

# ACPD 2009

Auxin and Cytokinins in Plant Development

International Symposium

July 10 – 14, 2009, Prague, Czech Republic



## LETTER OF CONFIRMATION

This is to confirm that

*Yunus effendi*

attend the International Symposium of Auxin and Cytokinins in Plant Development,

July 10-14, 2009, Prague, Czech Republic

Organizer

Eva Zažímalová, PhD.

Organized by

In cooperation with



Institute of Experimental  
Botany of the AS CR, v. v. i.





# ACPD 2009

Auxins and Cytokinins in Plant Development  
International Symposium  
July 10-14, 2009, Prague, Czech Republic

PROGRAMME

**BOOK OF ABSTRACTS**

**LIST OF PARTICIPANTS**



# ACPD 2009

Auxins and Cytokinins in Plant Development  
International Symposium  
July 10-14, 2009, Prague, Czech Republic

Organized by



**Institute of Experimental  
Botany of the AS CR, v. v. i.**

in co-operation with



CZECH  
UNIVERSITY  
OF LIFE SCIENCES PRAGUE

## Organizing Committee

Alena Březinová, Institute of Experimental Botany AS CR, Prague

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Eva Zažímalová, **Chair**, Institute of Experimental Botany AS CR, Prague

## Past meetings



Liblice

September 11-15

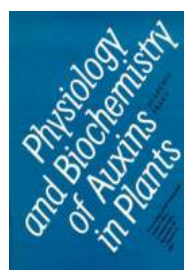
1972



Liblice

June 18-22

1984



Liblice

September 28-October 2

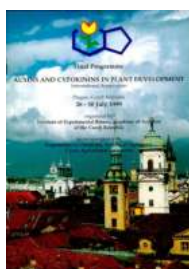
1987



Liblice

September 10-14

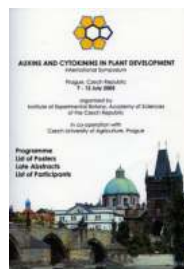
1990



Prague

July 26-30

1999



Prague

July 7-12

2005

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OPERAČNÍ PROGRAM PRAHA  
KONKURENCESCHOPNOST



EVROPSKÁ UNIE

The Institute of Experimental Botany of the Academy of Sciences of the Czech Republic obtained new equipment that will greatly facilitate its research in molecular and cellular plant biology. Instead of manually, routine laboratory work will now be performed by robots which are faster, more reliable, and more efficient. The equipment was financed by the European Fund for Regional Development via the Operational Programme Prague – Competitiveness.

The Institute purchased three automated systems for processing of plant samples. The systems will be used for isolation and analysis of nucleic acids, for proteomic analyses, and for *in situ* hybridisations and immunohistochemistry.

# Programme At a Glance

## Friday, July 10

16.00 - 20.00 Registration and poster mounting

## Saturday, July 11

08.00 - 08.45 Registration and poster mounting  
 08.45 - 09.00 Opening of the Symposium  
 09.00 - 10.30 Plenary lectures  
 10.30 - 11.00 Coffee  
 11.00 - 12.35 Session 1: Biosynthesis and Metabolism  
 12.35 - 14.05 Lunch  
 14.05 - 15.40 Session 1: Biosynthesis and Metabolism  
 15.40 - 16.10 Coffee  
 16.10 - 17.25 Session 2: Signalling and Development  
 17.30 - 19.30 Poster Session I (P1, P2, P3), light refreshment  
 19.30 - 21.00 Get-together Party

## Sunday, July 12

08.30 - 10.15 Session 2: Signalling and Development  
 10.15 - 10.45 Coffee  
 10.45 - 12.00 Session 2: Signalling and Development  
 12.00 - 13.30 Lunch  
 13.30 - 15.25 Session 3: Pattern Formation and Development  
 15.25 - 15.55 Coffee  
 15.55 - 17.50 Session 3: Pattern Formation and Development  
 18.00 - 20.00 Poster Session II (P4, P5, P6, P7), light refreshment

## Monday, July 13

08.30 - 10.15 Session 4: Transport and Development  
 10.15 - 10.45 Coffee  
 10.45 - 12.40 Session 4: Transport and Development  
 12.40 - 14.10 Lunch  
 14.10 - 15.55 Session 5: Hormone Interactions and Plant Architecture  
 15.55 - 16.25 Coffee  
 16.25 - 17.40 Session 5: Hormone Interactions and Plant Architecture  
 17.50 Departure to Liblice  
 19.00 - 23.00 Congress Dinner at Liblice Castle

## Tuesday, July 14

08.30 - 10.05 Session 6: Hormones, Environment and Applications  
 10.05 - 10.35 Coffee  
 10.35 - 12.30 Session 6: Hormones, Environment and Applications  
 12.30 - 14.00 Lunch  
 14.00 - 15.50 Session 7: Modelling and Advanced Methods  
 15.50 - 16.20 Coffee  
 16.20 - 18.10 Session 7: Modelling and Advanced Methods  
 18.10 - 18.30 Closing of the Symposium  
 18.30 - 22.00 Farewell Party





# ACPD 2009 Programme

## Friday, July 10

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16.00 - 20.00 Registration and poster mounting

## Saturday, July 11

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08.00 - 08.45 Registration and poster mounting  
08.45 - 09.00 Opening of the Symposium

### Plenary lectures

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Chair: Miroslav Kamínek

09.00 - 09.45 **Auxin transport - connecting cell polarity and patterning**  
Jiří Friml, VIB, Ghent University, Belgium

09.45 - 10.30 **Cytokinin signaling: Two components and more**  
Joseph Kieber, University of North Carolina, Chapel Hill, NC, USA

10.30 - 11.00 Coffee

### Session 1: Biosynthesis and Metabolism

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Chair: Karin Ljung

11.00 - 11.35 O1-1 **Cytokinin biosynthesis pathway: not as simple as it looks**  
Hitoshi Sakakibara, RIKEN Plant Science Center, Yokohama, Japan  
OIChemIm Honorary Lecture

11.35 - 11.55 O1-2 **Cytokinin interconversion is disrupted by adenosine kinase deficiency**  
Barbara Moffatt, University of Waterloo, Canada

11.55 - 12.15 O1-3 **Structural characterization of cytokinin oxidase/dehydrogenase mutants**  
David Kopečný, INRA, France and Palacký University, Olomouc, Czech Republic

12.15 - 12.35 O1-4 **Cis-zeatins in plants: their distribution, bioactivities, transport and metabolism**  
Václav Motyka, Institute of Experimental Botany AS CR, Prague, Czech Republic

12.35 - 14.05 Lunch

Chair: Hitoshi Sakakibara

14.05 - 14.40 O1-5 **Regulation of auxin and cytokinin metabolism during Arabidopsis root development**  
Karin Ljung, Umeå Plant Science Centre, Sweden  
OIChemIm Honorary Lecture

14.40 - 15.00 O1-6 **Proteomics and metabolomics of cytokinin-induced bud formation in *Physcomitrella patens***  
Anika Erxleben, University of Freiburg, Germany

15.00 - 15.20 O1-7 **Oxylipins contribute to the transcriptional regulation of YUC8 and YUC9, thereby controlling local auxin biosynthesis in *Arabidopsis thaliana***  
Stephan Pollmann, Ruhr-University Bochum, Bochum, Germany

15.20 - 15.40 O1-8 **Auxin amidohydrolases from *Brassica rapa* cleave conjugates of indole propionic and indole butyric acid as preferable substrates: a biochemical and modelling approach**  
Jutta Ludwig-Müller, Technische Universität Dresden, Dresden, Germany

15.40 - 16.10 Coffee

## Session 2: Signalling and Development

Chair: Tatsuo Kakimoto

16.10 - 16.45 O2-1 **Interpreting the tracks of cytokinin signaling during *Arabidopsis* gametophyte and embryo development**  
Bruno Müller, Harvard Medical School, Boston, USA and University of Zürich, Switzerland

16.45 - 17.05 O2-2 **Analysis of cytokinin receptor specificity in *Arabidopsis thaliana***  
Michael Riefler, Freie Universität Berlin, Germany

17.05 - 17.25 O2-3 **Cytokinin response factors in *Arabidopsis* and tomato**  
Aaron M. Rashotte, Auburn University, Auburn, AL, USA

17.30 - 19.30 **Poster Session I (P1, P2, P3)**, light refreshment. Posters with odd and even numbers should be presented from 17.30 to 18.30 and from 18.30 to 19.30, respectively.

