

D-glucose and D-fructose via the haustorium⁶. Indeed, the study has shown for the first time that the flow of sugars from a plant host to a rust fungus occurs, probably exclusively, through the haustorial complex. The work also provides a new locus of metabolic activity that can now be targeted to control this widespread and important plant disease, research that would also test some of the assumptions made from studies of function obtained indirectly in yeast.

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Meeting Report

Hormones at Mendel's birthplace

17th International Conference on Plant Growth Substances, Brno, Czech Republic, 1–6 July 2001.

Molecular genetics and, in particular, the recent completion of the *Arabidopsis* genome sequencing programme have brought about a resurgence in plant hormone research, resulting in spectacular advances in understanding their biosynthesis and signal transduction pathways, as well as their function in vegetative and reproductive development. These advances were discussed at the 17th International Conference on Plant Growth Substances in Brno, the birthplace of Gregor Mendel (Fig. 1). One of the traits (reduced stem height) used by Mendel in his studies with peas on the nature of inheritance is caused by a mutation in a gene (*Le*) that codes for the gibberellin-biosynthetic enzyme, GA 3-oxidase, which has now been cloned. A recurring theme in many of the talks was the interaction (cross-talk) between the signalling pathways, encompassing biosynthesis and signal transduction, of the different hormone classes, indicating

broad homeostasis in the hormonal control of plant growth and development. Some of the highlights of the meeting are discussed in this report.

Auxins

Alan Jones (University of North Carolina, Chapel Hill, NC, USA) reported that loss of function of the auxin binding protein, ABP1, results in early embryo lethality in *Arabidopsis*. Although inducible down-regulation of ABP1 in seedlings causes reduced hypocotyl length, there is no root phenotype. Thus, ABP1 appears to have a specialized function and is unlikely to be the receptor upstream of AXR1 and TIR1, which are components in an ubiquitin-dependent proteolysis system required for normal auxin responses. One target of the AXR1–TIR1 pathway might be Aux/IAAs, highly unstable proteins that interact with the more stable ARFs to regulate transcription. Stefan Kepinski (University of York, UK) reported that mutations in domain II of the Aux/IAA protein, AXR3, result in increased stability and reduced interaction with SCFTIR1. Auxin destabilizes AXR3

resulting in increased interaction with SCFTIR1. Major efforts are now needed to understand the function of the Aux/IAA and ARF families of transcriptional regulators. Paul Overvoorde (Plant Gene Expression Center, Albany, CA, USA) reported on efforts to isolate insertional mutants in members of these families. These lines will be made available through the stock centres and should help with characterizing the function of these genes. Thorsten Hamann (University of Tübingen, Germany) presented evidence from a yeast one-hybrid assay that the Aux/IAA protein BDL interacts with the ARF MONOPTEROS, suppressing its ability to activate transcription.

Cytokinins

Kentaro Takei (RIKEN, Wako, Saitama, Japan) and Tatsuo Kakimoto (Osaka University, Japan) reported that as a result of the *Arabidopsis* genome sequencing, the plant homologues of the *Agrobacterium ipt* gene have been identified, showing that the plant biosynthetic pathway is similar to that of *Agrobacterium*. However, the plant



Fig. 1. Statue of Gregor Mendel at the Monastery of St Thomas, Brno. Photograph courtesy of Andy Phillips.

enzymes use different substrates: *Atipt4* uses ADP and ATP, but not AMP (Kakimoto), whereas *Atipt1* can use all three nucleotides (Takei). Evidence for an alternative direct pathway to zeatin via a hydroxylated DMAPP donor was presented by Anders Nordström (Swedish University of Agricultural Sciences, Umeå, Sweden); the synthesis of this donor via tiglic alcohol was reported by Kakimoto, enabling it to be tested as a substrate for IPT. David Mok (Oregon State University, Corvallis, OR, USA) described a maize gene (*cisZOG*), which encodes *cis*-zeatin *O*-glucosyltransferase, suggesting parallel metabolic paths for the *trans*- and *cis*-zeatin isomers. Kakimoto reported that the *Arabidopsis* gene, *CRE1* (encodes a histidine kinase, also known as *WOL* and *AHK4*), functions in yeast as a cytokinin receptor. *CRE1* and its two homologues are perceived to act upstream of other signal elements, such as the two-component response regulators, *ARRs*, discussed by Joe Kieber (University of North Carolina, Chapel Hill, NC, USA), and perhaps *CKI*, which affects female gametophyte development.

