). Coupland presented a model in which an age-dependent pathway reduces the production of miR156 in older meristems, thereby allowing SQUAMOSA PROMOTER BINDING PROMOTER LIKE (SPL) transcription factors to increase in abundance and promote the transition to flowering during vernalization. This pathway is typical of perennial Arabis, in which the vernalization response is age dependent, but is not involved in the vernalization response of the annual A. thaliana in which even young meristems respond to vernalization.

The examples above illustrate the importance of sRNAs for several developmental processes. At least two other contributions made us understand that our current knowledge in this field is probably still very limited. Phillip Benfey reported on the identification, through Illumina sequencing, of at least 66 new high-confidence miRNAs using a computational pipeline (PPImiR) specifically developed for the identification of plant miRNAs (Breakfield et al., 2012), and Nam-Hai Chua (Rockefeller University, New York, USA) used a bioinformatics approach to detect ~6000 long intergenic non-coding RNAs (lincRNAs) in the Arabidopsis genome. lincRNAs are >200 nucleotides in length and differ from miRNA precursors. There is still no clear evidence for their functioning during plant development, but Chua and co-workers reported that genes encoding these non-coding RNAs show organ-specific expression patterns and many respond transcriptionally upon biotic and/or abiotic stress conditions.

Cell polarity in development

Cell polarity plays an integrated part of numerous plant developmental processes, ranging from embryogenesis and organogenesis to responses to environmental cues such as light, gravity or pathogen attack. Furthermore, plant cells are encapsulated by rigid cell walls, necessitating a strategy for modulating polarity of cells or groups of cells to mediate developmental processes at specific sites and time points during development (Dettmer and Friml, 2011). Phyllotaxy, the arrangement of leaves on the stem, clearly illustrates the importance of developmentally controlled cell polarity. New leaf primordia arise on the surface of the shoot apical meristem in precise positions characterized by local auxin maxima (Benková et al., 2003). Such maxima can be obtained by the action of the auxin transporter PIN1, polar localization of which converges towards these points of organ initiation (Reinhardt et al., 2003). Elliot Meyerowitz (California Institute of Technology, Pasadena, USA) presented a model, supported by experimental work, that grants a crucial role for local mechanical stresses driving the cell polarity patterns observed during flower initiation (Heisler et al., 2010). From the moment a given cell has a higher auxin content than its neighbors, it will expand more and will thus exert an anisotropic mechanical stress on the cell walls and plasma membranes of its neighboring cells. The result is that both microtubules and PIN1 become reoriented and align to the anisotropic stress. The localization of PIN1 to the plasma membranes adjacent to the cell walls with the highest stress provokes increased auxin efflux and consequently more mechanical stress. This self-reinforcing mechanism will only stop when new cellulose microfibrils are formed from cellulose synthase complexes that are guided by the newly aligned microtubules, or when the cell is reinforced by the formation of a new cell wall, after division. The implementation of such mechanical stress patterns combined with auxin transport appeared to be sufficient to predict the phyllotactic pattern found in the Arabidopsis shoot. This view is supported by the crucial importance of cell wall and cellulose synthesis for PIN polar distribution (Feraru et al., 2011) and by the studies of Jan Traas and colleagues on microtubule re-arrangements (Hamant et al., 2008) induced by mechanical stresses during morphogenesis.

Enrico Coen (John Innes Centre, Norwich, UK) delivered a charmingly conceptual talk on mechanisms of cell and tissue polarization, comparing minimal requirements for these processes in animals and plants. With the introduction of cell-to-cell coupling and intracellular partitioning of two mutually and feedback-regulating factors, the cells within a tissue were capable of local alignment of polarities. Furthermore, in the presence of a global organizer of polarity, for example an intercellular auxin gradient, the cells polarized in a coordinated fashion. This model, similar to the mechanical stress-based model from Meyerowitz or an auxin feedback model involving extracellular auxin perception (Wabnik et al., 2010), achieves coordinated polarization of cells without the need for hypothetical auxin flux sensors or auxin concentration measuring in the neighboring cells.

A nice study of hormonal crosstalk between brassinosteroid (BR) and auxin-mediated development presented by Antonio Leyva (Centro Nacional de Bioteconomía, Madrid, Spain) also involves effects on the polar localization of PINs. Leyva and his team showed that BR increased auxin maxima during lateral root initiation and generated wavy root growth phenotypes. They described a mutant displaying a wavy-root phenotype that bears a novel allele of the ACTIN2 gene. The mutant exhibits altered actin configuration and PIN delocalization consistent with constitutive BR responses. Interestingly, they showed that actin filament reconfiguration is sufficient to activate BR signaling leading to auxin hypersensitivity. They concluded that the actin cytoskeleton acts as a crucial node for BR and auxin crosstalk (Lanza et al., 2012).