19.30 - 21.00 Get-together Party

## Sunday, July 12

Chair: Mark Estelle

08.30 - 09.05 O2-4 **The TAF-related protein CKH1 and the chromatin remodeling-factor CKH2 negatively regulate cytokinin-induced callus formation in *Arabidopsis***  
Tatsuo Kakimoto, Osaka University, Japan

09.05 - 09.35 O2-5 **Histidine kinases CKI1, AHK2 and AHK3 control vascular tissue development in *Arabidopsis* shoots**  
Ildoo Hwang, Pohang University of Science and Technology, Pohang, Korea

09.35 - 09.55 O2-6 **Early cytokinin response proteins and phosphoproteins of *Arabidopsis thaliana***  
Martin Černý, Mendel University of Agriculture and Forestry & Institute of Biophysics AS CR, v.v.i., Brno, Czech Republic

09.55 - 10.15 O2-7 **The *Arabidopsis* cytokinin response is mediated by tissue-specific transcriptional cascades**  
Eric G. Schaller, Dartmouth College, Hanover, NH, USA

10.15 - 10.45 Coffee

Chair: Bruno Müller

10.45 - 11.20 O2-8 **Auxin signaling: A short (but complex) pathway**  
Mark Estelle, The University of California, CA, USA

11.20 - 11.40 O2-9 **A cellular expression map of the auxin response factor family reveals cell type-specific auxin responses**  
Barbara Möller, Wageningen University, Wageningen, The Netherlands

11.40 - 12.00 O2-10 **Activation mechanism of patatin-related phospholipase A by phosphorylation and function of phospholipases A in auxin and light signaling**  
Günther F.E. Scherer, University Hannover, Hannover, Germany

12.00 - 13.30 Lunch

### Session 3: Pattern Formation and Development

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Chair: Sabrina Sabatini

13.30 - 14.05 O3-1 **Integration of hormonal and genetic regulation during vascular morphogenesis in Arabidopsis**  
Ykä Helariutta, University of Helsinki, Finland

14.05 - 14.25 O3-2 **Molecular analysis of auxin regulation of wood formation**  
Rishikesh P. Bhalerao, Umeå Plant Science Center, Umeå, Sweden

14.25 - 14.45 O3-3 **DORNROESCHEN and DORNROESCHEN-LIKE function with the CUC genes and MP to modulate embryo symmetry via auxin-dependent pathways**  
John W. Chandler, Cologne, Germany

14.45 - 15.05 O3-4 **Multiple monopteros-dependent pathways are involved in leaf initiation**  
Jim Mattsson, Simon Fraser University, Canada

15.05 - 15.25 O3-5 **Auto-regulated expression of cytokinin biosynthesis confers drought tolerance in plants**  
Shimon Gepstein, Faculty of Biology, Technion, Haifa, Israel

15.25 - 15.55 Coffee

Chair: Ykä Helariutta

15.55 - 16.30 O3-6 **A genetic framework for the auxin/cytokinin control of cell division and differentiation in the root meristem**  
Sabrina Sabatini, Sapienza University of Rome, Italy

16.30 - 16.50 O3-7 **The role of cytokinin response factors during lateral root initiation**  
Giel van Noorden, VIB, Ghent University, Belgium

16.50 - 17.10 O3-8 **KNOX1 genes and cytokinin regulate leaf development**  
Naomi Ori, The Hebrew University of Jerusalem, Rehovot, Israel

17.10 - 17.30 O3-9 **Small RNAs facilitate polarity and laminar growth of tomato leaves**  
Tamar Yifhar, The Weizmann Institute of Science, Rehovot, Israel

17.30 - 17.50 O3-10 **Cytokinins can stimulate Arabidopsis hypocotyl elongation at decreased light intensity**  
Alena Reková, Mendel University of Agriculture and Forestry and Institute of Biophysics AS CR, v.v.i., Brno, Czech Republic

18.00 - 20:00 **Poster Session II (P4, P5, P6, P7)**, light refreshment. Posters with odd and even numbers should be presented from 17.30 to 18.30 and from 18.30 to 19.30, respectively.

**Monday, July 13****Session 4: Transport and Development**

Chair: René Benjamins

08.30 - 09.05	O4-1	<b>Lateral root development: an emerging story...</b> Malcolm J. Bennett, University of Nottingham, UK
09.05 - 09.35	O4-2	<b>Comparison of transport activity and interactions of ABCB, AUX1, and PIN auxin transporters</b> Angus S. Murphy, Purdue University, West Lafayette IN, USA
09.35 - 09.55	O4-3	<b>Auxin influx carriers are involved in regulating apical hook development of Arabidopsis</b> Filip Vandenbussche, Ghent University, Ghent, Belgium
09.55 - 10.15	O4-4	<b>PINOID controls PIN1 polar targeting through evolutionarily conserved phosphoserines</b> Fang Huang, Institute of Biology, Leiden University, Leiden, The Netherlands
10.15 - 10.45		Coffee
		Chair: Malcolm J. Bennett
10.45 - 11.20	O4-5	<b>Up and down and all around: PIN polarity regulation in Arabidopsis</b> René Benjamins, University of Utrecht, Utrecht, The Netherlands
11.20 - 11.40	O4-6	<b>Mechanistic framework for polar PIN targeting</b> Jürgen Kleine-Vehn, VIB , University Gent, Gent, Belgium
11.40 - 12.00	O4-7	<b>The NPA-binding protein TWISTED DWARF1 controls ABCB-mediated auxin transport</b> Hanna Valpuri Sovero, University of Zurich and Zurich-Basel Plant Science Center, Zurich, Switzerland
12.00 - 12.20	O4-8	<b>Post-transcriptional control of PIN expression by an Arabidopsis thaliana elongator complex</b> Johannes Leitner, University of Natural Resources and Applied Life Sciences, Vienna, Austria
12.20 - 12.40	O4-9	<b>ROCK1 encodes a putative transport protein of unknown function</b> Tomáš Werner, Free University of Berlin, Germany
12.40 - 14.10		Lunch

**Session 5: Hormone Interactions and Plant Architecture**

Chair: Christine A. Beveridge

14.10 – 14.45	O5-1	<b>Long range signalling in the control of shoot branching</b> Ottoline Leyser, University of York, York, UK
14.45 – 15.15	O5-2	<b>Auxin - cytokinin interaction shaping root architecture</b> Eva Benková, VIB, University Gent, Belgium

15.15 - 15.35	O5-3	<b>Apical dominance is controlled by interaction between cytokinin biosynthesis/degradation and auxin in stem</b> Hitoshi Mori, Nagoya University, Nagoya, Japan
15.35 - 15.55	O5-4	<b>Cytokinins modulate auxin-induced organogenesis in plants via regulation of the auxin efflux</b> Markéta Pernisová, Masaryk University, Brno, Czech Republic
15.55 - 16.25		Coffee  Chair: Ottoline Leyser
16.25 - 17.00	O5-5	<b>Regulation of axillary bud outgrowth by strigolactones</b> Christine A. Beveridge, University of Queensland, Brisbane, Australia
17.00 - 17.20	O5-6	<b>Spatial and temporal regulation of auxin and cytokinin gene expression and responses in pea ramosus mutants</b> Colin Turnbull, Imperial College London, London, UK and University of Massachusetts, Amherst, MA, USA
17.20 - 17.40	O5-7	<b>Competitive canalization of PIN-dependent auxin flow from axillary buds controls apical dominance in pea</b> Jozef Balla, Mendel University of Agriculture and Forestry, Brno, Czech Republic
17.50		Departure to Liblice
19.00 - 23.00		Congress Dinner at Liblice Castle

## Tuesday, July 14

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### Session 6: Hormones, Environment and Applications

