Institute of Experimental Botany

of the Czech Academy of Sciences

Scientific Report

2010–2014

Content

Introduction

The international evaluation of the institutes of Academy of Sciences is a good opportunity to look back and, in the printed form of the Research Report, take stock of important happenings at the Institute of Experimental Botany (IEB), and consider the institute's contributions to the knowledge pool of its field as well as the practical ramifications of its research.

Perhaps the greatest change at the IEB has been the recent completion of two new buildings. In 2012, the employees of the institute moved from its insufficient base in Prague–Dejvice to a new building in the academic research complex in Lysolaje, where most of Prague's scientific work is now concentrated. Concurrently, with the financial support of the European Union, the Centre of the Region Haná for the Biotechnological and Agricultural Research was completed in Olomouc, which benefited a team of our institute affiliated with the Center. This team of the Laboratory of Structural and Functional Genomics was able to abandon a building that had been in a flood zone (the building was damaged in the 1997 floods and again threatened in the 2002 floods), and move to a generously equipped modern space a safe distance from the Morava river. The successful parallel realization of both of these building projects was an enormous challenge that should be credited to the former director of the IEB prof. RNDr. Eva Zažímalová, CSc., who had lead the institute between 2007 and 2012.

Based on a previous international evaluation of scientific teams, as well as on our own internal annual assessment of our laboratories, 2012 saw changes in the IEB's organizational structure and a reduction in the total number of its laboratories. Currently, fifteen laboratories operate at the IEB, one of which is a service lab and another is focused on the production of applied research.

The greatest measure of scientific work on the plane of fundamental research are publications in high-quality scientific journals. In this regard, researchers at the IEB had been highly successful between 2010 and 2014: in total, they had authored or co-authored 565 articles in journals with an impact factor. This number, which corresponds to an almost 50% increase in comparison to the previous 5-year period, indicates that descriptions of results and directions on the following pages of laboratories will need to be limited to only the most important and highest-quality matters, while passing lightly over many other results that are undeniably also noteworthy and of very high quality. During the period, we published in the most prestigious journals: Nature (3×), Science (5×), Cell, Nature Biotechnology, Nature Genetics, Nature Chemical Biology (2×), Nature Communications (3×), Developmental Cell (4×), Genes & Development, Trends in Plant Sciences (2×), Genome Biology (2×), Progress in Lipid Research, Proceedings of the National Academy of Sciences of the USA (6×), Plant Journal (15×), Plant Cell (12×), Plant Physiology (11×), New Phytologist (14×) and others.

Few institutes of the Academy of Sciences have fulfilled its motto “quality research for public good” as impeccably as has the Institute of Experimental Botany. The team of prof. Ing. Jaroslav Doležel, DrSc., coordinates the program Foods for the Future, which is part of the larger project Strategy 21 of Academy of Sciences. Few of the Academy's institutes can boast a production of applied research this broad: between 2010 and 2014, researchers at the IEB got 29 new patents, most of them abroad including the US and the EU. Lead by Ing. Jaroslav Tupý, DrSc., Station of Apple Breeding for Disease Resistance cultivates scab-resistant apple trees. They 35 times registered breeding rights to newly bred apple varieties resistant to scab. We sell licences to grow these varieties all over the world, and revenue from these licences is an important component of the IEB's budget. Based on this licensing, over a million trees a year have been sold in recent years.

The IEB frequently hosts international scientific conferences. The largest one has been the Auxins and Cytokinins in Plant Development Conference, which was held between June 29 and July 4, 2014. The conference was attended by several hundred scientists from all over the world.

The last key part of the IEB's work – for over half a century now! – is the publication of academic scientific journals. I am proud that our *Biologia Plantarum* and *Photosynthetica* are rated among the top scientific publications in the Czech Republic. Both are indexed in the WOS database and their impact factor keeps rising.

Martin Vágner, director of IEB

Institute Representatives

Director:

prof. RNDr. Eva Zažímalová, CSc. (till May 30, 2012)
RNDr. Martin Vágner, CSc. (since June 1, 2012)

Deputy Director:

RNDr. David Honys, Ph.D. (till May 30, 2012)
RNDr. Jan Martinec, CSc. (since June 1, 2012)

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Ing. Jan Škoda – IBT CAS, Prague (since May 1, 2012)

Secretary:

Ing. Alena Trávníčková – IEB CAS

Abbreviations

Institutions of the Czech Academy of Sciences (CAS):

BC – Biology Centre
IBT – Institute of Biotechnology
IEB – Institute of Experimental Botany
IOCB – Institute of Organic Chemistry and Biochemistry
IPMB – Institute of Plant Molecular Biology
IVB – Institute of Vertebrate Biology

Others:

CRI, Prague – Crop Research Institute, Prague
MENDELU, Brno – Mendel University, Brno
PRI, Havlíčkův Brod – Potato Research Institute, Havlíčkův Brod
RIFC, Ltd., Troubsko – Research Institute for Fodder Crops, Ltd. Troubsko
UCT, Prague – University of Chemistry and Technology, Prague

Board of IEB

Chairman:

RNDr. Martin Vágner, CSc. – IEB CAS (till June 12, 2012)
RNDr. Radomíra Vaňková, CSc. – IEB CAS (since June 12, 2012)

Deputy Chairman:

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RNDr. Radomíra Vaňková, CSc. – IEB CAS (since January 20, 2012 till June 12, 2012)
prof. Ing. Miroslav Strnad, CSc., DSc. – IEB CAS (since June 12, 2012)

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RNDr. Miroslav Griga, CSc. – Agritec Šumperk
RNDr. Ladislav Kohout, DrSc. – IOCB CAS, Prague
RNDr. Jan Martinec, CSc. – IEB CAS
prof. Ing. Miroslav Strnad, CSc., DSc. – IEB CAS
doc. Ing. Jiří Šantrůček, CSc. – IPMB CAS, České Budějovice
prof. RNDr. Olga Valentová, CSc. – UCT, Prague
RNDr. Radomíra Vaňková, CSc. – IEB CAS
prof. RNDr. Eva Zažímalová, CSc. – IEB CAS

Members (since January 20, 2012):

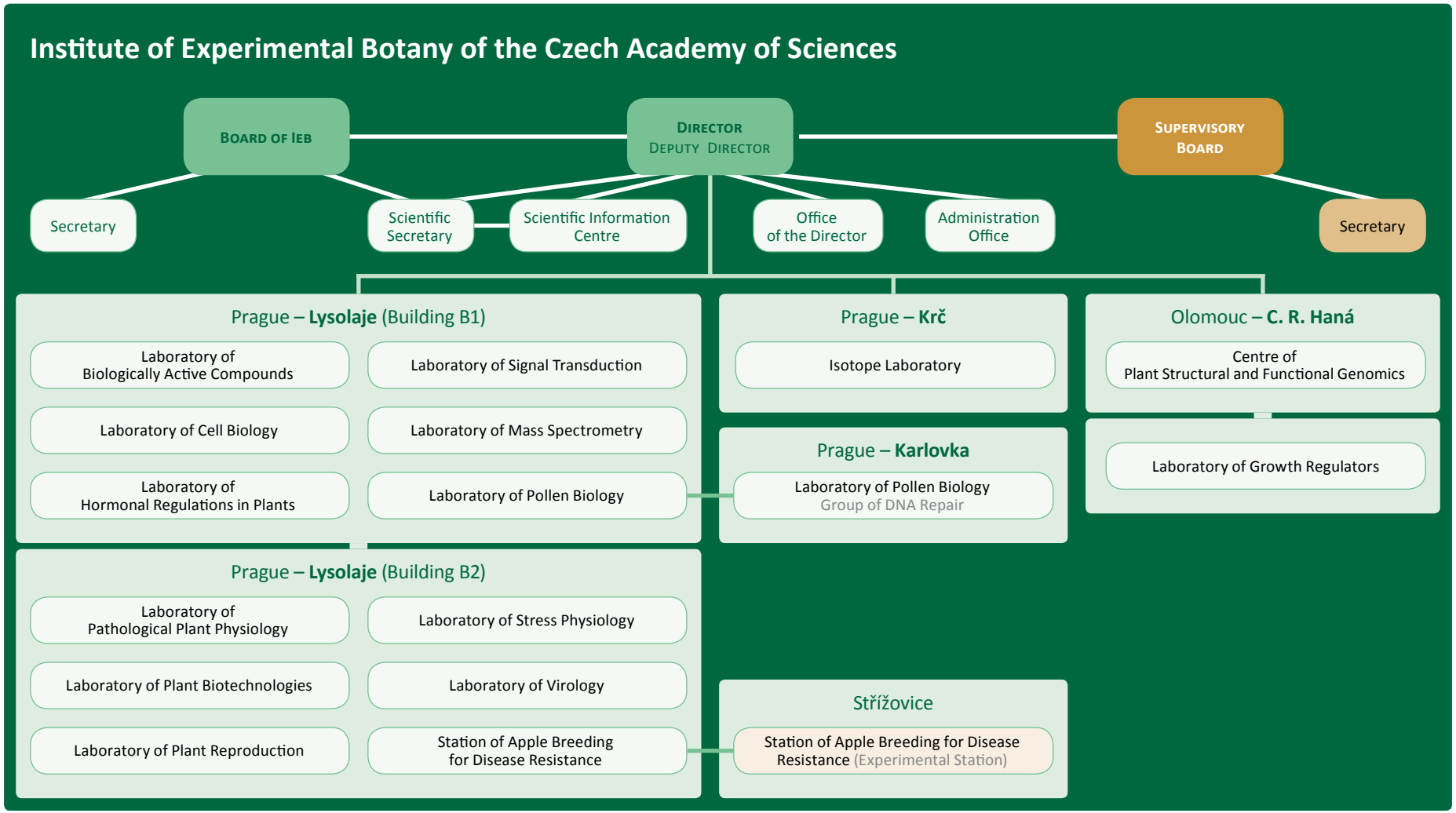
prof. RNDr. Břetislav Brzobohatý, CSc. – MENDELU, Brno
doc. Ing. Lenka Burketová, CSc. – IEB CAS
Ing. Petr Dědič, CSc. – PRI, Havlíčkův Brod (till January 23, 2013)
doc. RNDr. David Honys, Ph.D. – IEB CAS
Mgr. Jan Lipavský, CSc. – CRI, Prague
RNDr. Jan Nedělník, CSc. – RIFC, Ltd., Troubsko (since February 19, 2013)
Mgr. Lukáš Spíchal, Ph.D. – IEB CAS
RNDr. Martin Vágner, CSc. – IEB CAS
prof. RNDr. Olga Valentová, CSc. – UCT, Prague
prof. Ing. Zdeněk Wimmer, DrSc. – IEB CAS

Secretary:

Andrea Hourová – IEB CAS (till January 20, 2012)
Dr.rer.nat. Ing. Helena Plchová – IEB CAS (since January 20, 2012)

Scheme of the Organizational Structure of the Institute

According to the Organizational Series effective as of 31 December 2014



Buildings of IEB

Building B1: Rozvojová 263, 165 02 Prague 6 – Lysolaje

C. R. Haná: Šlechtitelů 31, 783 71 Olomouc

Building B2: Rozvojová 313, 165 02 Prague 6 – Lysolaje

C. R. Haná: Šlechtitelů 31, 783 71 Olomouc

C. R. Haná: Šlechtitelů 27, 783 71 Olomouc

Střížovice, 463 45 Pěnčín u Liberce

Not in the picture:
Vídeňská 1083, 142 20 Prague 4 – Krč,
Na Karlovce 1a, 160 00 Prague 6 – Dejvice

Centre of Plant Structural and Functional Genomics

Head of Laboratory:
prof. Ing. Jaroslav Doležel, DrSc.
Phone: +420 585 238 703
E-Mail: dolezel@ueb.cas.cz

In the picture (from the left):
Bottom row: Mgr. Eva Hřibová, Ph.D. /Researcher, Mgr. Miroslava Karafiátová, Ph.D. /Postdoctoral Fellow, Mgr. Helena Staňková /PhD Student, Elodie Rey /PhD Student, RNDr. Jan Šafář, Ph.D. /Researcher, Mahmoud Said, Ph.D. /Postdoctoral Fellow, Mgr. Veronika Burešová /PhD Student, Bc. Jitka Weiserová /Technician, Mgr. Pavla Christelová, Ph.D. /Postdoctoral Fellow
Second row: Mgr. Martina Horníková /PhD Student, Mgr. Kateřina Holušová /PhD Student, Michael Abrouk, Ph.D. /Postdoctoral Fellow, prof. Ing. Jaroslav Doležel, DrSc. /Head of the Centre, Mgr. Petr Cápal /PhD Student, Mgr. Jan Bartoš, Ph.D. /Researcher, Mgr. Zuzana Ivaničová /PhD Student, Mgr. Zuzana Tulpová /PhD Student, Ing. Hana Šimková, CSc. /Researcher
Third row: Ing. Marie Seifertová /Technician, Zdeňka Dubská /Technician, Radomíra Tušková /Technician, Helena Tvardíková /Technician, Mgr. Miroslav Valárik, Ph.D. /Researcher, Ludmila Švubová /Secretary, Mgr. Hana Jeřábková /PhD Student, Mgr. Eva Komínková /PhD Student, Eva Jahnová /Technician, Ing. Radoslava Kvasničková /Project Manager
Top row: Nicolas Blavet, Ph.D. /Postdoctoral Fellow, Mgr. Jan Vrána, Ph.D. /Researcher, Bc. Romana Šperková /Technician, RNDr. Roman Hobza, Ph.D. /Researcher, Ing. Zbyněk Milec, Ph.D. /Postdoctoral Fellow, Mgr. Štěpán Stočes /PhD Student, RNDr. David Kopecký, Ph.D. /Researcher, Mgr. Tomáš Beseda /PhD Student, Ing. Beáta Petrovská, Ph.D. /Researcher, Marie Vyhlídalová /Horticulturist

Not in the picture: RNDr. Jarmila Číhalíková /Researcher, Mgr. Jana Čížková, Ph.D. /Postdoctoral Fellow (maternity leave), Mgr. Eva Dvořák Tomaštíková, Ph.D. / Researcher (currently abroad), Mgr. Barbora Klocová /PhD Student, Mosses Nyine /PhD Student, Mgr. Martina Bednářová /PhD Student (maternity leave), Mgr. Anna Chmelařová /PhD Student, Mgr. Hana Vanžurová /PhD Student (currently abroad)

Our research team has been pursuing a long term program on the molecular organization and evolution of plant genomes. The emphasis is on crop plant species with polyploid genomes and, in particular, those which originated from interspecific hybridization. Apart from gaining insights into nuclear genome structure and evolution, an important goal was to produce novel data and biological resources to support the use of molecular and biotechnological tools in plant breeding. The research involved three groups of plants: (a) cereals of the tribe Triticeae (wheat, barley and rye); (b) forage grasses (fescue, ryegrass and their hybrids); and (c) banana. The latter was a continuation of international collaborative projects with IAEA/FAO and more recently Bioversity International. A unique character of the team is the extensive experience and expertise in a broad range of cytogenetic, flow cytometric, molecular biology and genomic methods that permit multidisciplinary and original experimental approaches. Due to its unique position, the team has been a popular partner in international projects and has also been working on species outside the above three groups of plants.