Environmental control

Drastic transcriptional changes occur when seedlings switch from heterotrophic to photosynthetic growth. Light plays a central role in this developmental transition and the group of Salomé Prat [Centro Nacional de Biotecnología (CNB), Madrid, Spain] showed that two plant hormones, brassinosteroids (BRs) and gibberellins (GAs), are crucial for this event. Previous work from the group showed that DELLA proteins, repressors of GA-regulated gene expression, interact with the light-regulated transcription factors, known as phytochrome-interacting factors or PIFs (Davière et al., 2008). This interaction prevents the PIFs from doing their job, namely sustaining etiolated growth. Prat presented convincing arguments to support a model in which the GSK3-like kinase BRASSINOSTEROID-INSENSITIVE 2 (BIN2), a central negative regulator of the BR signaling pathway, interacts with and phosphorylates PIF4 resulting in its degradation. In wild-type plants, BR inhibits BIN2, which leads to elongation growth. Part of this elongation growth can be attributed to the accumulation of PIFs, found also to work as obligate partners of the BR-response BRASSINAZOLE RESISTANT (BZR1) factors, appointing them as main integrators of light with GA and BR signaling.

Environmental regulation of elongation growth can be studied elegantly by analyzing hypocotyl growth in Arabidopsis. In the dark, hypocotyls elongate strongly (etiolation) and this can be reversed by light treatments (de-etiolation). Eirini Kaiserli from Joanne Chory’s laboratory (The Salk Institute, La Jolla, USA) reported on the de-etiolation mechanisms identified by this group (Loudet et al., 2008). Upon blue light irradiation, the tandem zinc finger/PLU3 domain-containing protein (TZP) is transcriptionally
induced. TZP protein localizes in the nucleus in the form of speckles that show a dynamic behavior to different light conditions; plants growing in day/night conditions show diurnal patterns in the density of the speckles with a drop during the night and at dawn, the period corresponding to maximal hypocotyl elongation growth. In their search for potential TZP-dependent growth controlling mechanisms, they identified ATHB23, an Arabidopsis class I homeodomain-leucine zipper gene by screening the complete Arabidopsis transcription factor library of Steve Kay (University of California, San Diego, USA). Furthermore, through co-immunoprecipitation in planta, PHYTOCHROME B (PHYB), the best-studied regulator of hypocotyl elongation so far, was picked up and shown to colocalize with TZP in the nuclear speckles. The identification of this interaction will certainly contribute to the understanding of the complex mechanism plants use to steer elongation growth in response to altered light conditions, a feature that is also used in the shade avoidance response. In this respect, Ferenc Nagy (Biological Research Centre, Szeged, Hungary) demonstrated that the activity of PHYB, together with its protein interactions, is also strongly determined by phosphorylation. Through the study of phospho-mutants of PHYB, they showed that phosphorylation on one specific residue inhibited the light-induced hypocotyl growth inhibition and shade avoidance capacity of PHYB.

In addition to the obvious abiotic factors, such as light, plants are subjected to various biotic factors, such as bacteria and fungi. However, interactions with bacteria or fungi do not necessarily have to be detrimental to the plant. A nice example was given by Heribert Hirt [French National Institute for Agricultural Research (INRA), Evry, France], who presented data on the interaction between Arabidopsis roots and the fungus Piriformospora indica. This endophytic fungus promotes plant growth and, more importantly, plants with the endophyte are more resistant to drought and to certain pathogens. In collaboration with Ralf Ölmüller’s group (Friedrich-Schiller-University, Jena, Germany), the Hirt group isolated an Arabidopsis mutant in the OXIDATIVE SIGNAL INDUCIBLE1 (OX1) gene in a genetic screen for plants that did not show the P. indica-induced growth response (Camehl et al., 2011). OX1 had previously been characterized as a protein kinase that plays a role in pathogen response, is regulated by water and 3-phosphoinositide-dependent protein kinase (PDK1), and activates a MAPK signaling cascade (Rentel et al., 2004). PDK1 is a member of the cAMP-dependent protein kinase A/protein kinase G/protein kinase C (AGC) kinase family, and the Arabidopsis homolog AtPDK1 is regulated by binding to phosphatidic acid (PA). Therefore a model was proposed in which a P. indica-derived signal stimulates plant growth through a PA-PDK1-OX1-MAPK signaling cascade.