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Chair: Thomas Schmülling

08.30 - 09.05	O6-1	<b>The importance of plant biotechnology for society and environment</b> Marc Van Montagu, Ghent University, Ghent, Belgium
09.05 - 09.25	O6-2	<b>Characterization and biological activity of novel purine-derived inhibitor of cytokinin oxidase/dehydrogenase INCYDE and its potential use for in vivo studies</b> Lukáš Spíchal, IEB AS CR & Palacký University, Olomouc, Czech Republic
09.25 - 09.45	O6-3	<b>Light/PHOT1-dependent polar translocation of PIN3 auxin carrier during phototropisms in Arabidopsis</b> Zhaojun Ding, VIB, Ghent University, Ghent, Belgium
09.45 - 10.05	O6-4	<b>Cytokinin regulates sodium homeostasis</b> Michael Mason, University of Queensland, Australia
10.05 - 10.35		Coffee  Chair: Marc Van Montagu
10.35 - 11.10	O6-5	<b>Applied perspective of cytokinin-mediated growth modulation in crop plants</b> Thomas Schmülling, Free University of Berlin, Germany

11.10 - 11.30	O6-6	<b>Molecular and functional analyses of changes in the pedicel abscission zone transcriptome following auxin depletion</b> Shimon Meir, ARO, The Volcani Center, Bet-Dagan, Israel
11.30 - 11.50	O6-7	<b>Cytokinin signalling in <i>Medicago truncatula</i> root and nodule organogenesis</b> Florian Frugier, Institut des Sciences du Végétal, CNRS, Gif-sur-Yvette, France
11.50 - 12.10	O6-8	<b>Comparison of cytokinin role in drought and heat stress response of tobacco plants</b> Radomíra Vaňková, Institute of Experimental Botany AS CR, Prague, Czech Republic
12.10 - 12.30	O6-9	<b>Metabolism and possible function of cytokinin during abiotic stress in maize</b> Petr Galuszka, Palacký University & Institute of Experimental Botany AS CR, Olomouc, Czech Republic
12.30 - 14.00		Lunch

### Session 7: Modelling and Advanced Methods

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Chair: Przemek Prusinkiewicz

14.00 - 14.35	O7-1	<b>Quantitative approaches to plant development</b> Cris Kuhlemeier, University of Bern, Switzerland
14.35 - 15.10	O7-2	<b>A computational model of phyllotaxis in <i>Costus</i></b> Przemek Prusinkiewicz, University of Calgary, Canada
15.10 - 15.30	O7-3	<b>Agent based modelling of auxin transport canalisation</b> Philip Garnett, University of York, York, UK
15.30 - 15.50	O7-4	<b>Towards a model of auxin response in root epidermis</b> Martin Kieffer, University of Leeds, UK
15.50 - 16.20		Coffee
		Chair: Cris Kuhlemeier
16.20 - 16.50	O7-5	<b>Modelling of auxin transport processes on a single cell level</b> Klára Hoyerová, Institute of Experimental Botany AS CR, Prague, Czech Republic
16.50 - 17.10	O7-6	<b>Modelling of positive-feedback mechanism for auxin carrier polarization during auxin-dependent plant development</b> Krzysztof Wabnik, VIB, Ghent University, Ghent, Belgium
17.10 - 17.30	O7-7	<b>Developing a real-time, quantitative biosensor for auxin and ABA</b> Richard Napier, University of Warwick, UK
17.30 - 17.50	O7-8	<b>Highly sensitive and high-throughput analysis of plant hormones using MS-probe modification and UPLC-ESI-qMS/MS: an application for hormone profiling in <i>Oryza sativa</i></b> Hitoshi Sakakibara, RIKEN Plant Science Center, Yokohama, Japan
17.50 - 18.10	O7-9	<b>New purification and mass spectrometric approach for cytokinin analysis</b> Ondřej Novák, Palacký University & Institute of Experimental Botany, Olomouc, Czech Republic
18.10 - 18.30		Closing of the Symposium
18.30 - 22.00		Farewell Party

**P2-5 AUXIN-BINDING PROTEIN1 (ABP1), THE SECOND AUXIN RECEPTOR****Yunus Effendi, Günther F.E. Scherer***Molecular Developmental Physiology, Leibniz University Hannover, Herrenhäuser Str. 2, D-30419 Hannover, Germany. scherer@zier.uni-hannover.de*

Despite of knowing the 3-dimensional structure ABP1 is not fully acknowledged as an auxin receptor. We used the ABP1 insertional mutant (Chen et al. 2001). It is lethal when homozygous but viable in the hemizygous *abp1/ABP1* state. Hemizygous plants produce 2:1 resistant:wild type progeny on kanamycin agar due to the T-DNA. Seedlings from *abp1/ABP1* plants are defect in phototropism and gravitropism of roots and shoots. Those populations are composed of a major slow reacting and a minor normal reacting group. *abp1/ABP1* seedlings show strong root slanting, longer hypocotyls, and slightly increased lateral root number. Root auxin responses in *abp1/ABP1* seedlings are slightly less sensitive than in wt. In short days and long days *abp1/ABP1* plants flower earlier. They have more branches and decreased main stem diameter, indicating decreased apical dominance. Auxin-induced genes (qPCR: *IAA2*, *IAA11*, *IAA13*, *IAA14*, *IAA19*, *IAA20*) respond to auxin (0.1µM/1µM/10µM) 2-10 fold stronger in wt than in *abp1/ABP1* seedlings (30 & 60 min). Thus ABP1 is a receptor with probable functions in auxin transport and gene regulation. The apparent functional link to TIR1-linked gene regulation could be provided by phospholipase A (Scherer et al., 2007)

**P2-7 THE ROLE OF FUSICOCCINE-LIKE SECONDARY HORMONE IN THE CYTOKININE SIGNAL TRANSDUCTION.****Gilmanov M.K., Ibragimova S.A., Kudaibergenov K.K., Dukumbayeva A.U.***M.A. Aytkhozhin's Institute of Molecular Biology and Biochemistry; baltakay@mail.ru*

It was shown that cytokinin causes the formation of cytokinin secondary hormone (CSH) in embryos of germinating wheat seeds. CSH was purified by chromatography on nanostructured carbon sorbent "Nanocarbosorb". It was established by mass-spectra that CSH related to fusicoccine. The CSH showed the typically cytokinin activities such as: the derepression of apical dominance, the greening of yellow leaves and synthesis of amarantin. CSH was active at concentration 1000 times less at 2-3 times quicker, than cytokinin. The one of interesting property of CSH is its ability to increase the tolerance of germinating wheat seeds to salt stress. We developed very interesting enzyme sensor model for investigation of signal transduction of cytokinin. It was established that cytokinin causes the formation of NADP-GDH in aleurone layer of wheat seeds. We suggest the next scheme of signal transduction of cytokinin. First step is the formation of CSH. Then molecules of CSH are bound with fusicoccine receptors of plasmatic membrane. This let to increase the level cytosolic  $Ca^{2+}$ . The last step of signal transduction is switching on the activity of protein kinase C. But this process demands the presence of another low molecular regulator which is formed under the effect of CSH on wheat seeds embryos.