Cereal genome analysis

The analysis of many plant genomes, including those of the Triticeae species is complicated by their enormous size and sequence redundancy resulting from high DNA repeat content and the presence of homoeologous genomes in polyploids. To overcome these difficulties, the team pioneered a chromosome genomics strategy which relies on dissection of nuclear genomes to chromosomes or chromosome arms by flow cytometric sorting and preparation of chromosomal DNA suitable for downstream genomics applications. During the past five years, the team has employed the strategy in its own research projects as well as in collaborative projects with international research teams. They have also continued to improve and expand the range of tools so that the strategy can be easily integrated into any genome mapping and sequencing program.

The work involved refinement of a protocol for construction of large insert BAC libraries from flow-sorted chromosomes, and the team remains the only one in the world that can construct this type of DNA library. These unique resources are making the biggest impact in the development of ready to sequence physical map of bread wheat. The team is one of the key members of the International Wheat Genome Sequencing Consortium (IWGSC) and after a huge effort, they constructed BAC libraries from all chromosomes of bread wheat [81]. The availability of chromosome BAC libraries permitted estimation of the fidelity of BAC contig assembly using genomic libraries [50]. This was a collaborative project with prof. Jan Dvořák (UC Davis) in which the team provided a set of chromosome BAC libraries and participated in data analysis and publication of the results. The availability of chromosome BAC libraries from homoeologous chromosomes enabled characterization of changes in genic sequences during wheat genome evolution, including the rates of non-collinear gene insertion and gene duplication [212].

The suitability of chromosome genomics for producing reference sequence of the wheat genome was definitely confirmed in a collaborative project in which the first reference sequence of (the largest) wheat chromosome (3B) was produced after sequencing BAC clones from its physical map. This result was published in Science [473] and provided so far, the most detailed information on genome structure of bread wheat. To date, members of IWGSC constructed physical maps from 16 out of 21 wheat chromosomes, including the map of chromosome 6A [526]. During the process of constructing physical maps, BAC contigs are ordered and oriented predominantly using genetic markers. However, genetic linkage maps suffer from poor resolution in (peri)centromeric regions. To tackle this problem, the team developed a FISH technique to localize cDNA probes shorter than 3.5 kb on plant mitotic metaphase and prometaphase chromosomes and demonstrated that it could be a valuable tool to order physical maps and provide a complementary approach to genetic mapping for chromosome regions with limited or no recombination [372].

Despite some limitations, genetic linkage maps remain one of the main tools in gene mapping and positional gene cloning projects. These projects benefit from high density maps and an attractive approach to constructing such maps is to develop new markers specifically from target genome regions. In collaborative projects, the team demonstrated that this can be

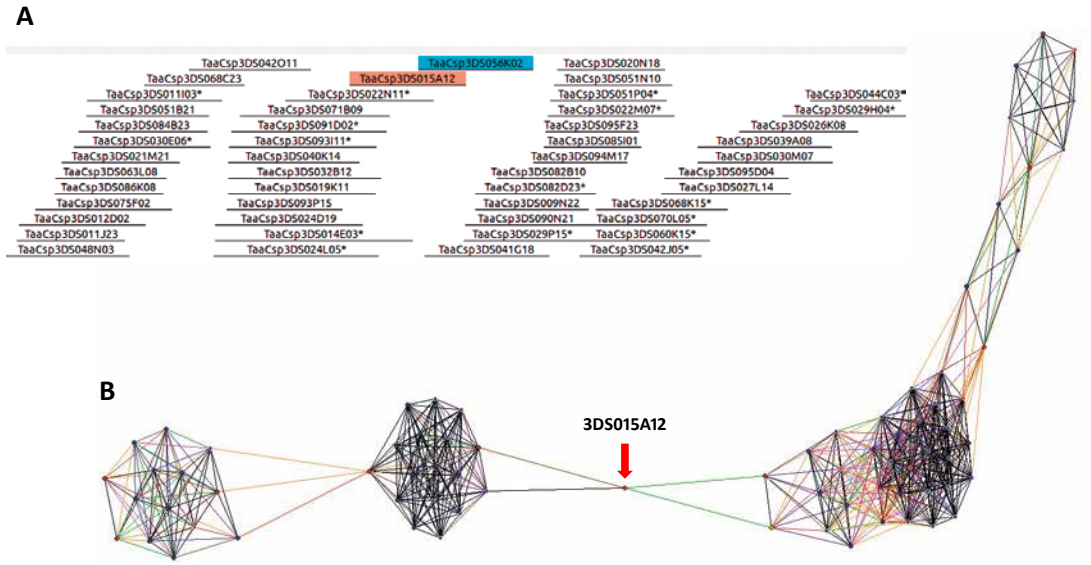


Figure 1: Example of a contig of overlapping BAC (Bacterial Artificial Chromosome) clones from short arm of wheat chromosome 3D (3DS). The contig was assembled using FPC program (A), and the assembly was validated using LTC program (B). The analysis using LTC confirmed the assembly with the exception of incorrectly included BAC clone 3DS015A12.

done using DNA from flow-sorted chromosomes [420]. For example, they showed that the Diversity Arrays Technology (DArT) can be coupled with chromosome sorting to increase the density of genetic maps for specific chromosomes or chromosome arms of wheat. Since only a small amount of chromosomal DNA (5 ng) is needed to develop DArT markers, this approach can be readily applied to any crop for which chromosome sorting is available [96].

Sequencing DNA amplified from flow-sorted chromosomes by next generation sequencing (NGS) technologies is another powerful application of chromosome genomics developed by the team. Although not suitable for producing gold standard reference sequence assemblies, it has many important applications. The main advantage is low cost and the speed with which a draft chromosome/genome sequence can be produced. Thus, sequencing DNA of flow-sorted chromosomes of barley allowed assembly of a majority of its genes and establishment of their putative linear order along all chromosomes. This was the first blueprint of a diploid Triticeae genome and provided a framework for the study of Triticeae genome evolution and the development of novel strategies in cereal breeding [154]. In a similarly novel study, virtual linear gene order models were established for all chromosomes of rye. A genome-wide high-density comparative analysis of synteny between rye, barley and model grass genomes indicated that introgressive hybridizations and/or a series of whole-genome or chromosome duplications played a role in rye speciation and genome evolution [391].

In collaboration with other groups, the team demonstrated the utility of chromosome sequencing for the analysis of the complex genome of bread wheat in several studies [112, 198, 201, 217, 238, 279, 335, 387, 496, 550]. For example, sequencing both arms of chromosome 4A [245] facilitated construction of an ordered gene map of the chromosome, embracing over 85% of its genes. The work provided new insights into the evolutionary dynamics between homologous chromosomes and syntenic chromosomal regions and enabled precise localization of translocation and inversion breakpoints on the chromosome. Following these pioneering studies, IWGSC decided to sequence all chromosomes of bread wheat using NGS technology. This large-scale exercise was successfully completed in 2014 and the results were published in Science [505]. The work provided novel insights into the genome biology of a polyploid species and the results will facilitate faster gene isolation, genetic marker development, and precise breeding of this important crop.

Given the success of chromosome genomics in obtaining draft genome sequences of cultivated Triticeae, the team decided to expand this work to wild relatives of bread wheat (see also the section 3 below). As a first step, they developed a protocol for chromosome sorting in a set of species from genus *Aegilops* [158].

The chromosome-centric approaches developed by the team provide an attractive opportunity for studying the molecular organization and evolution of specialized chromosomes, such as B chromosomes. Their analysis using whole genomic DNA is hampered by the presence of sequences from all remaining chromosomes. Analysing DNA from the chromosome of interest provides an important advantage, including the reduction of sample complexity. The team employed this approach to study the evolution of the B chromosome of rye. After sequencing DNA amplified from flow-sorted A and B chromosomes, the origin of Bs could be traced to parts of the A genome. The origin of the rye B chromosome could be dated and a comprehensive model was proposed for the stepwise evolution of Bs, which included insertions of organellar DNA [282].

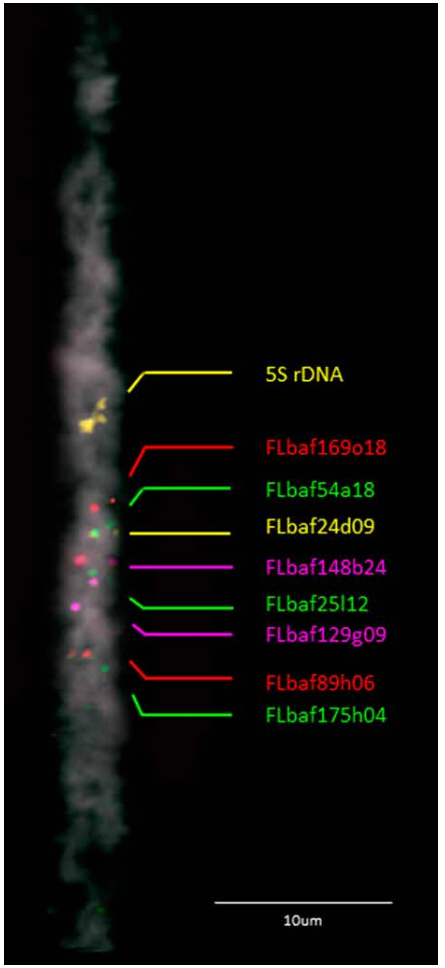


Figure 2: Localization of genes on barley chromosome 7H using multicolor fluorescence *in situ* hybridization (FISH).The genes were selected from non-recombining regions of the chromosome and the results indicated that this region spans over 40% of the chromosome length. Moreover, errors in genetic map of this region were discovered. The chromosome was identified using 5S rDNA as marker.

Genome analysis in forage and amenity grasses

The research in forage grasses (*Festuca* spp., *Lolium* spp. and their hybrids), focused on analysis of their genome structure and evolution at a cytogenetic and DNA level. The experiments prior to 2010 established molecular karyotypes of fescue and ryegrass using FISH and they determined the genomic constitution in a majority of commercially available hybrid Festulolium cultivars using GISH. With the aim of increasing the resolution of genome analysis and achieve higher throughput, the team developed DArT markers specific for fescue and ryegrass. Validation of the DArTFest array confirmed its suitability for determining genome constitution in *Festuca* × *Lolium* hybrids at high resolution and its ability to discriminate between Festulolium cultivars. The results also confirmed the potential of the array to follow changes in genome composition of *Festuca* × *Lolium* hybrids over successive generations [145].

The DArTFest array was also used to saturate genetic maps of *F. pratensis* and *L. multiflorum* and identify markers associated with traits of interest. Three genomic loci associated with freezing tolerance co-localized to chromosome segments and QTLs previously implicated in freezing tolerance. Moreover, sequencing the markers enabled comparison of genome structure of both species with the genomes of rice and *Brachypodium* and revealed their syntenic relations [110]. These results again confirmed the potential of the DArTFest array in genetic studies of the *Festuca–Lolium* complex. The annotated DArTFest array resources could accelerate further studies and improvement of desired traits in *Festuca–Lolium* species.

Given the lack of detailed information on genome structure of *F. pratensis*, the team applied their chromosome genomics approach to generate a draft genome sequence assembly. As a first step, they flow sorted chromosome 4F and sequenced it by NGS technology. This provided the first insight into the composition of the fescue genome, permitted estimation of gene content, enabled the construction of virtual gene order of the chromosome, and facilitated detailed comparative analysis with the sequenced genomes of rice, *Brachypodium*, sorghum and barley. The analysis of chromosome sequences enabled identification of new tandem repeats, which were mapped using FISH and were found to be suitable cytogenetic markers for karyotyping *F. pratensis*, *Lolium* species and their hybrids. This was the first report on dissection of a complex and large forage grass genome using chromosome sorting [380].