Natural variation
Plants adapt to their environment and show genetic diversity according to the ecological context in which they are living. Arabidopsis, for example, grows in a wide range of environments and this makes it an excellent system with which to dissect the molecular variation underpinning adaptive variation. Caroline Dean (John Innes Centre, Norwich, UK) and colleagues investigated the molecular basis for variation in vernalization. They searched in 192 Arabidopsis natural accessions adapted to different climates for adaptation in vernalization related to flowering (Coustham et al., 2012). A major variable they found among the ecotypes was the capacity to maintain epigenetic silencing of the floral repressor gene FLOWERING LOCUS C (FLC). Dean’s earlier work had established the Polycomb mechanism necessary for vernalization. Now they have identified non-coding single-nucleotide polymorphisms (SNPs) within the FLC domain (in which histone methylation accumulates in the cold) that attenuate the accumulation of epigenetic silencing. This results, for example, in the Northern Swedish accession requiring a longer period of cold (9 rather than 4 weeks) to fully saturate the vernalization requirement. Detlef Weigel’s group [Max Planck Institute (MPI), Tübingen, Germany] performed a genome-wide association study of a collection of Arabidopsis accessions and demonstrated that a hyperactive ACCELERATED CELL DEATH 6 (ACD6) allele of Arabidopsis is responsible for increased camalexin and salicylic acid production and enhanced resistance to a broad range of pathogens in comparison with the reference allele (Todesco et al., 2010). However, the ACD6 allele has a smaller rosette size which leads to the conclusion that the acquired increased resistance is traded off at the same time. Products of many immunity-related genes that are responsible for acquiring enhanced resistance to pathogens also appear to inhibit growth, which will in extreme situations lead to cell death, as is the case for ACD6. This led Weigel to introduce the concept of ‘hybrid necrosis’ (Bomblies and Weigel, 2007). Allelic variation at such loci results in increased defense, which is at the same time associated with a reduced growth capacity. Boosting the plant’s defense capacity is only possible to a certain point beyond which growth stops and necrosis sets in. The pervasive presence of negative epistatic interactions also prompted Weigel to investigate how frequent new mutations and new epimutations are, as these are the raw materials of evolution. They found epigenetic polymorphisms, such as differential cytosine methylation, between different Arabidopsis descendants of the Col-0 accession that had evolved and diverged for 30 generations in the laboratory (Becker et al., 2011). Such differential methylated positions are not permanent but appear to be able to reverse from generation to generation. Their instability also depends on their positioning on chromosomes; telomeric methylations seem to show a higher tendency to become preserved in the offspring. Such studies of the methylome can therefore assist in reconstructing the colonization history of plants.

Conclusions
This was another fantastic EMBO Plant Molecular Biology meeting that demonstrated great progress in multiple aspects of plant science. At the end of the meeting, it became obvious to all of us that our field of research has matured into a discipline in which complex networks of genetic and environmental factors are currently investigated, and one that is distantly removed from the earlier descriptive fields of plant research. It showed, through increased knowledge of crosstalk between different signaling pathways, identification of common genetic components and signaling modules involved in seemingly unrelated processes, as well as the development of state-of-the-art technologies for multiple research topics, that coordination of research efforts and exchange of concepts and ideas is of greatly increasing importance. The undisputable success of all three previous EMBO plant meetings clearly calls for continuation of this series. This was unanimously and enthusiastically agreed on in the panel discussion at the end of the meeting. The organizers of previous meetings represented mainly by Czaba Koncz (MPI, Cologne, Germany) proposed that ‘younger’ colleagues should become actively involved in organizing next series of EMBO Conferences on Plants Molecular Biology. Salomé Prat, Jiri Friml and Heribert Hirt [who currently also acts as head of the European Plant Science
Organization (EPSO) were thus proposed as organizers and tentatively agreed to take over this responsibility. It has also been agreed to alternate the EMBO Plant Molecular Biology Conferences and EPSO meetings to avoid overlap in the same year.

Last, but not least, the meeting highlighted the importance of novel fundamental insights into plant development for agriculture and plant biotechnology. Improving plant growth and yield through genetic engineering is therefore becoming within realistic reach. In Europe especially, this is a delicate political issue, as illustrated by the animated panel discussion on the final day, which reflected some of the frustration in the plant community regarding the difficulties in changing public opinion on transgenic plant technologies and in influencing policy makers in this aspect. Various proposals for how to improve this were made, including the organization of ‘plants day’ events and similar activities that would convey the beauty and potential of plant science to the broader public. Thus, we can only hope that the great progress made in fundamental plant science and impressively demonstrated at this EMBO Plant Molecular Biology meeting in Matera will go hand in hand with an increasing broader awareness of its importance and future potential for agriculture and society.

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Competing interests statement

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