**P2-6 LIGHT ALTERS PLANT ELONGATION RESPONSES TO EXOGENOUS AUXIN****Martin Fellner<sup>1,2</sup>, Renáta Plotzová<sup>1</sup>, Jana Bořucká<sup>1</sup>, Tereza Vaclová<sup>1</sup>, Jirí Řehulka<sup>1</sup>, David Zalabák<sup>1</sup>, Marta Hlobilová<sup>1</sup>***<sup>1</sup> Laboratory of Molecular Physiology, Department of Cell Biology and Genetics, Palacky University in Olomouc, Šlechtitelů 11, 783 71, Olomouc, Czech Republic <sup>2</sup> Laboratory of Growth Regulators, Palacky University in Olomouc and Institute of Experimental Botany ASCR, v.v.i, Šlechtitelů 11, 783 71, Olomouc, Czech Republic*

Many fundamental issues of interaction between light and hormone signaling pathways involved in plant growth remain to be uncovered. In model plants *Arabidopsis*, tomato and maize we investigated effects of light on plant growth responses to exogenous auxins. In dark, blue light (BL) and red light (RL), exogenous auxin inhibits long-term growth in intact *Arabidopsis* and tomato hypocotyl, and in corn coleoptile. Compared to dark- and RL-grown plants, inhibitory effect of auxin on elongation of *Arabidopsis* hypocotyl developed in BL is weak. Mutant analyses revealed that CRY1 mediates BL-induced reduction of hypocotyl sensitivity to exogenous auxin, and that ZTL1 is required for maintenance of hypocotyl response to exogenous auxin in BL and RL. Photoreceptor CRY1 is also involved in BL- and RL-induced reduction of hypocotyl sensitivity to NAA in tomato. Data indicate that tomato hypocotyl responses to the inhibitory effects of NAA and 2,4-D are regulated by light via different mechanisms. Analysis of *elm1* mutant in corn indicated that phytochromes mediate the BL- and RL-induced decline in coleoptile response to exogenous auxin. Our results confirmed the existence of interaction between light and auxin signaling in plant growth. Analyses also suggest the existence of diverse mechanisms of the cross-talk between light and auxin in different plant species.

*This work was supported by grant from Ministry of Education of the Czech Republic to MF (grant no. 1P05ME792).*

**P2-8 UNCOVERING THE DISTINCT ROLES OF AUXIN SIGNALING F-BOX (AFB) 4 AND 5 AS AUXIN RECEPTORS****Katie Greenham & Mark Estelle***Section of Cell and Developmental Biology, University of California San Diego, La Jolla, California*

The auxin receptor family is comprised of six members; TIR1 and AFB1-5. Phylogenetic analysis reveals that the AFB4/5 clade diverged from the other members before seed plant radiation whereas the TIR1/AFB1 and AFB2/3 clades diverged within the angiosperm lineage (Prigge & Estelle, unpublished). The conservation of these receptors across seed plants suggests that they maintain a distinct function. Our goal is to understand the diverse functions of AFB4/5 in relation to other members of the family. Preliminary studies reveal that picloram works specifically through AFB4/5. The *afb4-2* and *afb5-5* single mutants are resistant to picloram compared to wild type while *tir1-1* is not. Biochemical analysis confirms that picloram enhances the affinity of Aux/IAA with AFB4/5 but not with TIR1. The basis for this specificity remains unknown. The *afb4-2afb5-5* double displays hypersensitivity to root growth at 29°C, a condition that results in increased levels of auxin biosynthesis. In contrast, the *tir1-1afb2-3* mutants are resistant at 29°C. To improve our understanding of TIR1/AFB function we are generating and characterizing all mutant combinations in conjunction with an investigation of the biochemical properties of AFB4/5 compared to TIR1.



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## Auxin-Binding Protein 1 (ABP1), the second auxin receptor

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### Abstract

Despite knowing 3-dimensional structure ABP1 is not fully acknowledged as an auxin receptor. We used the insertional ABP1 mutant (Chen et al., 2001). It is lethal when homozygous but viable in the hemizygous *abp1*/ABP1 state. A hemizygous plant produces 2:1= resistant:wildtype progeny on kanamycin agar due to the T-DNA and this lethality. Seedlings from *abp1*/ABP1 plants are defect in phototropism and gravitropism of shoots and roots. Those populations are composed of a major slow reacting and a minor normal reacting group. ABP1/*abp1* seedlings show strong root slanting, longer hypocotyls, and slightly increased lateral root numbers. Root auxin responses (lateral root, main root length) in *abp1*/ABP1 seedlings are slightly less sensitive than in wt. In short days and long days *abp1*/ABP1 plants flower earlier. They have more branches and decreased main stem diameter, indicating decreased apical dominance. Auxin-induced genes (qPCR: IAA2, IAA11, IAA13, IAA14, IAA19, IAA20, GH3.5, SAUR9, SAUR15, SAUR23) respond to auxin (0.1µM/1µM) 2-15 fold stronger in WT than in *abp1*/ABP1 seedlings (30 and 60 min). Thus, ABP1 is a receptor with probable functions in auxin transport and gene regulation. The apparent functional link to TIR1-link gene regulation could be provided by phospholipase A (Scherer et al., 2007, FEBS Lett.581:4205-4211).

Keyword: ABP1, Receptor, Auxin, early auxin-induced genes

### Introduction

AUXIN-BINDING PROTEIN 1 (ABP1) was the first protein described as having specific auxin-binding activity (Napier et al., 2002). Previously, auxin-binding activity, probably resulting from ABP1, had been reported for membranes isolated from maize coleoptiles (Hertel et al., 1972). Initially, research on ABP1 functions focused on rapid regulation of membrane potential and potassium channels (Barbier-Brygoo et al., 1989, 1991; Thiel et al., 1993). Clear evidence of a link to typical auxin functions such as cell elongation, cell division or lateral root formation was lacking at first, as no ABP1 mutants or antisense plants were available. The *Arabidopsis thaliana* genome contains only one ABP1 gene, and its knockdown resulted in embryo lethality of homozygous progeny (Chen et al., 2001b). Although the embryo lethality of the *Arabidopsis* homozygous *abp1* knockout mutant demonstrated the functional importance of ABP1, it hindered investigations on the post-embryonic functions of ABP1. Determination of the 3D structure of ABP1 revealed a specific binding site for auxins (Woo et al., 2002). Moreover, ABP1 is a small glycoprotein that is abundant in the ER, with only a small proportion exposed on the outer leaflet of the plasma

membrane (Napier et al., 2002). As ABP1 has no transmembrane domain, a docking protein was postulated to exist that linked auxin perception to intracellular signaling (Klaumt, 1990). However, no such membrane anchor for ABP1 has yet been identified.

Progress was made by investigating tobacco cell culture cells over-expressing the ABP1 gene in the sense or antisense orientation (Jones et al., 1998) and tobacco plants over-expressing ABP1 (Chen et al., 2001a). These studies suggested that ABP1 does indeed positively regulate cell division and cell elongation. In another approach, a specific antibody against ABP1 was expressed in tobacco cell cultures, secreted into the ER, and thus onto the cell surface. This resulted in down-regulation of ABP1 function (David et al., 2007). Down-regulation of ABP1 function was not found when the antibody was expressed in the cytoplasm. The study showed that ABP1 functions as an extra-cytoplasmic protein and that ABP1 inhibition hinders the cell cycle at the G1/S and G2/M phase transitions. This concept of suppression of ABP1 function by antibody binding was expanded by ethanol-controlled expression of the antibody in planta (Braun et al., 2008; Tromas et al., 2009). Suppression of ABP1 function by ethanol-stimulated antibody expression inhibited both cell expansion and cell division in these plants. Moreover, expression of the anti-ABP1 antibody for 8 h also led to down-regulation of several IAA genes, suggesting that ABP1 also functions in auxin-induced gene regulation, which, at that time, was attributed exclusively to TIR1 and its homologs (Mockaitis and Estelle, 2008). We previously showed that auxin activates phospholipase A, and that inhibitors of phospholipase A inhibited hypocotyl elongation and up-regulation of early auxin-induced genes (Paul et al., 1998; Scherer et al., 2007), although the inhibitors did not directly affect TIR1 activity. In this way, we provided indirect evidence that an auxin receptor other than TIR1 participates in gene regulation of auxin-induced genes.

In an ongoing study to generate viable mutants of ABP1 in order to provide a ‘missing link’ between the lethal *abp1* knockouts and the wild-type, we performed experiments on heterozygous *abp1*/ABP1 plants. The heterozygous plants are viable, whereas homozygosity leads to embryo lethality (Chen et al., 2001b). Surprisingly, heterozygous plants showed physiological and morphological features that clearly deviated from wild-type. In addition, even as early as 30 min after auxin challenge, a number of IAA genes and other early auxin-regulated genes were up-regulated to a much lower extent in *abp1*/ABP1 seedlings compared to wild-type seedlings.