Analysis of banana genomes

A majority of banana (*Musa* spp.) cultivars are parthenocarpic triploid clones which originated from natural intra- and interspecific hybridizations between various subspecies of at least two different *Musa* species. However, their exact origin is not known. The research on *Musa* focused on two areas: genetic diversity and phylogeny, and genome structure. The team has been appointed by Bioversity International to serve as *Musa* Genotyping Centre and genotyping and phylogenetic analyses are part of this mandate [570]. As the classification of species of the Musaceae (banana) family and their phylogenetic inter-relationships remain controversial, the team studied evolutionary relationships using 13 species and DNA sequences obtained from a set of unlinked nuclear genes. The study contributed significantly to the classification of the Musaceae family species. The first estimates for the divergence times of the four sections of the genus *Musa* were obtained and the study provided a substantial insight into the course of speciation within the Musaceae. An understanding of the main phylogenetic relationships between banana species provided data to fine-tune the taxonomy of Musaceae [133].

Internal transcribed spacer (ITS) loci show high level of interspecific divergence and have been used frequently in genetic diversity and phylogenetic studies in various taxa. The team obtained the first detailed information on ITS sequence diversity in the genus *Musa* and characterized the structure and diversity of the ITS region in 87 representatives of the family Musaceae. Phylogenetic reconstruction based ITS sequences showed that the genus is divided into two distinct clades. A need to identify putative pseudogenic ITS sequences, which may have negative effect on phylogenetic reconstruction at lower taxonomic levels was shown. Independent evolution of parental rDNA in hybrids enabled determination of genomic constitution of hybrids using ITS sequences [131].

In order to provide more insight into the *Musa* genome structure and evolution, the team characterized the genomic organization of two main banana DNA satellites together with other DNA sequences in

nineteen accessions of *Musa*, including inter-specific hybrids. Molecular analysis of DNA satellites revealed their sequence conservation within and between the accessions. The pattern of their genomic distribution makes them suitable as cytogenetic markers. The study expanded the number of individual chromosomes which can be identified cytogenetically and provided tools to support determination of genomic constitution in inter-specific hybrids [347].

In order to provide the knowledge needed to apply molecular and genomics tools in improving the banana and contribute to understanding *Musa* evolution, the team participated in a large-scale sequencing project, which produced a draft sequence of the 523-megabase genome of *M. acuminata*. The banana genome sequence was the first of its kind for a monocotyledon outside Poales and represented an essential bridge for comparative genome analysis in plants. The study revealed three rounds of whole-genome duplications in the *Musa* lineage, which were followed by gene loss and chromosome rearrangements, resulting in little synteny conservation between lineages. The results of the work, which also led to discovery of conserved non-coding sequences predating monocotyledon–eudicotyledon divergence, were published in Nature [230].

Legume genome analysis

The team has also made significant contributions to sequencing nuclear genomes of some other species, with the biggest efforts concentrating on legumes, and chickpea in particular. In this species, they used DNA of flow-sorted chromosomes to assign all genetic linkage groups to chromosomes and thus completed the efforts on integration of genetic and physical maps of this crop [202]. The team has also developed a powerful approach to validate genome sequence assemblies obtained after whole genome shotgun sequencing (typically using NGS technologies). In two whole genome chickpea assemblies (kabuli and desi types of chickpea) the chromosome-centric approach highlighted short defined regions that were misassembled in the kabuli genome and identified large-scale misassembly in the desi genome [533]. The results of the study showed that the integration of chromosome genomics tools within genome sequencing projects has great potential as whole genome approaches are prone to errors and misassemblies.

Research projects: 3, 29, 116, 140–162

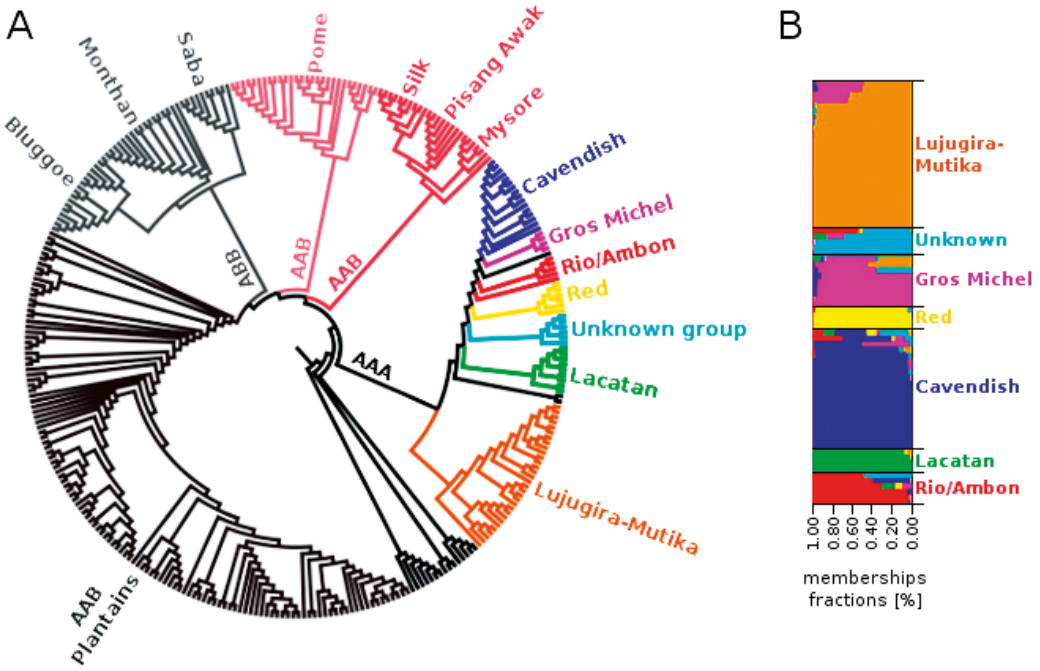


Figure 3: Characterization of genetic diversity of a set of triploid banana clones. The analysis using 19 microsatellite (SSR) markers enabled identification of groups of clones with AAA, AAB and ABB genomic constitution (A). The examination of multi-locus genotype data using the Structure program confirmed the grouping and indicated subpopulations sharing particular alleles (B).

Figure 4: Microscopic investigation of chromosomes of *Agropyron cristatum*, a wild relative of wheat

Isotope Laboratory

Head of Laboratory: **prof. Ing. Zdeněk Wimmer, DrSc.**
Phone: +420 241 062 457; E-Mail: wimmer@ueb.cas.cz

Research in the Isotope Laboratory has been focused at the three basic directions:
(1) Investigation of medicinally important plant products with special attention paid to their derivation resulting in semisynthetic compounds with improved physico-chemical characteristics and mostly with higher cytotoxicity. High antimicrobial activity was achieved with several new compounds. Multifarious activity (i.e. pleitropic effect) was found in several highly active compounds. Ability to form supramolecular aggregates in aqueous media and/or in organic solvents was found and investigated.
(2) Development of heterocyclic derivatives of synthetic origin (purine-based compounds), including radiolabeling whenever required.
(3) Preparation of cytokinin derivatives and other required compounds with radiolabeling.

In the picture (from the left):
RNDr. Bohuslav Černý, CSc./Researcher, Dr. Josef Holík/Researcher, Ing. Zulal Özdemir/PhD Student, doc. Ing. Libor Havlíček, CSc./Researcher, doc. Ing. Milan Pavlík, CSc./Researcher, Bc. Pavla Štangelová/Diploma Student, PharmDr. Lenka Zahajská, Ph.D./Research Assistant, Bc. Tereza Jíšová/Diploma Student, Mgr. Ivona Blažková/PhD Student, Ing. Jana Šusteková/PhD Student, Mgr. Uladzimir Bildziukevich/PhD Student, Martina Wimmerová/Technician, Ondřej Čáslavský/Technician, prof. Ing. Zdeněk Wimmer, DrSc./Head of Laboratory

Not in the picture:
RNDr. Sándor T. Forczek, Ph.D./Researcher, RNDr. Martin Vlk/PhD Student, Jana Maňáková/Technician (maternity leave)

The research is oriented to biomolecules, their structure and analysis, activity, molecular and cellular mechanism of action as well as applications in different fields.

The comprehensive screen through the land plants is presented suggesting that cytokinins (CKs) of *cis*-zeatin (cZ)-type occur generally in plant kingdom. Survey of employed bioassays illustrates ability of high doses of cZ-type CKs to induce various physiological responses and CK signaling. These data argue against the image of cZ-type CKs as the non-active or weakly active natural adjuncts to the *trans*-isomers suggesting their conceivable function as delicate regulators of CK responses in growth-limiting conditions. This work was possible because of new cZ synthesis was developed [126].

Natural phytochemicals as potential drug candidates

We developed drug candidate with unknown molecular mechanism of action. These usually exist because of our expertise in cellular and molecular testing on new drug candidates.

Phytosterols and triterpenoids – Phytosterols and cholesterol were subjects of structural modifications with the objective to get novel compounds displaying either cytotoxicity and antimicrobial activity or ability to self-assemble into chiral supramolecular systems.

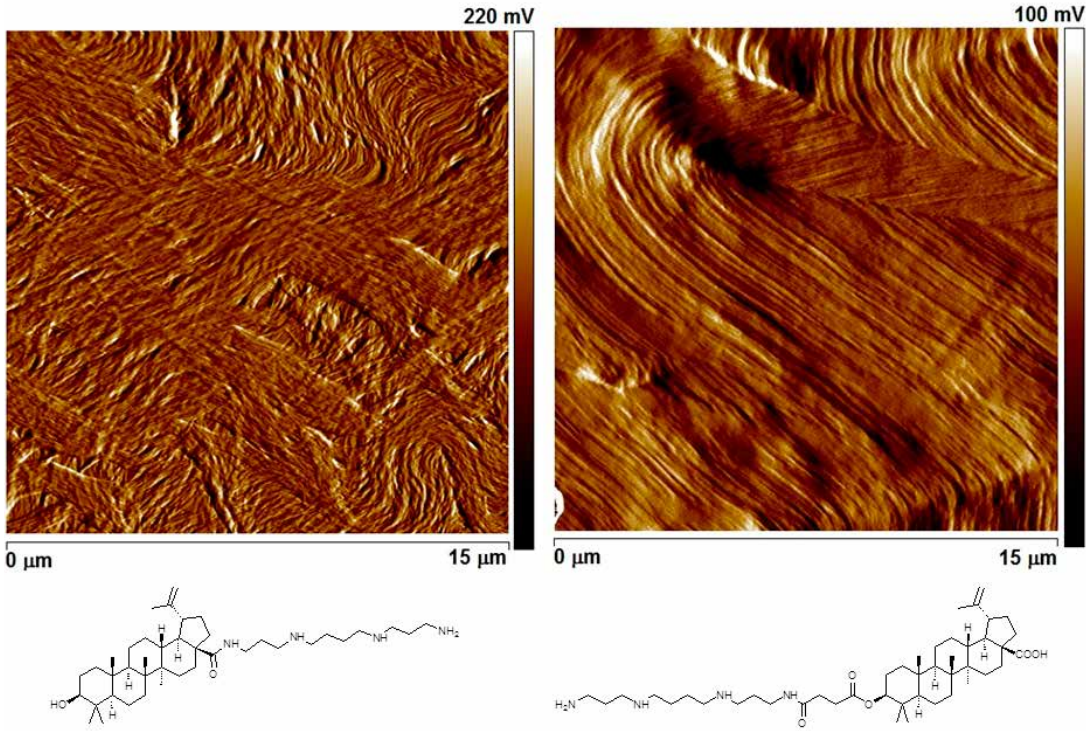
The current interest of the IL team has also been focused on investigation of novel amides of sterols and triterpenoid acids with potential cytotoxicity. The synthetic protocol was designed in as simple as possible way, and divided into several general methodologies applicable to the compounds synthesized. The cytotoxicity was tested on cells derived from human T-lymphoblastic leukemia, breast adenocarcinoma and cervical cancer, and compared with tests on normal human fibroblasts. ADME parameters as well as selected

physico-chemical parameters were either measured or calculated to support experimentally obtained results [329, 341].

Physico-chemical characteristics of the prepared compounds were studied. This is important for investigation of supramolecular behavior of potential biological systems, and contributes to the newly emerging area of supramolecular chemical biology [188, 194, 195, 203, 319]. A number of the prepared compounds, especially those derived from natural triterpenoid acids, suffer from low biovailability due to their low solubility in aqueous media. Even triterpenoid acids themselves display low solubility in those media. Despite of this fact, several of them (betulinic acid, oleanolic acid or ursolic acid) are known by their positive effects in treating different types of cancer. A series of cationic polyamine-based amides of plant sterols and triterpenoids was prepared. These compounds are able to bind to negatively charged DNA and are also able to enter lipid bilayer to participate in formation of ion channels.