Ethylene

Anthony Bleecker (University of Wisconsin, Madison, USA) reported on the *Arabidopsis etr1 ers1* double null receptor mutant phenotype. Although both single mutants are normal, the double mutant is highly stunted, showing a severe constitutive response, unlike other double and triple receptor mutant combinations, but similar to a quadruple receptor mutant that contains only wild-type *ERS1*. All five *Arabidopsis* ethylene receptors negatively regulate ethylene responses, but subfamily-1 receptors, *ETR1* and *ERS1*, play a greater role than the three subfamily-2 receptors. Consistent with this, Caren Chang (University of Maryland, College Park, MD, USA) presented data indicating that the subfamily-2 receptor, *ETR2*, signals to the downstream *CTR1* kinase via interactions with subfamily-1 receptors, mediated by the receptors' GAF domain. Bleecker also showed evidence that seedling response time to ethylene is dependent upon receptor synthesis. Igor Moshkov and Galina Novikova (Timiryazev Institute, Moscow, Russia) reported rapid activation of monomeric G proteins and a MAP kinase(s) in response to ethylene.

Gibberellins

With most of the genes of gibberellin (GA) biosynthesis identified, the focus of GA metabolism research is on regulation and genetic manipulation. Using green fluorescence protein fusions, Chris Helliwell (CSIRO, Canberra, ACT, Australia) showed that *ent*-copalylidiphosphate synthase (*CPS*) and *ent*-kaurene synthase are located within plastids, *ent*-kaurene oxidase (*KO*) and *ent*-kaurenoic acid oxidase are associated with the plastid envelope and endomembrane system, respectively, and GA 20-oxidase is cytoplasmic. By contrast, in germinating *Arabidopsis* embryos, Yuji Kamiya (RIKEN, Wako, Saitama, Japan) and colleagues showed expression of *CPS* and *KO* in different tissues and suggested that *ent*-kaurene might be mobile between tissues. Andy Phillips (IACR-Long Ashton Research Station, UK) described collaborative experiments in which dwarf plants of several crop species, including wheat, apple and sugar beet, were produced by manipulating GA biosynthesis or catabolism. In GA signalling, Alyssa Dill (Duke University,

Durham, NC, USA), Frank Gubler and Peter Chandler (both at CSIRO, Canberra, ACT, Australia) reported that *Arabidopsis* *RG1* and a barley homologue, *SLENDER*, were rapidly degraded upon application of bioactive GAs. Miyako Ueguchi-Tanaka (Nagoya University, Japan) described a new GA-insensitive, recessive mutant of rice, *gid1*, in which the rice homologue of *SLENDER*, *SLR1*, is no longer degraded after GA-treatment; *GID1* encodes a serine protease that might act on *SLR1*. Salome Prat (CID-CSIC, Barcelona, Spain) described a new GA-signalling component from potato, *PHOR1*, which is nuclear localized after GA treatment; transgenic plants overexpressing *PHOR1* have a reduced GA response.

Abscisic acid

The prediction that 9-*cis*-epoxycarotenoid dioxygenase (*NCED*) is rate-limiting in abscisic acid (ABA) biosynthesis was substantiated by over-expressing *NCED* in tomato and tobacco, reported by Andrew Thompson (HRI, Wellesbourne, UK), and also in *Arabidopsis*, reported by Kazuo Shinozaki (RIKEN, Tsukuba, Japan). This resulted in over-accumulation of ABA with associated phenotypes, such as reduced stomatal conductance. Julian Schroeder (UC-San Diego, USA) described how ABA-induction of stomatal closure requires an oscillation in cytosolic Ca^{2+} concentration of defined frequency. The *gca2* mutation, which disrupts the oscillation frequency, could be rescued by imposing wild-type oscillations. ABA-hypersensitivity, with reduced stomatal conductance, resulted from mutation in *ABH1*, which has homology with an RNA cap-binding protein. Peter McCourt (University of Toronto, Canada) described multiple examples of cross-talk between ABA and other hormone signalling pathways. For example, auxin and ABA induce expression of *ABI3* in root primordia, the GA-insensitive mutant *sly1* suppresses *abi1* (ABA insensitive), and *era3* (ABA hypersensitive) is allelic to the ethylene insensitive *ein2*. Jen Sheen (Massachusetts General Hospital, Boston, MA, USA) highlighted the link between ABA and sugar signalling; for example, *GIN1*, the mutation of which causes glucose insensitivity, is allelic with *ABA2*, an ABA-biosynthesis gene.