## **RESULT**

### **Morphological differences and physiological responses in *abp1*/ABP1 mutants**

We grew seeds from heterozygous *abp1*/ABP1 plants on kanamycin-containing agar plates under a 16 h/8 h light/dark cycle to eliminate wild-type plants (Ws background), before transferring resistant seedlings to soil. Resistant plants appeared to be smaller than wild-type plants (data not shown). This observation prompted us to investigate phenotypic properties of the *abp1*/ABP1 plants. PCR genotyping with primers against the insertion allele of ABP1 (Chen et al., 2001b) confirmed that resistant plants were heterozygous for *abp1*. Furthermore, viable seeds from *abp1*/ABP1 plants segregated 2:1 into resistant and wild-type seedlings on kanamycin-containing

plates. Siliques of *abp1/ABP1* contained approximately 25% non-viable white seeds, as described by Chen et al. (2001b).

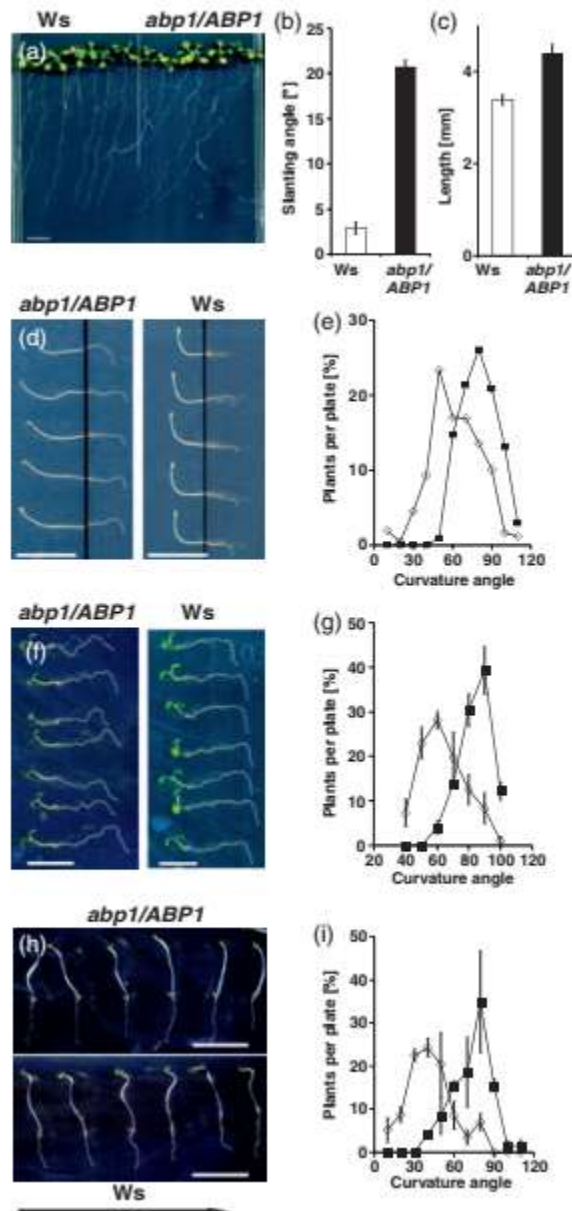


Fig.1. Phenotype and responses to gravity and light in wild-type *Ws* and heterozygous *abp1/ABP1* seedlings. (a) *Ws* seedlings (left) and *abp1/ABP1* seedlings (right). Scale bar = 1 cm.

(b) Slanting angles of seedlings grown for 7 days in the light. White bar, *Ws*; black bar, *abp1/ABP1*. Values are means  $\pm$  SE (n = 20, P < 0.01 for mutant versus wild-type).

(c) Hypocotyl length of 7-day-old light-grown seedlings. White bar, *Ws*; black bar, *abp1/ABP1*. Values are means  $\pm$  SE (n = 20, P < 0.01 for mutant versus wild-type).

(d) Representative images showing the gravitropic response of 4-day-old light-grown *Ws* seedlings and an *abp1/ABP1:Ws* segregating population after 24 h. Scale bar = 1 cm.

(e) Gravitropic response of the hypocotyls of dark-grown 4-day-old seedlings.

(f) Representative images showing the gravitropic response of 7-day-old light-grown *Ws* seedlings and an *abp1/ABP1:Ws* segregating population after 24 h. Scale bar = 1 cm.

(g) Gravitropic response of roots of 7-day-old light-grown seedlings after 24 h. Growth and quantification were performed as described in (e).

(h) Representative images showing the phototropic response of 4-day-old dark-grown *Ws* seedlings and an *abp1/ABP1:Ws* segregating population after 10 h. The arrow shows the direction of light. Scale bar = 1 cm.

(i) Phototropic response of the hypocotyls of dark-grown 4-day-old seedlings. Seedling growth and quantification were performed as described in (e).

When we grew seeds from an *abp1/ABP1* plant on kanamycin-free upright agar plates, we observed two seedling phenotypes: seedlings with roots growing downwards, with only a small slanting angle, and seedlings with a strong slanting angle and roots that grew in a wavy pattern. Seedlings with a strong slanting angle were transferred to new agar plates after 4 days and grown side by side with wild-type seedlings treated the same way (Figure 1a,b). After 7 days, the selected mutant seedlings had a greater slanting angle (Figure 1a,b) and longer hypocotyls (Figure 1c) compared to wild-type seedlings. The greater slanting angle suggested that heterozygous roots might be agravitropic. Therefore, we tested hypocotyls of 3-day-old dark-grown seedlings and roots of 14-day-light-grown seedlings for defects in gravitropism by tilting the agar plates through



90 (Figure 1c–f). No pre-selection on kanamycin free plates was performed prior to the experiment in order not to disturb or wound the seedlings as a result of transfer to a second medium. Seeds from wild-type and *abp1*/ABP1 plants were tested as separate populations. The distribution of bending angles of wild-type plants had a single peak centred at approximately 80 for hypocotyl gravitropism and approximately 90 for root gravitropism after 24 h. The population segregating for *abp1* showed a peak at an angle of 50 and a smaller peak at 70–80 for hypocotyls, consistent with a segregation ratio of 2:1 for heterozygous versus wildtype plants (Figure 1d,e). Similar results were obtained for the gravitropic response of roots. While wild-type root bending angles peaked at 90, the segregating population showed a peak at 60, with a shoulder at 90 (Figure 1f,g). We then tested hypocotyl phototropism in dark-grown seedlings in a segregating population by application of 10  $\mu\text{mol m}^{-2} \text{s}^{-1}$  of lateral blue light for 10 h. We again found a strong and uniform response in wild-type seedlings, with a peak of bending angles at approximately 80, while a major response angle at 40 and a minor peak at 80 was observed in *abp1*/ABP1 progeny seedlings, reflecting the 2:1 segregation of this population (Figure 1h,i). The *abp1* mutation therefore results in defects of gravitropism and phototropism, both developmental processes that are mainly controlled by auxin. We tested auxin sensitivity in heterozygous and wild-type seedlings placed side by side on upright agar plates containing increasing auxin concentrations. Only small differences between wild-type and mutant in the length of the main root, lateral root formation and lateral root density were found in response to auxin (Figure 2a–c). These small differences were reproducible and may indicate a slight insensitivity of root and hypocotyl growth to auxin in the mutant.

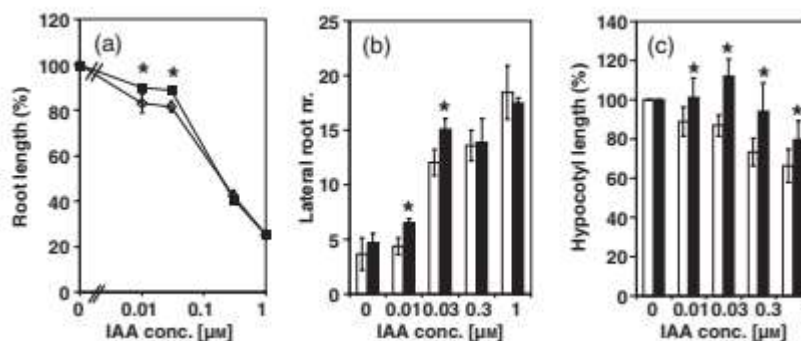


Fig.2. Auxin sensitivity of wild-type Ws and *abp1*/ABP1 seedlings. All seedlings were grown on vertical agar plates without auxin for 4 days, and then transferred to plates containing increasing concentrations of IAA. The *abp1*/ABP1 seedlings were selected from the segregating population after 3 days on the basis of their strong slanting angle, and both Ws and mutant seedlings were transferred to a fresh plate for 4 days. Response to auxin of (a) the relative length of the main root, (b) lateral root number, and (c) relative hypocotyl length. Values are means  $\pm$  SE ( $n = 20$ ). Filled bars/filled squares, *abp1*/ABP1 plants; open bars/open diamonds, Ws. Asterisks indicate values that are significantly different from wildtype ( $P < 0.01$ ).