Most of the prepared compounds displayed self-assembly behavior, and several of them formed hydrophilic and chiral supramolecular gels. The most important compounds have so far been studied by a combination of VT-DOSY-NMR measurements (variable temperature dependence of the diffusion coefficient) and UV-VIS-NIR measurements realized in the mixtures of water/organic solvent (miscible with water) systems with stepwise change of the solvents ratios and with a constant concentration of the studied compound. Non-linear temperature dependence of the diffusion coefficient is the proof of supramolecular behavior of the studied system. Change in the concentration of the free monomeric molecules is detected by this method, and it is non-linear with temperature change. No self-assembly in the system is explained by the constant concentration of the free monomeric molecules in the system which status results in linear dependence of the diffusion coefficient. In the UV-VIS-NIR spectra measured by the described method a bathochromic shift of the maxima was observed most in the range 1000–850 nm wavelength with increasing water content in the studied system. This behavior indicates formation of the J-type supramolecular aggregates (fibrous nanostructure formed by a head-to-tail superassembly). Atomic force microscopy (AFM) imaging made on a multimode scanning probe microscope on freshly cleaved highly oriented pyrolytic graphite (HOPG) or mica resulted in nice view of the fibrous nanostructures superassembled into two dimensional supramolecular hydrophilic systems (*Figure*). The same result was proven by scanning electron microscopy (SEM) in collaboration with scientists from the University of Jyväskylä in Finland.

Figure: AFM images of the fibrous supramolecular systems formed by compounds, the formulae of which are presented.



Research projects: 91, 97–99, 103, 105, 108, 109, 111

Laboratory of Biologically Active Compounds

Head of Laboratory: **RNDr. Martin Vágner, CSc.**
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The majority of findings published by the Laboratory of Biologically Active Compounds (LBAC) can be assigned to three fields: 1) studies of somatic embryogenesis in conifers; 2) studies of endogenous polyamines, phenolic compounds and phytohormones; and 3) studies of abiotic stresses. Our published papers often address the intersection of these three areas.

Somatic embryogenesis of conifers and polyamines

We examined the role of actin cytoskeleton in somatic embryo development. We proved that a decrease of endogenous IAA level is necessary for the development of fir somatic embryos. The role of endogenous polyamines has been studied both during the preparation of embryogenic culture of Norway spruce prior to cryopreservation and during culture regrowth after cryopreservation. We also examined the effect of cold stress, drought stress, heat stress on level of endogenous phytohormones and a combination of the latter two on polyamines metabolism in plants. The studied abiotic stresses also include salinity and long-term exposure to elevated CO_2.

In a pair of papers [73, 559], we examined the role of actin cytoskeleton in somatic embryo development. The first paper uprooted the dominant opinion that use of the actin-depolymerizing drug latrunculin B conclusively arrests the development of somatic embryos in conifers. We found that latrunculin applied in a particular concentration and at a particular phase of embryo development damaged only the suspensor cells but not the meristematic cells of developing embryos. Moreover, the chemical cleavage of suspensors triggered additional, more synchronized development of embryos. Although the number of fully matured embryos decreased, these embryos were characterized by a higher germination rate and lower incidence of malformations. We describe the functioning of latrunculin (the only anti-actin compound with this effect) as well as a different effect of another actin-depolymerizing drug – cytochalasin. The effect of latrunculin is currently being tested in several laboratories gathered under the IUFRO program. Our findings could be important for automatized commercial production of somatic embryos, where the uniformity and quality of embryos is crucial.

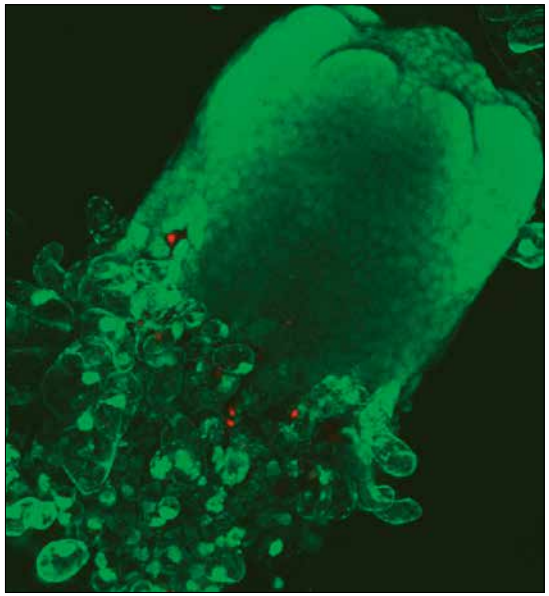
Additional work examining the role of auxins and their antagonists during the development of somatic embryos in *Abies alba* was described [199]. That project proved that a decrease of endogenous indole-3-acetic acid (IAA) level is necessary for the development of fir somatic embryos. The blocking of IAA synthesis did not produce the same effect.

Studies of endogenous polyamines in plants based upon an excellently elaborated method of extraction remains our laboratory's long-term specialization. The role of endogenous polyamines has been studied both during the preparation of embryogenic culture of Norway spruce prior to cryopreservation and during culture regrowth after cryopreservation [94]. The changes in the endogenous levels of polyamines due to external treatment by putrescine are important for the development of embryos.

In the picture (from the left): RNDr. Zuzana Vondráková CSc. /Researcher, Kateřina Raková / Technician, Jaroslava Špačková /Technician, RNDr. Martin Vágner, CSc. /Head of Laboratory, Mgr. Kateřina Eliášová, Ph.D. /Researcher, RNDr. Milena Cvikrová /Researcher, RNDr. Lucie Fischerová, Ph.D /Postdoctoral Fellow

Not in the picture: Mgr. Pavlína Bečvářová, Ph.D. /Technician, Mgr. Lenka Gemperlová, Ph.D. / Postdoctoral Fellow, Jana Kališová /Technician, Mgr. Jan Kolář, Ph.D. /Researcher, Ing. Olga Martincová /Technician

Figure 1: Somatic embryo of Norway spruce with developing cotyledons and rest of suspensor cells



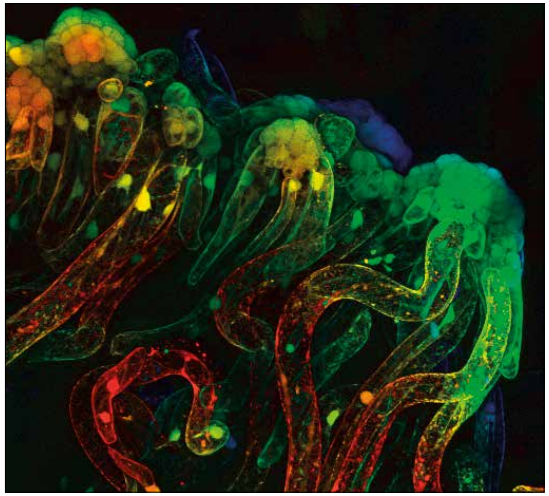


Figure 2: Early somatic embryos of Norway spruce

Polyamines are active in the defense reaction of cells of spruce embryogenic culture after infection by fungus *Gremmeniella* [5]. Similarly, two fractions isolated from mycelia of the fungus *Sirococcus strobilinus* evoked a defense reaction comprising changes in the spectrum and concentrations of phenolic compounds and stilbenes [573]. Our experiences with the role of polyamines in the somatic embryogenesis of Norway spruce have been reviewed [572].

Stresses

Aside from conifer somatic embryogenesis, we focus our research on plant stress. The application of cold stress resulted in a decrease in the levels of endogenous phytohormones associated with cell growth and division. During the acclimation phase of the stress response, the plants increased their frost tolerance and began accumulation of dehydrines. Active gibberellins, cytokinins and auxin were elevated, accompanied by a decrease of abscisic acid. Up-regulation of phenolic acids was observed [556] We also examined the effect of drought stress, heat stress, and a combination of the two on polyamines metabolism in a tobacco plant, characterizing it by an overproduction of proline [227, 345]. The studied abiotic stresses also include salinity. In salt-sensitive and salt-tolerant barley varieties the retention of K^+, a key determinant of salinity tolerance, was observed to depend upon the endogenous levels of polyamines and reactive oxygen species (ROS) [327]. Long-term exposure of Norway spruce trees to elevated CO_2 led to increase in the CO_2 assimilation rate and decrease of dark respiration, whereas the structure of needles' mesophyll and the accumulation and localization of phenolic compounds remained unchanged [277].

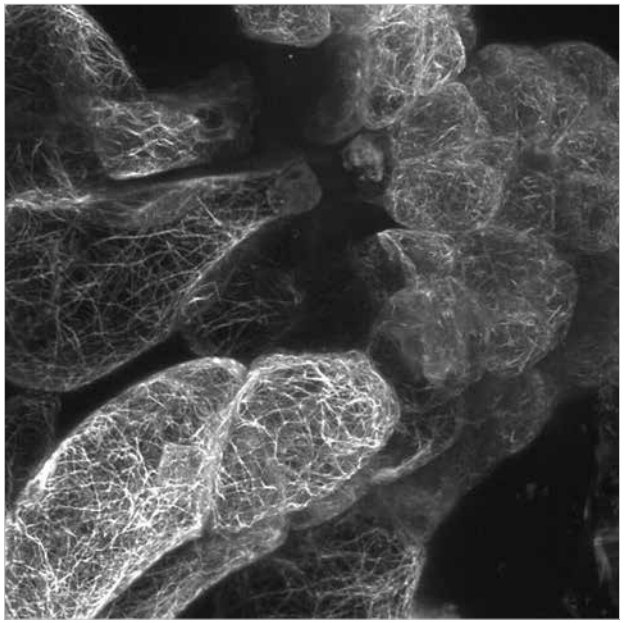


Figure 3: Actin in Norway spruce early embryos

Collaboration

Our collaboration with other teams, both within the Institute of Experimental Botany and from other institutes and universities in the Czech Republic and abroad, is evident from the profile of the published papers. The laboratory frequently participates in projects that are international in scope. Several papers were born in cooperation with scientists in Israel and other states in an international research program involving bioactive compound content in fruits [65, 165]. The aforementioned paper [327] was prepared under the auspices

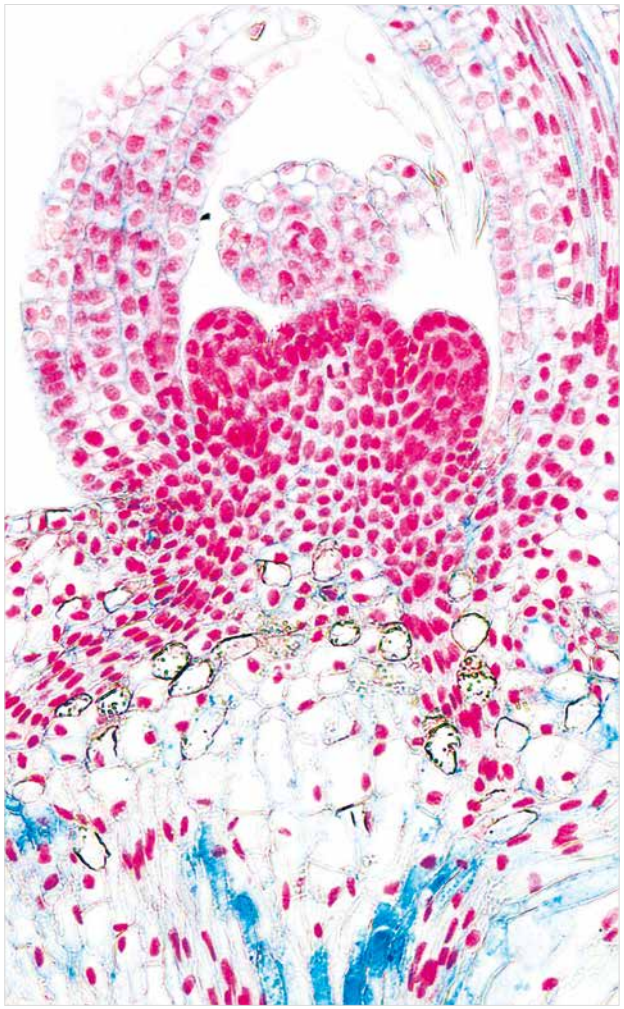


Figure 4: Apical bud of Norway spruce embling (seedling derived via somatic embryogenesis)

of the COST Program. Two more papers resulted from bilateral cooperation with Poland [19, 189]. Another paper, which originated in Czech–French cooperation under the Barrande program [511], dealt in a rather complex way with the development of somatic embryos of *Pinus pinaster* under conditions of reduced water availability. This study comprises proteomic, transcriptomic and morphologic analyses, as well as monitoring of endogenous abscisic acid and carbohydrate levels during pine somatic embryo development. The study remains the first paper to describe early molecular mechanisms during pine somatic embryo development and the first paper to combine transcriptomic and proteomic data in the somatic embryogenesis of conifers.

One paper on the regulation of photoperiodicity in *Chenopodium* was done in cooperation with the Laboratory of Plant Reproduction [462]. We also have contributed to other papers, such as a microscopic study [557] and a study on accumulation of radionuclides [76].

Research projects: 55, 118, 119, 124, 125, 129, 134, 136, 137

Figure 5: Mature somatic embryos of Norway spruce

Laboratory of Cell Biology

Head of Laboratory: **doc. RNDr. Viktor Žárský, CSc.**
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The Laboratory of Cell Biology explores selected molecular regulatory modules of plant cell polarity and morphogenesis operating mostly at the plasma membrane, at the interface of secretory pathway, membrane lipids and cytoskeleton.

The laboratory made a major progress in the characterization of plant vesicle tethering complex exocyst culminating in the publication of the review on the current state of arts in this field [441] and in the understanding of phospholipase D (PLD) involvement in the cytoskeletal regulations [407].