Brassinosteroids

Impressive advances in the metabolism and perception of brassinosteroids (BRs) were reported. Miklós Szekeres (Institute of Plant Biology, Szeged, Hungary) showed that many of the P450 genes in BR biosynthesis were feedback regulated. Zhi-Yong Wang (Salk Institute, La Jolla, CA, USA) described the cloning of BZR, a novel protein, which, when mutated, confers resistance to brassinazole, a BR-biosynthesis inhibitor. Tadao Asami (RIKEN, Wako, Saitama, Japan) also reported a similar mutation. Jianming Li (University of Michigan, Ann Arbor, MI, USA) discussed the BR-insensitive mutation *bin2* and suggested that BIN2 interacts with BRI, an essential component of the BR receptor. Furthermore, BIK, a kinase, was also shown to interact with BRI. Thomas Altmann (Max-Planck-Institut, Golm, Germany) presented genomic approaches to BR research, describing a comprehensive transcriptome analysis of BR-responsive genes.

Oxylipins

Plant cells can produce innumerable oxylipins, oxygenated derivatives of fatty acids, and they do so not only in times of stress but also during development. New work on the jasmonate family of regulators was presented. Elmar Weiler (Ruhr University, Bochum, Germany) described his recent discovery of large cellular pools of galactolipid-esterified oxophytodienoic acid (OPDA), raising the possibility that OPDA could be released rapidly from these pools during an attack. Further illustrating the complexity of jasmonate pools, Claus Wasternack (Institute of Plant Biochemistry, Halle, Germany) showed that each organ of tomato flowers contains different quantities of jasmonates and jasmonic acid–amino acid conjugates. New mutants

in jasmonic acid perception were described by John Turner (University of East Anglia, Norwich, UK). Screening for constitutive jasmonate-dependent gene expression led to the discovery of the *CEVI* gene that encodes a negative regulator of jasmonic acid signalling. Ted Farmer (University of Lausanne, Switzerland) described results from a collaboration with John Browse (Washington State University, Pullman, WA, USA) that led to the identification of genes that were activated by cyclopentenone jasmonates, such as OPDA, but not by jasmonic acid.

Flowering

Recent studies on hormonal regulation of flowering have exposed strong environmental and molecular themes. GAs regulate flowering of some long-day plants. As described by Phillips, lines over-expressing GA-catabolism genes flower late and over-expression of GA-biosynthesis genes causes early flowering. Siegbert Melzer (ETH Zürich, Switzerland) reported that over-expression of the *FPF1* gene also induces early flowering in *Arabidopsis* and suggested that it may participate in GA-regulated pathways. Molecular studies with two long-day plants, *Lolium* and *Arabidopsis*, have linked GA-induction of a *MYB* gene with activation of the floral gene, *LEAFY*. Detlef Weigel (Salk Institute, La Jolla, CA, USA) and Rod King (CSIRO, Canberra, ACT, Australia) highlighted the importance of an 8 bp *MYB*-recognition motif in the *LEAFY* promoter. King reported that the GA₅ content in *Lolium* apices, determined by a sensitive gas chromatography-mass spectrometry method, doubles during the early stages of floral evocation, which suggests that it might be a primary effector. Later, during inflorescence differentiation, there are large increases

in GA₁ and GA₄ at the apex, and expression of the *MYB* and *LEAFY* genes also increases. Georges Bernier (University of Liege, Belgium) reported that long days or cytokinin treatment induce expression of the *MADSA* flowering-associated gene in sub-epidermal cells in the shoot apex of *Sinapis*, although applied cytokinin does not cause flowering. Given the similar sub-epidermal localization of the *SMADSA* and *WUS* genes in *Arabidopsis*, reported by Weigel, examination of hormonal control of *WUS* would be interesting because this gene controls the pattern of *AGAMOUS* expression at the *Arabidopsis* shoot apex.

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