Plants selected on kanamycin agar and later grown in the greenhouse were smaller than wild-type plants. We therefore investigated apical dominance in *abp1*/ABP1 plants grown under long- and short-day conditions (Figure 3). The primary inflorescence of wild-type plants was always thicker than the secondary inflorescences (Figure 3a,c). The progeny from an *abp1*/ABP1 plant grown under long-day conditions segregated into plants that showed the same distinction between

primary and secondary inflorescences described above, and plants with a strongly reduced diameter of the primary inflorescence but an equal diameter for the secondary inflorescences. PCR genotyping revealed that the plants with a thinner primary inflorescence were heterozygous for *abp1* (Figure 3c,d). Under short-day conditions, the diameter of the primary inflorescences was nearly equal for wild-type and heterozygous plants; however, slightly more secondary inflorescences formed in the *abp1/ABP1* plants (Figure 3e,f). Taken together, these results indicate a decrease in apical dominance in heterozygous plants.

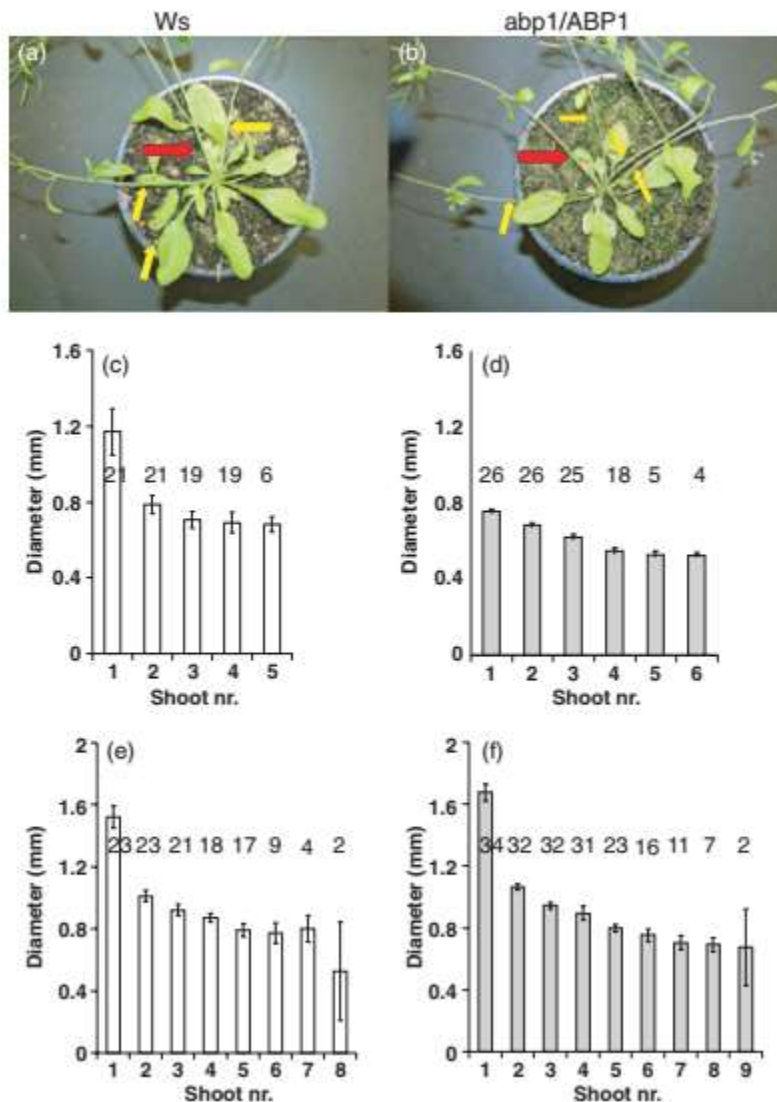


Fig. 3. Apical dominance of wild-type Ws and heterozygous *abp1/ABP1* plants grown under long- (16 h/8 h light/dark) or short-day conditions (8 h/16 h light/dark). Representative wild-type Ws plant (a) and heterozygous *abp1/ABP1* plant (b), both grown under long-day conditions. Red arrow, main inflorescence; yellow arrows, lateral inflorescences. Plant genotypes were determined by PCR. Note the lower number of rosette leaves and absence of a prominent main stem in mutant plants.

(c) Inflorescence thickness and inflorescence number of wild-type Ws plants grown under long-day conditions. Values are means  $\pm$  SE (n as indicated). (d) Inflorescence diameter and total number of inflorescences of heterozygous *abp1/ABP1* plants grown under long-day conditions. Values are means  $\pm$  SE (n as indicated). (e) Inflorescence diameter and inflorescence number of wild-type Ws plants grown under short-day conditions (n as indicated). (f) Inflorescence diameter and total number of inflorescences of heterozygous *abp1/ABP1* plants grown under short-day conditions (n as indicated).

Heterozygous plants grown under long-day conditions not only had reduced apical dominance but often had fewer rosette leaves. Therefore, we determined the flowering time and rosette and cauline leaf numbers in plants grown under short- and long-day conditions (Figure 4). The photograph (Figure 4a) taken shortly before the wildtype plants started flowering shows that the population of seeds grown from a kanamycin-resistant *abp1/ABP1* plant segregated into approximately one-third that were not as yet flowering and two-thirds that were flowering. When plants of the segregating



population were sorted by PCR genotyping, the early-flowering plants had an *abp1/ABP1* genotype, whereas the late-flowering plants were homozygous for the wild-type allele. Under short-day conditions, heterozygous *abp1/ABP1* plants flowered approximately 5 days earlier than wild-type plants, and rosette leaf numbers were lower in heterozygous plants than in wildtype plants (Figure 4b,c). Under long-day conditions, flowering occurred only slightly earlier in heterozygous plants ( $P < 0.05$ ) and they had fewer rosette leaves (not statistically significant) (Figure 4d,e).