We showed crucial contribution of exocyst to plant cell division and detailed dynamics studies imply exocyst especially in phragmoplast initiation and then final fusion and maturation of the new cell wall. We contributed to a report on a co-ordination between TRAPP and exocyst complexes in Arabidopsis cytokinesis. We described for the first time the eukaryotic exocyst complex dynamics at the cytoplasmic membrane and the importance of exocyst complex for the recycling and cellular localization of PIN auxin efflux carriers and regulation of polar auxin transport. We also discovered that EXO70B1-containing exocyst subcomplex plays a role in the Golgi-independent autophagic transport into the vacuole. For its close homologue EXO70B2 our report showed for the first time an active exocyst role in the defense against both bacteria and fungi. Our work on phospholipase D signalling and regulation resulted in the uncovering of a positive feed-back loop between phospholipase D, its product phosphatidic acid and actin cytoskeleton. New specific interaction domain (GOE) in plant class I F-actin nucleators formins was also unexpectedly uncovered.

In the picture (from the left):
Mgr. Martina Růžičková /PhD Student, doc. RNDr. Viktor Žárský, CSc. /Head of Laboratory, RNDr. Michal Hála, Ph.D. /Researcher, Ing. Martin Potocký, Ph.D. /Researcher, Mgr. Anamika Ashok Rawat /PhD Student, Mgr. Hana Soukupová, Ph.D. /Researcher, Mgr. Denisa Oulehlová, Ph.D. / Postdoctoral Fellow, Mgr. Nemanja Vukašinović /PhD Student, Mgr. Edita Janková Drdová, Ph.D. / Postdoctoral Fellow, Mgr. Lucie Brejšková, Ph.D. /Postdoctoral Fellow, Mgr. Lukáš Synek, Ph.D. / Researcher (currently abroad), Mgr. Jitka Ortmannová /PhD Student, Bc. Klára Aldorfová /Diploma Student, Mgr. Juraj Sekereš / PhD Student, Bc. Jana Šťovíčková /Technician, Mgr. Vedrana Marković / PhD Student, doc. RNDr. Jiří Luštinec, CSc. /Researcher Emeritus, Tamara Pečenková, Ph.D. /Researcher, Ing. Andrea Potocká, Ph.D. /Researcher, Ing. Roman Pleskot, Ph.D. /Postdoctoral Fellow

Not in the picture:
Mgr. Radek Bezvoda, Ph.D. /PhD student (until 2013), Mgr. Matyáš Fendrych, Ph.D. /PhD student (until 2011), Mgr. Michal Kuchár /Technician (until 2014), Mgr. Ivan Kulich, Ph.D. /PhD student (until 2013), Ing. Petra Šarochová /Technician (until 2011), Mgr. Hana Toupalová, Ph.D. /PhD student (until 2011), Mgr. Pavlína Trpkošová /PhD student (until 2012)

Analysing *exo84b* and *exo70A1* Arabidopsis mutants, we for the first time not only show crucial contribution of exocyst to plant cell division, but show detailed dynamics implying exocyst especially in phragmoplast initiation and then final fusion and maturation of the new cell wall. Using co-immunoprecipitation interaction of EXO84 subunit with other exocyst subunits was proven [18]. Later in collaboration with the laboratory of Farhah Assaad at TUM, Munich, Germany we contributed to a report on a co-ordination between TRAPP and exocyst complexes in Arabidopsis cytokinesis. Both vesicle tethering complexes participate in the initiation of cytokinesis – assembly of phragmoplast. In the expansion phase TRAPP dominates

the process, while during new cell wall insertion and maturation exocyst is maximally present [534].

Using high resolution Total Internal Reflection Fluorescent Microscopy/Variable Angle Microscopy (TIRF/VAEM), we described for the first time the eukaryotic exocyst complex dynamics at the cytoplasmic membrane [356]. Along with the expected proof of significant co-localization with exocytotic v-SNARE, half-life and co-localization of exocyst subunits indicate, that there is also possible vesicles independent dynamics of the assembled complex at the membrane [356].

Phenotypic deviations of our first Arabidopsis exocyst mutant *exo70A1* showing reduced apical dominance and impaired root and root hairs growth prompted us to look into the possible participation of exocyst in polar auxin transport regulation. Using variety of methods including radioactive auxin transport assays we for the first time show the importance of exocyst complex for the recycling and cellular localization of PIN auxin efflux carriers and regulation of polar auxin transport [369].

We also documented specific participation of vesicles tethering complex exocyst in cell wall pectins deposition on the model of seed coat maturation in Arabidopsis – another evidence for the exocyst engagement in cell wall biogenesis. New plant-specific interactor of exocyst RHO1 was described in this study – possibly a candidate for negative regulator of plant secretory pathway [45].

We consider our discovery that EXO70B1-containing exocyst subcomplex plays a role in the Golgi-independent autophagic transport into the vacuole as possibly the most important one from our laboratory over the last years [383]. The *exo70B1* mutant has spontaneous leaf lesions/hyper sensitive reaction due to overaccumulation of salicylic acid and anthocyanin accumulation defect [383]. It is possible, that autophagy-related endomembrane transport is a hidden and so far neglected branch of the plant membrane trafficking [488].

Our report showing for the first time an active role of plant exocyst complex in defense against both bacterial and fungal pathogens points to a close homolog of EXO70B1 – EXO70B2 [167]. Along with EXO70H1 we describe their transcriptional pathogen inducibility and demonstrate, that respective Arabidopsis mutants are significantly more sensitive to *Pseudomonas syringiae* and produce abnormal defensive papillae in response to *Blumeria graminis* [167]. Working on phytopathogen interactions context of exocyst complex we discovered also a direct interaction between the SNARE protein, SNAP33 with EXO70B1 and EXO70B2 [167].

In collaboration with the Trujillo lab at the IPB Leibnitz inst. in Halle, Germany we contributed to the follow up discovery of EXO70B exocyst subunits as a subject to specific E3 ligase ubiquitination-dependent regulatory degradation in biotic interactions [313]. Also extraordinary evolutionary dynamics of exocyst subunits, especially EXO70s - possibly driven by competition between host and parasite - indicates an involvement in the plant-microbe interactions [229].

In collaboration with Andrea Genre from University of Torino we showed participation of exocyst in the perifungal membrane biogenesis during the symbiosis establishment [240].

Our efforts to study functions of exocyst using phenotypic analyses of Arabidopsis T-DNA mutants resulted in the uncovering of an unrecognized and therefore un-annotated gene duplication of SEC10 locus [560].

As exocyst was discovered as an effector of RAB and RHO GTPases we are studying in our lab also some aspects of their cell biology related to the regulation of secretory pathway. RAB GTPases are post-translationally modified by Geranylgeranyl transferase. Using LOF Arabidopsis mutant in one of two beta-subunits of this transferase we published a first report on RAB GTPases prenylation modifying complex in plants[22]. Along with expected biochemical defect in beta-subunit Arabidopsis mutant resulting in a agravitropic shoot, it uncovered a surprising developmental aspect of RAB function in switch between etiolation and photomorphogenesis, supported by our transcriptomic data used to interpret this result [22].

In collaboration with the laboratory of Attila Feher at the BRC, Szeged, Hungary we contributed to the characterization of ROP6 activity regulation by phosphorylation [124]. An important contribution of ROP GTPases activity (along with other factors) we observed also in case of the NADPH oxidase activity regulation in pollen tubes [298].

We have also adopted over last years moss *Physcomitrella* patens as an ideal model to study exocyst functions in cell polarity and morphogenesis and are preparing first data to be published (Brejšková *et al.* in prep.; Rawat *et al.* in prep.).

Crucial aspect of cell polarity reciprocally connected to the targeted secretion is the functioning of cytoskeleton – especially a F-actin one. Crucial F-actin nucleators in plants are formins – studied in collaboration with the group of Fatima Cvrčková at Charles university, Prague. New specific interaction domain (GOE) in plant class I F-actin nucleators formins was unexpectedly uncovered in collaboration with the laboratory of Patrick Hussey (Durham university, UK); it mediates interaction with microtubular cytoskeleton [9]. This new link between F-actin and microtubular cytoskeletons is crucial to understand their interactions with the endomembranes, as GOE-domain formins are anchored into the lipid membranes via transmembrane domain.

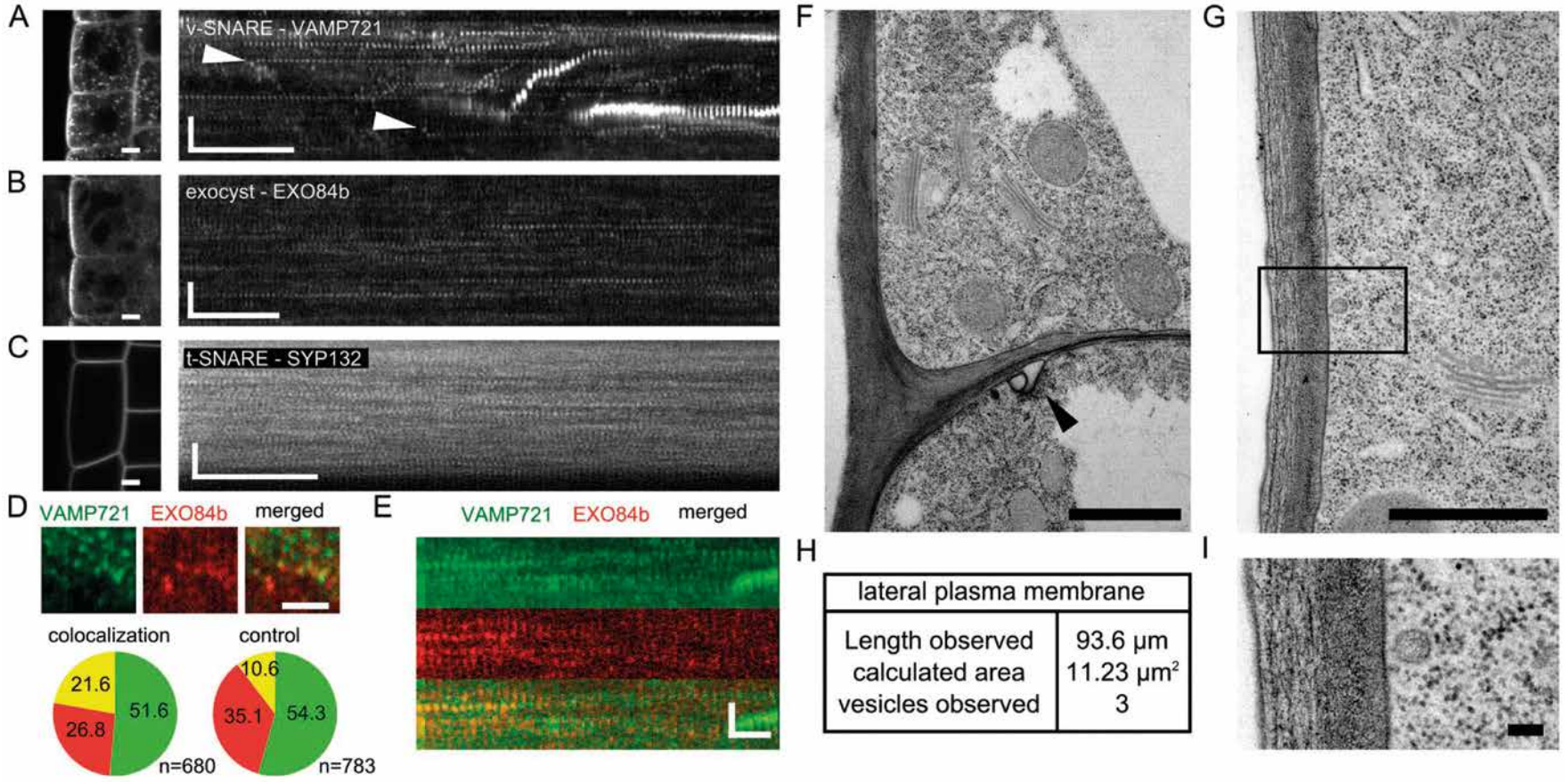

Figure 1: **Colocalization of exocyst foci with vesicle marker and electron microscopy analysis of the lateral plasma membrane of root epidermal cells.** (A–C) Comparison of VAMP721 (A), exocyst foci (B), and SYP132-GFP (C) CLSM localization (left) and dynamics visualized by VAEM (right). GFP-VAMP721 localizes to epidermal PM and endosomes and EXO84b-GFP signal is prominent at the outer epidermal PM, whereas SYP132-GFP is evenly distributed along the entire PM; the seemingly stronger signal of the intercellular membranes results from summing of the adjacent PM signal. Kymographs demonstrate that VAMP721 and exocyst label PM-localized foci with similar appearance (A, B). VAMP721 foci dwelling at the PM are preceded by movement of the foci (arrowheads). Motile foci and endosomes are visible in the kymograph (B). SYP132-GFP (C) is highly dynamic compared with EXO84b-labeled foci. Scale bars, 5 µm (left); horizontal and vertical bars (right) represent 5 s and 3 µm, respectively. (D) Colocalization of GFP-VAMP721 and EXO84b-mRFP foci (scale bar, 2 µm), and quantification (%) of the colocalization (left). The random overlap quantification is shown on the right. (E) Kymographic representation of the colocalization between GFP-VAMP721 and EXO84b-mRFP; horizontal and vertical bars represent 10 s and 2 µm, respectively. (F, G) HPF-AFS electron microscopy analysis of the lateral PM of Arabidopsis root epidermal cells. (H) Table summarizing the length and area of lateral PM analyzed and number of visible vesicles. From the actual vesicle number observed it is clear that only a subset of exocyst foci are tethering a vesicle. An example of vesicle tethered at the PM is shown in G; note also the presence of numerous vesicles in the cytoplasm close to the Golgi. (I) Magnified inset from (G); the distance of the vesicle from the PM is 23 nm. Scale bars, 1 µm in F and G and 100 nm in I. Reproduced from [356].