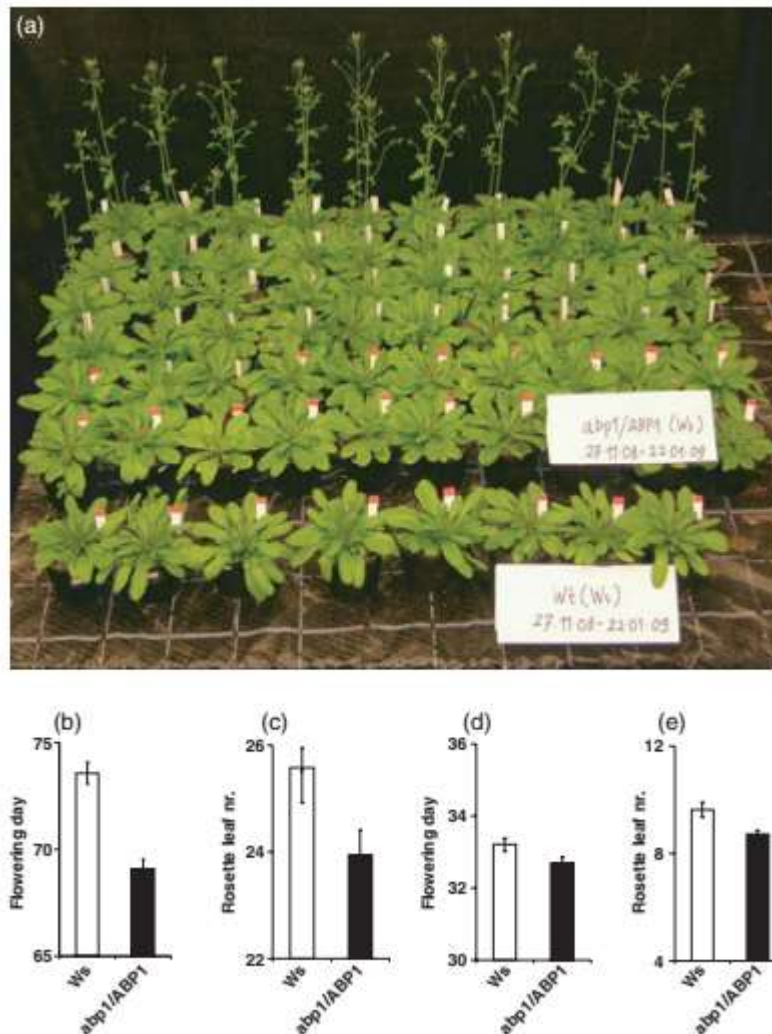


Fig.4. Early-flowering phenotype of wildtype Ws and heterozygous *abp1/ABP1* plants grown under short-day conditions (8 h/16 h light/dark) (a–c) or long-day conditions (16 h/ 8 h light/dark) (d, e). (a) Plants from seeds of a kanamycin-resistant heterozygous *abp1/ABP1* plant and Ws wild-type plants, as indicated, grown under short-day conditions. Plants were ordered as follows: those with open flowers were placed at the back (small white tags) and non-flowering plants were placed at the front (small red tags). All plants were PCR-genotyped prior to statistical analysis. (b, c) Flowering date (b) and number of rosette leaves (c) of plants grown under short-day conditions. Open bars, wild-type Ws ( $n = 31$ ;  $P < 0.05$  for flowering date and number of rosette leaves, by Student's *t* test). Filled bars, heterozygous *abp1/ABP1* plants ( $n = 37$ ;  $P < 0.01$  for flowering date and  $P < 0.05$  for number of rosette leaves, by Student's *t* test). The results shown are from one of two experiments. (d, e) Flowering date (d) and number of rosette leaves (e) of plants grown under long-day conditions.

### Gene regulation in *eir1* mutants

The defect in root basipetal auxin transport could be due to mis-regulation of a PIN protein. The localization and inverted polarity of PIN2 in the outer layer of cells in the root tips of PIN2 mutants (Abas et al., 2006; Wisniewska et al., 2006; Sukumar et al., 2009) suggested that transport activity of this PIN protein could be affected in the *abp1/ABP1* heterozygote. We therefore tested the expression of the same auxin-inducible test genes as for *abp1/ABP1* heterozygotes in the PIN2

mutant *eir1* (Chen et al., 1998; Luschnig et al., 1998; Müller et al., 1998) in the presence and absence of 1  $\mu$ M IAA (Figure 8). Of 12 genes tested, three (IAA2, IAA13 and ABP1) were more strongly induced in *eir1* than in the Col wild-type, the regulation of one (IAA12) was indistinguishable from that in the Col wild-type, and the regulation of two (IAA20 and SAUR9) was indistinguishable during the first 30 min. In summary, the presence of a non-functional PIN2 protein caused similar consequences as in the heterozygous *abp1/ABP1* mutant, but with a clearly different ‘signature’..

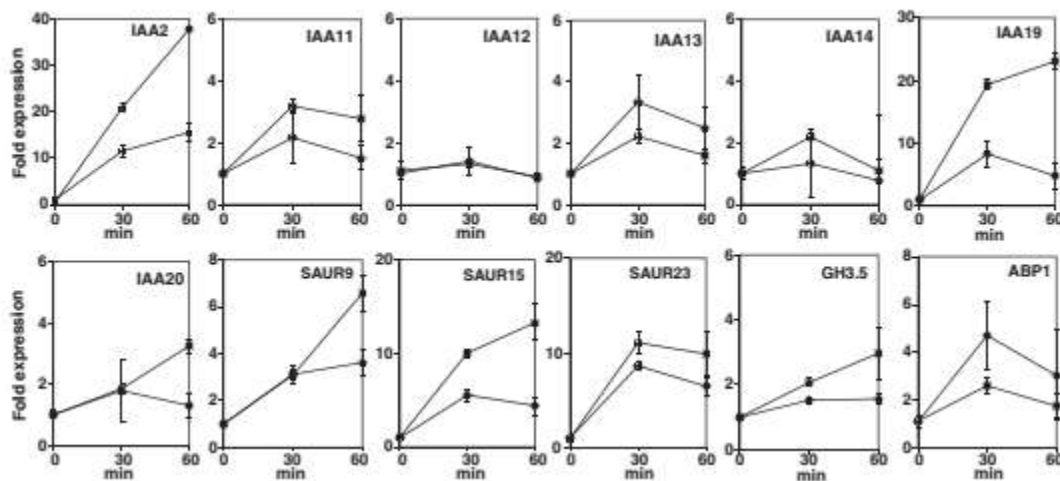


Fig. 5. Regulation of early auxin-regulated genes and ABP1 in light-grown wild-type (Col) and *eir1* seedlings. Wild-type and *eir1* seedlings were grown on half-strength MS agar. After 14 days, seedlings were washed three times in the medium, and transferred to fresh liquid half-strength MS medium and grown for another 5 days. Treatment with 1  $\mu$ M IAA was performed using fresh medium for the times indicated. For details of RNA extraction and real-time PCR quantification, see Experimental Procedures. The results are from two biological treatments with three technical replicates for each measurement. Statistical analysis was performed as described by Pfaffl and Horgan G.W. (2002).

## DISCUSSION

### Heterozygous *abp1/ABP1* mutants exhibit

morphological alterations Heterozygous *abp1/ABP1* plants were previously described as having a similar phenotype to the wild-type (Chen et al., 2001b). Because the homozygous *abp1/abp1* mutant is embryo-lethal, only experiments with seed mixtures of 2:1 heterozygous:wild-type seeds are possible, and this may obscure investigations of the morphological phenotype. However, we found that heterozygous seedlings have a waving and slanting root phenotype. Plants with similar phenotypes are often affected in auxin-related processes such as gravity perception or auxin physiology-related processes, or, alternatively, have defects in microtubule-associated proteins (Sedbrook and Kaloriti, 2008).

The *abp1/ABP1* mutant had a defect in the gravitropic response of the root, which probably caused the root slanting. The heterozygous mutants also had longer hypocotyls, which could be related to defective auxin or light signaling (Gray et al., 1998; Ljung et al., 2001; De Grauwe et al., 2005). Additionally, their phototropic response was impaired. In these respects, the *abp1/ABP1* seedlings

resemble mutants that are defective in phototropin-triggered phototropism. Phototropin1 mutants exhibit long hypocotyls and defective phototropism (Chen et al., 2008), hence an association between the long-hypocotyl phenotype of *abp1/ABP1* mutants and their phototropism defect seems possible. In addition to altered gravitropism and phototropism and hypocotyl length, apical dominance was decreased in heterozygous plants (Figure 3), resulting in a semi-dwarf stature under long-day conditions. However, under shortday conditions, the size of the adult mutant plants was not different from that of adult wild-type plants, except for a slightly lower number of leaves in the early-flowering heterozygous plants, and the decrease in apical dominance was subtle (Figures 2 and 3). As the major contributor to apical dominance is auxin transport (Ongaro and Leyser, 2008), it is likely that the loss of apical dominance may be explained as a defect related to auxin physiology in the heterozygous *abp1/ABP1* mutant.

### **Similar Delay responses in auxin-induced genes expression in *eir1* mutants and *abp1/ABP1***

Our data on early auxin-induced gene regulation show that all tested IAA genes were mis-regulated in the heterozygous *abp1/ABP1* mutant, including IAA19, the SAUR genes, GH3.2 and ABP1 (Figure 5). In an attempt to elucidate the mechanism behind this mis-regulation, we investigated the regulation of these test genes in the PIN2 mutant *eir1* (Chen et al., 1998; Luschnig et al., 1998; Müller et al., 1998). Mis-regulation of PIN2 could be the reason for the observed defect in root basipetal auxin transport (Abas et al., 2006; Wisniewska et al., 2006; Sukumar et al., 2009). Indeed, eight of 12 genes tested were up-regulated to a lower extent in the *eir1* background compared with the wildtype, one gene was not differentially expressed, and three were up-regulated by auxin to a greater extent (Figure 5).