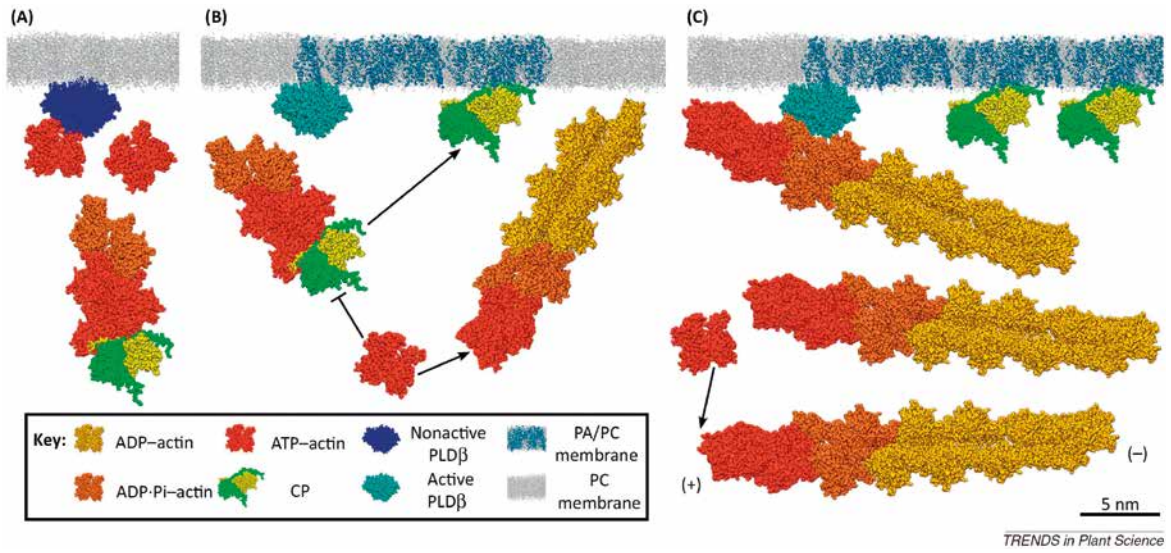

Figure 2: **A positive feedback loop model of actin dynamics regulation by PLDβ and PA.** (A) Monomeric actin binds and inhibits PLDβ. Actin is mainly in monomeric form or as short filaments. Actin polymerization is blocked by CP heterodimer binding to the plus end of the filament. (B) Activation of PLDβ leads to localized PA production; CP binds to PA, and the barbed end of the actin filament is released to polymerize into longer filaments. The barbed end of actin filaments prefers to add ATP–actin monomers, whereas the minus or pointed end of filaments loses ADP–actin. (C) PLDβ binds to and is further activated by actin filaments. Elevated PLDβ activity causes local enhancement in PA concentration and more CP is bound to the membrane. The inhibition of CP by PA results in increased F-actin levels, which further activates more PLD molecules, resulting in a positive feedback loop. Abbreviations: CP, capping protein; PA, phosphatidic acid; PC, phosphatidylcholine; PI, phosphate; PLD, phospholipase D. Reproduced from [407].

One of our major interests in the Laboratory of Cell Biology is the regulatory relationship between secretory pathway, membrane lipids and cytoskeleton. In collaboration with the laboratory of Chris Staiger at Purdue we made major progress in the analysis of plant actin cytoskeleton regulation by membrane lipid phosphatidic acid (PA) and phospholipase D (PLD).

We characterized the mutual interaction and regulation between F- or G-actin and PLDβ activity. We then identified the PLD actin-binding domain and using sequence-, structure- and mutational analysis we characterized PLD-actin binding in detail. Polymeric F-actin binding stimulates PLDβ activity and production PA; while interaction with monomeric G-actin inhibits PLD activity and PA production [63]. This report was done in collaboration with the Laboratory of signal transduction (IEB) and Institute of Chemical Technology (lab of O. Valentová). Based on published data on the regulation of actin polymerization by PA through inhibition of actin capping protein (CP) interaction with actin (Staiger laboratory – see further) we proposed and experimentally tested in pollen tubes a specific positive feed-back loop between F-actin and PLDβ activity [63].

Using combination of experimental evidence and methods of molecular dynamics computations recently introduced in our laboratory, we reported detailed insight into the molecular mechanism of CP-mediated actin regulation via interaction with PA and phosphatidylinositol (4,5)-bisphosphate (PIP_2). We explained enhanced affinity of plant CP to PA, which is evolutionary unique [295]. By analysing PA turnover through distinct signaling pathways we discovered that multiple aspects of tip growth machinery are distinctly regulated through various PA pools [577].

The understanding of PA-enriched membrane domains functioning in plant cells is hampered by a lack of useful PA marker. We established and verified genetically-encoded fluorescent marker for sub-population of PA in plant cells, which is based on the specific PA-binding protein domain of yeast SNARE protein Spo20p (from the laboratory of Nicolas Vitale, Strasbourgh). We documented specific overaccumulation of PA in endocytic subapical pollen tubes domain and we described specific PA-PIP_2 colocalization restricted to the secretory domain at the cell apex [525].

The progress in this new field of cytoskeletal regulation (both actin and microtbular) by PA was summarized in a joint review with the laboratory of Chris Staiger [407]. This along with reports on PA turnover [577], PA and PIP_2 effect on NADPH oxidase activity in pollen tubes [298] and especially recently developed computational molecular dynamics approaches [295] opens both conceptually as well as methodologically new avenues for the multiscale analyses of membrane lipids-proteins interface functioning in the regulation of the cell polarity and morphogenesis.

Research projects: 3, 21–28

Laboratory of Growth Regulators

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Second row: Pharm.Dr. Lubor Urbánek Ph.D. /Researcher, Mgr. Jakub Hrdlička /PhD Student, Asta Zukauskaite Dr., Ph.D. /Researcher, Mgr. Marie Vitásková /Researcher, Eva Hirnerová /Technician, Mgr. Kateřina Šmídová /Research Assistant, Mgr. Zuzana Skrášková /PhD Student, Mgr. Martin Hönig /PhD Student, Mgr. Jana Oklešťková, Ph.D. /Researcher, Mgr. Lucie Rárová, Ph.D. /Researcher, Mgr. Ota Blahoušek /Research Assistant, doc. RNDr. Martin Fellner, Ph.D. /Associate Professor
Third row: Mgr. Aleš Pěnčík, Ph.D. /Researcher, Ing. Věra Doleželová /Research Assistant, Mgr. Jiří Skořepa /Researcher, Mgr. Ivan Petřík /Research Assistant, Mgr. Andrea Novotná /Researcher, Mgr. Jan Buček /PhD Student, Bc. Dita Jordová /Technician, Mgr. Barbara Nardelliová /Researcher, Mgr. Alena Kadlecová /Researcher
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Not in the picture: Jitka Hansgutová, DiS /Secretary, doc. RNDr. Jitka Frébortová, Ph.D. /Associate Professor, doc. RNDr. Jan Krekule, DrSc. /Associate Professor, Mgr. Karel Doležal, Dr. DSc. /Researcher, RNDr. Miroslav Kvasnica, Ph.D. /Researcher, Ing. Ludmila Ohnoutková Ph.D. /Researcher, Mgr. Lucie Plíhalová, Ph.D. /Researcher, RNDr. Jiří Pospíšil, Ph.D. /Researcher, Mgr. Jiří Voller, Ph.D. /Researcher, Mgr. Zdeňka Kamarádová /Research Assistant, Ing. Jakub Vylíčil /Research Assistant, Olga Hustáková /Technician, Bc. Jana Kočířová /Technician, Pavel Sedláček /Technician, Mgr. Ondřej Bíba /PhD Student, Mgr. Tomáš Vlčko /PhD Student

Research at the Laboratory of Growth Regulators (LGR) is directed to biomolecules: structure, analysis and activity and, molecular and cellular mechanisms of action as well as applications in various fields. LGR pursues research mainly on cytokinins but recently on other groups of plant growth regulators as well. One globally renowned contribution of the LGR in this field, is expansion of a number of cytokinins, especially the aromatic cytokinins and their olomoucine-derived derivatives. These compounds are used in cancer treatment. Olomoucine was the first in a line of anti-tumor agents derived from cytokinins. The development of other, more effective inhibitors of cyclin-dependent kinases, key enzymes in the cell division cycle, followed, such as bohemine, roscovitine, olomoucine II and others . Roscovitine is completing phase II clinical trials for cancer treatment in Europe and in the USA. The development of anti-cancer drugs is not the only field that the LGR conducts advanced research in. It is also successful in the agricultural research area. For example, we discovered how to increase endogenous cytokinins using an inhibitor of cytokinin oxidase/dehydrogenase called INCIDE, which supports growth. Owing to this discovery, we were able to increase the yield of a number of agricultural crops and plant stress resistance. Recently, we developed a product which restores the skin to its youthful state and aids in the treatment of skin diseases. Cytokinins which also retard ageing in humans, were used in this development. The product with the trade name Pyratine not only treats skin roughness, wrinkles, and

pigmentation, it is also effective for treating various forms of acne. LGR engages in scientific research especially in the preparation of new, purine-based growth regulators with potent biological activities, the development of relevant analytical methods, study of the functions and effects on growth and developmental processes in normal and tumor cells, including the development of anti-tumor agents derived from plant hormones. Research on tumor suppressor genes, mechanisms that regulate their expression and the design of mutant organisms with controlled gene expression, are included in our scientific profile.

New phytohormone probes and biomolecules

New phytohormone standards, probes and labelled derivatives

Our laboratories have long standing experience in organic synthesis, labelling of phytohormones and production of heavy and radioactively labelled phytohormones [2, 61, 79, 88, 92, 93, 95, 140, 203, 215, 221, 251, 286, 318, 375, 431, 444, 465, 564]. For example, we developed a bioactive, fluorescent BR analogue, Alexa Fluor 647-castasterone (AFCS), and we visualized the endocytosis of leucine-rich repeat receptor-like kinases in plants, BRASSINOSTEROID INSENSITIVE 1 (BRI1)-AFCS complexes in living *A. thaliana* cells. To the best of our knowledge, our findings provide the first visualization of receptor-ligand complexes in plants and reveal clathrin- and ARF-GEF-dependent endocytic regulation of BR signalling from the plasma membrane [155]. We also described a new reversed phase HPLC-MS detection method for quantifying intact cytokinin nucleotides in human K-562 leukaemia cells. Identification of the intracellular metabolites was confirmed by synthesis [2]. We also published the first analysis of the relationship between the chemical structure of cytokinins and their cytotoxic effects against a panel of human cancer cell lines with diverse histopatotological origin. Most cell lines showed greatest sensitivity to *ortho*-topolin riboside. The study showed that the structural requirements for the cytotoxic activity of cytokinins against human cancer cell lines differed from their activity in plant bioassays [93]. A capillary zone electrophoresis (CZE) method for separation of adenosine and isopentenyladenosine (cytokinin) nucleotides (prepared for the first time) was developed, optimized and validated. The identities of the reaction products: isopentenyladenosine di- and triphosphate were confirmed by HPLC-QqTOE-MS [215]. We also revealed that an ATP-binding cassette transporter in Arabidopsis, AtABCG14, is essential for the acropetal (root to shoot) translocation of the root-synthesized cytokinins. In planta feeding of new C-14 or C-13-labelled tZ, suggests that it acts as an efflux pump and its presence in the cells directly correlates with the transport of the fed cytokinin. For this reason, AtABCG14 is a transporter likely involved in the long-distance translocation of cytokinins in planta [564]. We developed a sensitive mass spectrometry-based method to simultaneously profile the majority of known auxin precursors and conjugates/catabolites in small amounts of Arabidopsis tissue. The method also includes a new derivatization technique for quantification of the most labile of the auxin precursors and new labelled IAA derivatives [286].

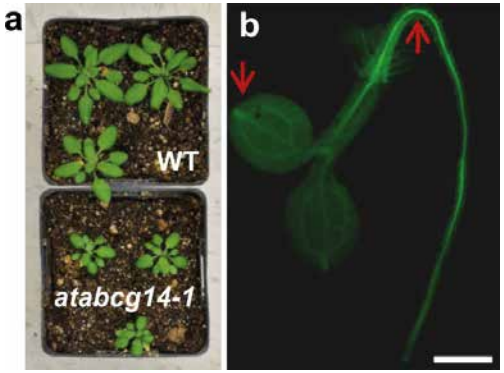

Figure 1: Phenotypes of atabcg14 mutant and localization of AtABCG14. (a) 25-DAG wild-type (above) and *atabcg14-1* (below) mutant plants. (b) Distribution of GFP signals in a 4-DAG AtABCG14::EGFP-ABCG14 transgenic seedling. Arrow indicates the primary expression in roots. Scale bar, 500 µm.

New compounds modulating phytohormone perception, biosynthesis and degradation

Recently, we have contributed to studies of transgenic plants with cytokinin receptor loss-of-function mutations [32, 328], plants with mutations in cytokinin-synthesizing genes [381, 494], and cytokinin-deficient plants with genetically enhanced cytokinin degradation [20, 41, 97, 111, 278, 308, 388, 396, 430, 481]. These studies showed that such changes lead to distinct alterations in shoot growth parameters, retarded leaf senescence, increased seed size, accelerated germination and enhanced root systems. Chemical inhibitors of cytokinin perception, biosynthesis and degradation are thus very promising as powerful tools for studying further the mechanism of cytokinin action as an alternative to genetic approaches. Further, they would be expected to influence plant growth and development and might thus find interesting applications as growth regulators for modifying traits in crop plants. Several compounds regulating both the perception and metabolism of brassinosteroids and cytokinins have been developed over the last five years [36, 155, 156, 205, 297, 418] (*for patents see* [*1, 5, 12, 13, 14, 15, 16, 17, 18, 19, 22, 23, 26, 27, 28, 29*] *and* ***www.espacenet.com***) and their beneficial activity for plant growth and development have been described. Recently we reported

6-(2-hydroxy-3-methylbenzylamino)purine (PI-55) as the first molecule to antagonize cytokinin activity at the receptor level. The effect of INCYDE at 10 nM on growth, biochemical and photosynthetic efficiency in sodium chloride (NaCl)-stressed tomato plants was investigated [444]. Wealso reported the synthesis and *in vitro* biological testing of eleven BAP derivatives substituted in the benzyl ring and in the C2, N7 and N9 positions of the purine moiety. 6-(2,5-Dihydroxybenzylamino)purine (LGR-991) was identified as a cytokinin receptor antagonist. At the molecular level, LGR-991 blocks the cytokinin receptor CRE1/AHK4 with the same potency as PI-55 [55]. From X-ray structure, NMR and stability-in-solution study of 6-(furfurylamino)-9-(tetrahydropyran-2-yl) purine (Pyratine), a new very active cytokinin derivative was determined [95]. We further prepared a series of eight N9-substituted kinetin derivatives, and characterized them with available physicochemical, biochemical and biological assays [156]. A series of isopentenyladenine (iP) derivatives specifically substituted at the N9 atom of purine moiety by tetrahydropyran-2-yl, ethoxyethyl, and C2-C4 alkyl chains terminated by various functional groups were prepared. The rationale for this design was to reveal the relationship between specific substitution at the N9 position and cytokinin activity [155]. A sensitive and reliable high-performance liquid chromatographic method with tandem mass spectrometric detection has been developed and used for the determination of 2-methylthio-cytokinin derivatives produced by the phytopathogenic actinomycete *Rhodococcus fascians*. New 2-methylthio- CK probes were prepared for this study [88]. An inhibitory investigation with a large number of urea derivatives was undertaken using he maize cytokinin oxidase/dehydrogenase (ZmCKO1) and the crystal structure of ZmCKO1 in a complex with CPPU was solved. Subsequently, site-directed mutagenesis of L492 and E381 residues involved in inhibitor binding was performed. All studied compounds were further analysed for cytokinin activity [36]. The comprehensive screen through land plants is presented suggesting that cytokinins (CKs) of the *cis*-zeatin (cZ)-type occur generally in the plant kingdom. Survey of employed bioassays illustrates the ability of high dose cZ-type CKs to induce various physiological responses and CK signalling. These data argue against the image of cZ-type CKs as the non-active or weakly active natural adjuncts to the *trans*-isomers suggesting their conceivable function as delicate regulators of CK responses in growth-limiting conditions [126]. We also investigated the effect of meta-topolin tetrahydropyran-2-yl – a novel derivative of the aromatic cytokinin *meta*-topolin on shoot proliferation, photosynthetic pigment content, phytochemicals and antioxidant activity of two widely used medicinal plants, *Aloe arborescens* and *Harpagophytum procumbens* [443]; tissue-cultured and acclimatized 'Williams' bananas subjected to new cytokinin treatments – 6-(3-methoxybenzylamino)-9-tetrahydropyran-2-ylpurine [446].

Chemical modulators of kinases (cytokinin-derived)

Over the last five years, we have continued development of increasingly effective cyclin-dependent-kinase (CDK) inhibitors, leading to the discovery of several other potent compounds with various structural motifs [21, 27, 135, 138, 359, 366, 437, 479, 558]. The potential of CDK inhibitors in different therapeutic areas has also been reviewed several times [43, 44, 254, 268]. New generations were prepared following well-established methods, including our previously described syntheses of purines, pyrazollo[4,3-d]pyrimidines, 8-azapurines and arylazopyrazoles (*for patents see* [*6, 7, 8, 9, 20, 21, 24*] *and* ***www.espacenet.com***). Selected examples are enclosed: A series of 1,5-diaryl-3-(3,4,5-trihydroxyphenyl)-1H-pyrazolo[4,3-e][1,2,4]triazines [21] and 3-(2-pyridyl)-6-(hetero)aryl-1H-pyrazolo[4,3-c]pyridines [558] were synthesized and their kinase inhibitory activity and cytotoxicity against several cancer cell lines has been evaluated. A new potent CDK2 inhibitor with pyrazolo[4,3-d]pyrimidine scaffold has been synthesized, characterized, and evaluated in cellular and biochemical assays [138]. For a series of roscovitine derivatives bearing the 2-(hydroxyalkylamino) moiety, cytotoxic potency strongly correlated with anti-CDK2 activity. The most potent compounds were investigated further to assess their ability to affect cell cycle progression, p53-regulated transcription and apoptosis [437]. A series of 2,9-substituted 6-guanidinopurines, structurally related to the CDK inhibitors olomoucine and roscovitine, have been synthesized and characterized. Their increased inhibitory activity and decreased selectivity offer a good starting point for further development of new protein kinase inhibitors [352]. Recently, we synthesized and screened a novel series of 2-substituted-6-biarylmethylamino-9-cyclopentylpurine derivatives for improved CDK inhibitory activity and antiproliferative effects. [359]. We further focused on the efficacy of the novel compounds BA-12 and BP-14 that antagonize CDK1/2/5/7 and CDK9. Inhibition of these CDKs in human hepatocellular carcinoma cell lines reduced the clonogenicity by arresting cells in S-G(2) and G(2)-M phase of the cell cycle and inducing apoptosis. In contrast, primary human hepatocytes failed to show cytotoxicity and apoptosis. *In vivo* treatment of xenografted human hepatocellular carcinomas with BA-12 or BP-14 effectively repressed tumour formation [361]. We also showed that roscovitine and TRAIL demonstrate synergistic cytotoxicity in hematologic malignant cell lines and primary cells. Pre-treatment of TRAIL-resistant leukemia cells with roscovitine induced enhanced cleavage of death-inducing signalling complex-bound

proximal caspases after exposure to TRAIL [392]. We analysed the effect of inhibition of CDKs by olomoucine II on gene expression from viral promoters. We found that both roscovitine and olomoucine II blocked the phosphorylation of RNA polymerase II C-terminal domain. However the repression of genes regulated by viral promoters was strongly dependent on gene localization – expression only when the viral promoter was not integrated into chromosomal DNA [470]. We further reported that new CDK9 3,5-diaminopyrazole inhibitor CAN508 inhibits endothelial cell migration and tube formation. In addition, it reduces phosphorylation of the C-terminus of RNA polymerase II and inhibits mRNA synthesis in endothelial cells. It has high selectivity towards the positive transcriptional regulator P-ular endothelial growth factor in several human cancer cell lines [146]. We also described a novel member in the library of the arylazo-3,5-diaminopyrazole family, AAP1742, that reduces the viability of multiple myeloma cell lines in low micromolar concentrations. Consistent with the inhibition of CDK9, AAP1742 decreases the phosphorylation of RNA polymerase II and inhibits mRNA synthesis of anti-apoptotic proteins Mcl-1, Bcl-2, and XIAP, followed by apoptosis in the RPMI-8226 cell line in a dose- and a time-dependent manner [479]. Recently, we showed that roscovitine exerts potent antiangiogenic effects and found Cdk5 to be a new player in angiogenesis. We also reported the antiangiogenic profile of 15 derivatives of roscovitine *in vitro* and *in vivo* and provided structure activity relationships of roscovitine analogues [148]. We also demonstrated that trisubstituted pyrazolo[4,3-d]pyrimidines constitute a novel class of compounds which potently inhibit angiogenesis [434]. We pharmacologically characterized N-5-(2-aminocyclohexyl)-N-7-benzyl-3-isopropyl-1(2)H-pyrazolo[4,3-d]pyrimidine-5,7-di-amine (LGR1406), a novel derivative of the CDK inhibitor roscovitine (ROSC), in PDGF-BB-activated VSMC. Abnormal vascular smooth muscle cell (VSMC) proliferation contributes to the pathogenesis of restenosis. Thus, drugs interfering with cell cycle progression in VSMC are promising candidates for anti restenotic therapy [78]. We also reported the results of screening of new anti-leishmanial drugs among 2,6-disubstituted purines and corresponding 3,7-disubstituted pyrazolo[4,3-d] pyrimidines. Since some compounds reduced the viability of axenic amastigotes of *Leishmania donovani*, we screened them for interaction with recombinant leishmanial cdc-2 related protein kinase (CRK3/CYC6). Some compounds (9A, 12A and 13A) show activity against amastigotes with EC(50) in a range 1.5–12.4 μM [137]. To determine which CDKs were involved in regulating neutrophil lifespan, we first examined CDK expression in human neutrophils and found that only CDK5, CDK7 and CDK9 were expressed in these cells. Treatment of neutrophils with a potent CDK9 inhibitor increased apoptosis and caused a rapid decline in the level of the anti-apoptotic protein Mcl-1, while Bcl2A was unaffected. We propose that CDK9 activity is a key regulator of neutrophil lifespan, preventing apoptosis by maintaining levels of short-lived anti-apoptotic proteins such as Mcl-1. Furthermore, CDK9 represents a novel therapeutic target in such diseases [332].

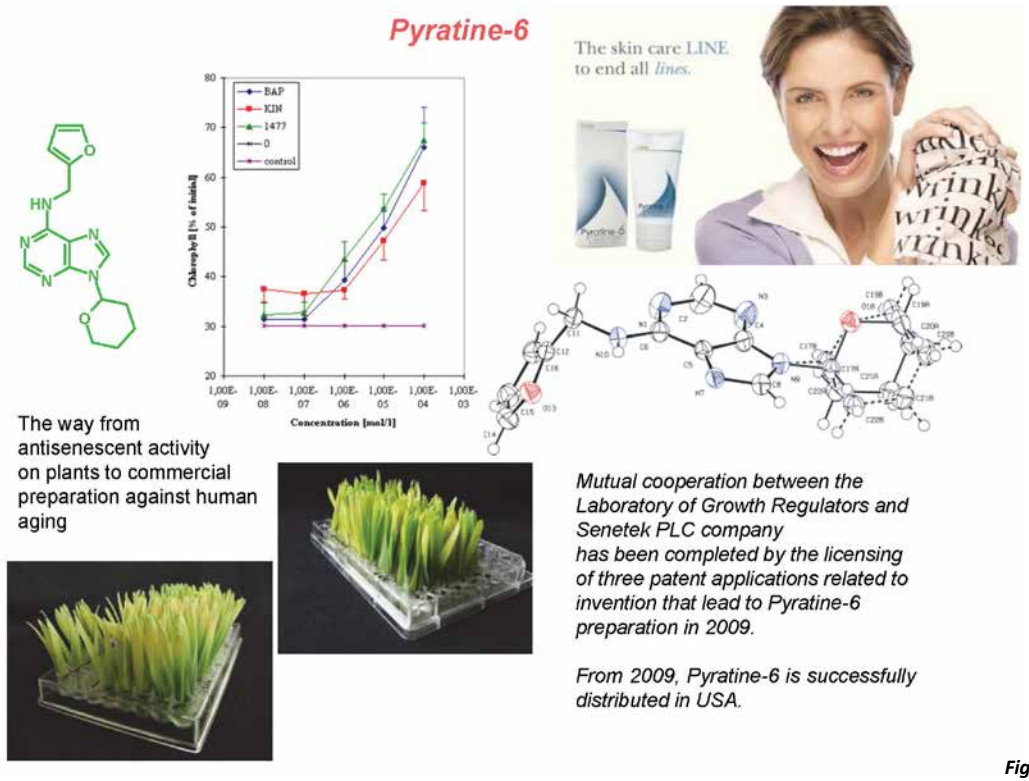

Figure 2

New phytohormone bioanalytical methods and their applications

In order to understand better the network regulation of hormone action, we need to measure multiple hormone concentrations simultaneously, i.e. characterize the 'hormone-metabolome'. Most plant hormones are found in plant tissues in extremely low concentrations which makes qualitative and quantitative analysis difficult and therefore very sensitive analytical tools are required. The analysis of plant hormones is challenging not only because these compounds are present in trace amounts but also because many other substances in plant extracts interfere with the analysis, such as pigments, lipids, phenolics and proteins. Currently, the most suitable and most used analytical technology for phytohormone analysis is based on liquid chromatography-tandem mass spectrometry ((U)HPLC-MS/MS) as evidenced in our reviews [290, 296, 551]. Since 2008, this methodology has gradually been developing in LGR for plant hormone analyses (cytokinins, auxins, JAs, ABAs, gibberellins, brassinosteroids, phenolics, intact cytokinin nucleotides in human K-562 leukemia cells, 2-methylthio-cytokinin derivatives produced by the phytopathogenic actinomycete *Rhodococcus fascians*, roscovitine oxidation products, isoflavonoids and other phenylpropanoids) [140, 300, 431, 465]. Further, analysis of cytokinin nucleotides by capillary zone electrophoresis with diode array and mass spectrometric detection as well as LC-NMR, has also been introduced [215, 365]. Plant products can be extracted efficiently from plant tissue by supercritical carbon dioxide technology. We have applied this technology to investigate plant phytosterols and phytoecdysteroids. Supercritical carbon dioxide also offers the possibility of mediating enzymic reactions. Examples of this research appear in our papers [71, 99]. The ability of LC-NMR to detect simultaneously free and conjugated phytosterols in natural extracts was tested. The results of qualitative and quantitative analyses are in a good agreement with the literature [365].