A defect in PIN2 could become manifest by defects in regulation of the same set of genes, suggesting that ABP1 and PIN2 occur in largely overlapping regulatory pathways. Our suggestion is that ABP1 and PIN proteins cooperate in a tight regulatory circuit (Figure 9). The differences in the ‘signature’ of regulation of early auxin genes between *abp1/ABP1* and *eir1* could be explained by participation of additional proteins that regulate cellular auxin concentration. The most likely candidates are other PIN proteins and AUX1 or LAX proteins. Alternatively, mis-expression of early auxin genes could be due to a direct effect of ABP1 on TIR1-dependent IAA ubiquitination. However, there is currently no evidence for this second explanation. The mechanisms are not mutually exclusive (Figure 9). Common to all aspects of the *abp1/ABP1* phenotype is that they may be explained by changes in polar auxin transport regulation and local auxin concentration. Braun et al. (2008) tested transcription of early auxin regulated genes after a minimum of 8 h of induction of antiABP1 antibody expression. Thirteen of 14 IAA genes tested were down-regulated transiently or for up to 48 h compared to the non-induced status. Among them, IAA12 was downregulated by auxin. These findings are consistent with our results. As we did not need to induce functional downregulation of ABP1, we were able to monitor changes as soon as 30 min after auxin addition. Braun et al. (2008) did not investigate gravitropism and phototropism. In conclusion, our results support the notion that ABP1 is required for early auxin functions.

## **EXPERIMENTAL PROCEDURES**

## Plant material

Heterozygous *abp1*/*ABP1* mutant seeds (stock number N6489) were obtained from the Nottingham Arabidopsis Stock Center (<http://arabidopsis.info/>), and these proved to be kanamycin-resistant. For long- or short-day experiments, seedlings were not selected on kanamycin agar but were sown directly on peat-based compost soil (Einheitserde, <http://www.einheitserde.de/>) containing 30% silica sand. The genotypes were determined by PCR. Seeds from *abp1*/*ABP1* plants were sown on kanamycin-containing medium and transferred to kanamycin-free medium after 4 days of growth on upright agar plates. Afterwards, they were selected according to their slanting angle. The experiments shown in Figures 1(a,b) and 2 were performed this way on upright agar plates. In the experiments shown in Figure 1(c–e), all seedlings were planted on kanamycin-free medium and the results confirmed the segregation of 2:1 *abp1*/*ABP1* to wild-type (Chen et al., 2001b). For quantifications, seedlings were scanned using a CanonScan 8800F (resolution of 600 dots per inch; Canon, <http://www.canon-europe.com>). Root lengths and angles were measured using AXIOVISIO LE version 4.6 software (Zeiss, <http://www.zeiss.com/>). For transcription measurements and auxin uptake experiments (Figures 5 and 6), seedlings were grown in half-strength MS agar medium for 14 days under long-day conditions, the wild-type without kanamycin, and seeds from a kanamycin resistant *abp1*/*ABP1* plant in medium containing 50 µg/ml kanamycin. Then resistant *abp1*/*ABP1* seedlings were selected, washed three times for 5 min in medium without kanamycin, and grown for a further 5 days in half-strength MS liquid medium without kanamycin. Wildtype seedlings were treated the same way, but without kanamycin. For auxin treatment, the medium was removed and replaced by fresh medium without or with the IAA concentration indicated. Seedlings were blotted on filter paper and frozen in liquid nitrogen for further use.

## Nucleic acid analysis

For quantitative RT-PCR, 4 µg of total RNA was prepared using a NucleoSpin RNA plant kit according to the manufacturer's instructions (Macherey & Nagel, <http://www.mn-net.com>), and transcribed to first-strand cDNA using a RevertAid™ H Minus

first-strand cDNA synthesis kit (Fermentas, <http://www.fermentas.com>). Primers were selected using PRIMER 3 software ([http://www.broad.mit.edu/cgi-bin/primer/primer3\\_www.cgi](http://www.broad.mit.edu/cgi-bin/primer/primer3_www.cgi)) and NETPRIMER software (<http://www.premierbiosoft.com/netprimer/netprlaunch/netprlaunch.html>), and checked for primer efficiency and against primer dimer formation. The primers used were 18S rRNA forward (5'-GGCTCGAAGACGATCAGATACC-3'), 18S rRNA reverse (5'-TCGGCATCGTTTATGGTT-3'), *ABP1* forward (5'-ACGAGAAAATCATACCAATTCGGACTAACC-3'), *ABP1* reverse (5'-GTATCTACGTAGTGTACAAAACCTCAAC-3'), IAA2 forward (5'-GGTTGGCCACCAGTGAGATC-3'), IAA2 reverse (5'-AGCTCCGTCCATACTCACTTTCA-3'), IAA11 forward (5'-CCTCCCTTCCCTCACAATCA-3'), IAA11 reverse (5'-AACCGCCTTCCATTTTCGA-3'), IAA12 forward (5'-CGTTGGGTCTAAACGCTCTG-3'), IAA12 reverse (5'-TTCCGCTCTTGCTGCCTTCA-3'), IAA13 forward (5'-CACGAAATCAAGAACCACAAACGA-3'), IAA13 reverse (5'-

CACCGTAACGTCGAAAAGAGATC-3'),	IAA14	forward	(5'-
CCTTCTAAGCCTCCTGCTAAAGCAC-3'), IAA14 reverse			
(5'-CCATCCATGGAAACCTTCAC-3'),	IAA19	forward	(5'-
GGTGACAACCTGCGAATACGTTACC-3'),	IAA19	reverse	(5'-
CCCGGTAGCATCCGATCTTTTCA-3'),	IAA20	forward	(5'-
CAATATTTCAACGGTGGCTATGG-3'),	IAA20	reverse	(5'-
GCCACATATTCCGCATCCTCTA-3'), GH3.5 forward (5'-AGCCCTAACGAGACCATCCT-			
3), GH3.5 reverse (5'-AAGCCATGGATGGTATGAGC-3'), SAUR9 forward (5'-			
GACGTGCCAAAAGGTCACCT-3'), SAUR9 reverse (5'-AGTGAGACCCATCTCGTGCT-			
3'), SAUR15 forward (5'-ATGGCTTTTTTGAGGAGTTTCTTGGG-3), SAUR15 reverse (5'-			
TCATTGTATCTGAGATGTGACTGTG-3'), SAUR23 forward (5'-			
ATGGCTTTGGTGAGAAGTCTATTGGT-3), and SAUR23 reverse (5'-			
TCAATGGAGCCGAGAAGTCACATTGA-3'). Quantitative PCR reactions were performed			

using 1 ll of sixfold diluted cDNA, 200 nM primers and 0.2· Power SYBR Green PCR master mix (Invitrogen, <http://www.invitrogen.com/>) in a StepOnePlus™ system (Applied Biosystems, <http://www.appliedbiosystems.com/>). For each pair of primers, the threshold value and PCR efficiency value were determined using cDNA diluted tenfold each time in five dilution steps. For all primer pairs, including the internal standard gene, 18S rRNA, the PCR efficiency was >99%. The specificity of PCR amplification was examined by monitoring the presence of a single peak in the melting curves for quantitative PCR. Amplicons were checked for fragment length on 4% agarose gels. For each determination, two to three biological repeats and three technical replicates for each determination were performed for the subsequent PCR reaction. Relative expression was calculated according to the DDCT method using the equation: relative expression = 2<sup>-(DC tsample - DC tcontrol)</sup>, where DCt = Ct(sample gene) - Ct(reference gene) and Ct refers to the threshold cycle determined for each gene in the early exponential amplification phase (Livak and Schmittgen, 2001). The expression level for the control treatment was set as 1-fold. For statistical analysis, REST 2008 software (Pfaffl et al., 2002) was used.

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