We were able to develop a new separation technology UHPLC. UHPLC uses columns packed with sub-2µm particles which results in higher peak capacity, greater resolution, and increased sensitivity compared to HPLC. As a result the analytical parameters of mass spectrometry measurements are significantly enhanced after implementation of UHPLC. Few publications to date have described the use of this analytical technique for qualitative and quantitative analysis of plant extracts [2, 88, 286, 318, 402]. Mass spectrometry has developed towards increasingly higher sensitivity and selectivity in the analyses, which now makes it possible to perform tissue and cell specific quantification of phytohormones and different phytohormone metabolites – simultaneous profile of the majority of known auxin precursors and conjugates/catabolites (auxin metabolome) in small amounts of Arabidopsis tissue [286, 402]. For minute tissue samples, miniaturization of the extraction and purification steps can improve the sensitivity of the analytical method, since it can minimize analyte losses due to adsorption to surfaces and/or increase analyte recovery in the solid phase extraction (SPE) step [318].

The application of new technologies has led to several important discoveries. For example:

1) The phytopathogenic actinomycete *Rhodococcus fascians* D188 secretes six cytokinin bases that synergistically redirect the developmental program of the plant

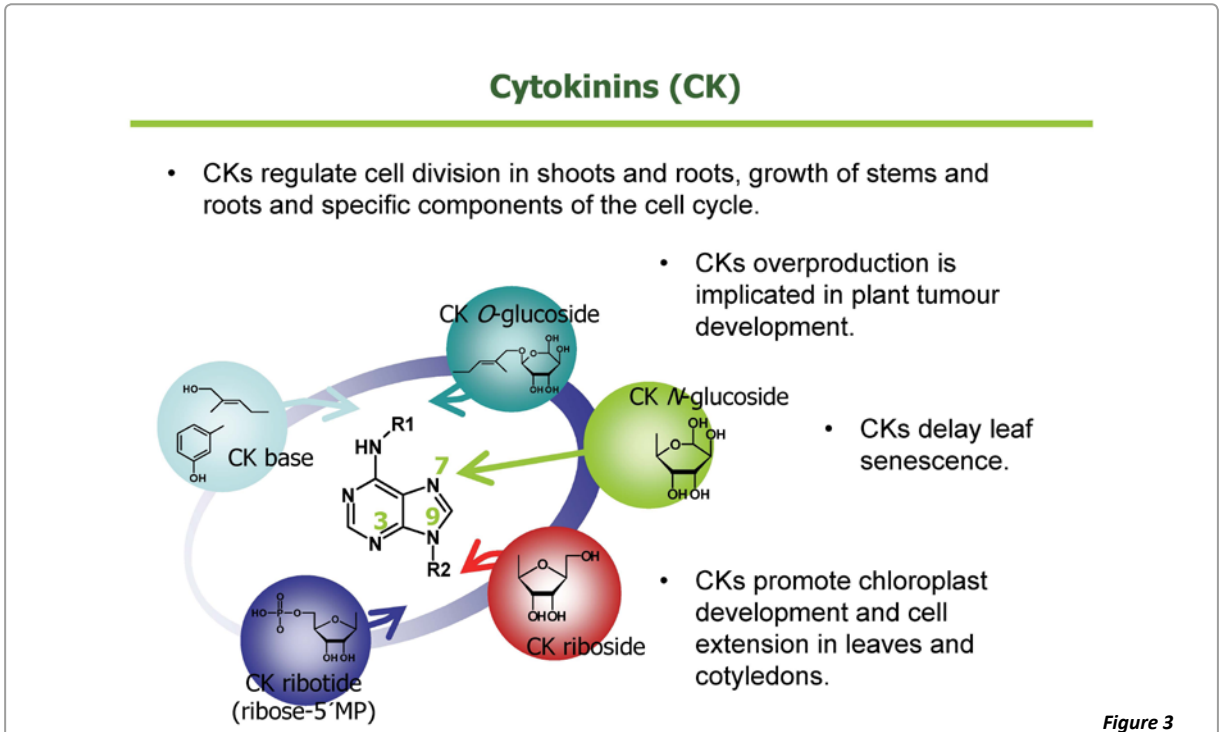

Figure 3

to stimulate proliferation of young shoot tissue, thus establishing a leafy gall as a niche [61]. Typical symptoms of *Verticillium longisporum*-induced disease are stunted growth and leaf chlorosis. Our analyses show that, concomitant with the development of chlorosis, levels of tZ decrease in infected plants. Stabilization of Arabidopsis cytokinin levels by both pharmacological and genetic approaches, inhibited *Verticillium* proliferation and this coincided with reduced disease symptom development [418]. Cytokinins (CK) play an important role in the formation of nitrogen-fixing root nodules. CK profiling showed that the most abundant CKs secreted by Bradyrhizobium sp. strain ORS285 are the 2-methylthio derivatives of tZ and iP. In their pure form, these CKs can activate legume CK receptors *in vitro*, and their exogenous addition induced nodule-like structures on host plants. [408].

2) Endogenous cytokinins (CKs), auxins, and abscisic acid (ABA) were identified and quantified in 11 red algae collected from the Brazilian coast. These results confirm that plant hormones are common constituents of red seaweeds, with this being the first report of the occurrence of ABA in Rhodophyta [101]. Next, the endogenous auxins and cytokinins were quantitated in 24 axenic microalgal strains from the Chlorophyceae, Trebouxiophyceae, Ulvophyceae, and Charophyceae. IAA and IAM were present in all microalgal strains; nineteen cytokinins were identified in the microalgal strains [426]. Endogenous gibberellins and brassinosteroids were also quantified. Between 18 and 20 gibberellins were quantified in all strains.

GA profiles were similar in all strains and the active GA detected in the highest concentration was GA(6), the predominant intermediates were GA(15) and GA(53) and the main biosynthetic end products were GAB(13) and GA(51). Brassinolide and castasterone were determined in all strains [425]. The effect of light on growth and endogenous phytohormone concentrations in *Chlorella minutissima* MACC 360 was also investigated [547]. It was also our aim to quantify plant growth regulators ABA, GAs and brassinosteroids present in *E. maxima* and Kelpak as a biostimulant used in agriculture [546]. In the oleaginous eustigmatophyte *Nannochloropsis oceanica* IMET1, UHPLC-MS/MS also detected a wide array of plant hormones. The presence of such functional flowering plant-like phytohormone signalling systems in *Nannochloropsis* sp. suggests a much earlier origin of phytohormone biosynthesis and degradation than previously believed [499].

3) Furthermore, cytokinin metabolism and function were analysed in different plant tissue cultures. In the three types of embryogenic and non-embryogenic calli, all cytokinins were found in each type. These results suggest that the difference in somatic embryo formation capacity observed between embryogenic and non-embryogenic calli is related to their endogenous cytokinin content [70]. Changes in cytokinin (CK) profiles and their physiological implications in micropropagated *Harpagophytum procumbens* [(Burch.) DC. ex Meisn.] tissues in relation to shoot-tip necrosis (STN) and CK treatments were studied. We also assessed the use of topolins in PTC with emphasis on their metabolism, structure-activity relations and effect on morphogenesis *in vitro* [109, 205, 337, 395], on micropropagation of 'Williams' bananas [207, 206, 209, 336, 446], on the micropropagation efficiency and shoot quality of smoke bush (*Cotinus coggygria* S cop.) 'Royal Purple' [297], on the *in vitro* multiplication and senescence of wych elm (*Ulmus glabra* Huds.) [390], on the micropropagation of *Aloe arborescens* and *Harpagophytum procumbens* [443], on the micropropagation of *Hypoxis hemerocallidea* Fisch [513], and on phytochemical levels and antioxidant potential in greenhouse grown *Merwilla* [445]. The endogenous cytokinin and auxin levels were also analysed during adventitious caulogenesis in *Pinus pinea* cotyledons [226], during *in vitro* organogenesis from vegetative buds of *Pinus radiata* adult trees [394], in *in vitro* cultures and inflorescences from normal and mantled oil palm (*Elaeis guineensis* Jacq.) [400], after exogenously applied cytokinins in micropropagated *Merwilla plumbea* [447].

4) In Arabidopsis and most plant species, dormancy absolutely requires an unidentified seed coat germination-repressive activity and constitutively higher abscisic acid (ABA) levels upon seed imbibition. We developed a "seed coat bedding" assay monitoring the growth of dissected embryos cultured on a layer of seed coats. This assay, combined with direct ABA measurements, revealed that, upon imbibition, dormant coats, unlike nondormant coats, actively produce and release ABA to repress embryo germination, whatever the embryo origin [48]. Using a seed coat bedding assay, we further showed that canopy light specifically inactivates phyB activity in the endosperm to override phyA-dependent signalling in the embryo. Under the canopy, endospermic ABA opposes phyA signalling through the transcription factor (TF) ABI5, which shares with the TF PIF1 several target genes that negatively regulate germination in the embryo; ABI5 enhances the expression PIF1, SOMNUS, GAI, and RGA genes but also of ABA and GA metabolic genes [275]. Using *Lepidium sativum* as a model target species, experiments were conducted to investigate how environmental cues modulate MyA's interference with key processes of seed germination. Testa permeability and early water uptake by imbibition is enhanced by myrigalone A (MyA). During late germination, MyA also inhibits endosperm weakening and embryo growth [330]. *Tagetes minuta* L. achenes are thermoinhibited at temperatures above 35 °C and have accelerated radicle emergence (germination) when subsequently

transferred to an optimal temperature (25 °C) – endogenous cytokinins and cytokinin oxidase/dehydrogenase (CKX) activity were compared [315]. The aims of a further study were to monitor endogenous cytokinin levels during germination and early seedling establishment in oats, maize, and lucerne [316].

5) In Arabidopsis, AHK2 and AHK3 were found to be primarily involved in mediating cold, to express A-type ARRs despite CK deficiency - cold might induce ARR expression via the AHK2 and AHK3 proteins. These results suggest that AHK2 and AHK3 and the cold-inducible A-type ARRs play a negative regulatory role in cold stress signalling via inhibition of the ABA response, occurring independently of the cold acclimation pathway [32]. In subsequent report, the question was addressed whether AHK2, AHK3,and CRE1/AHK4 are required for BA-induced programmed cell death (PCD). The results showed that CRE1/AHK4, the strongest expressed CK receptor gene of this family in cultured cells, is required for PCD, thus linking this process to the known CK signalling pathway [328].

6) Directional auxin distribution within tissues depends on PIN transporters that are polarly localized on the plasma membrane. We identified an evolutionarily conserved phosphorylation site within a central hydrophilic loop of PIN proteins that is important for apical and basal polar PIN localizations. Inactivation of the phosphorylation site in PIN1(Ala) resulted in a predominantly basal targeting and increased the auxin flow to the root tip. In contrast, the outcome of the phosphomimic PIN1(Asp) manipulation was a constitutive, PINOID-independent apical targeting of PIN1 and an increased auxin flow in the opposite direction [103]. We also identified a novel putative auxin transport facilitator family, called PIN-LIKES (PILS). PILS proteins regulate intracellular auxin accumulation at the endoplasmic reticulum and thus auxin availability for nuclear auxin signalling [211]. We reported, in addition, the discovery and the functional characterization of the first vacuolar auxin transporter. WALLS ARE THIN1 (WAT1), a plant-specific protein that dictates secondary cell wall thickness of wood fibres, facilitates auxin export from isolated Arabidopsis vacuoles in yeast and in Xenopus oocytes. We unambiguously identified IAA and related metabolites in isolated Arabidopsis vacuoles, suggesting a key role for the vacuole in intracellular auxin homoeostasis [417]. In maize, at least five auxin-binding proteins (ABPs) have been identified but their functions remain unclear. This study reported the use of maize abp1, abp4, and abp1abp4 mutants to investigate the role of ABPs during maize growth and development. We concluded that ABP1 and ABP4 participate in the growth of maize seedlings, mediate seedling responses to auxin, and interact with light signalling pathway(s) [256]. We also found that knockout of ABP1 or ABP4 results in essentially reduced expression of the PHYB gene in dark-grown mesocotyl but not in the expression of PHYA gene and in auxin-induced suppression of PHYA transcript accumulation. The results support the existence of cross-talk between auxin and light signalling and indicate for the first time that ABP1, ABP4 and PHYB genes could share common signalling pathway(s) [220]. Further study was performed to investigate the possible role of ABP1 and ABP4 in Ca^{2+}/auxin-regulated growth in maize (*Zea*

Figure 4

mays L.). We provided evidence for cross talk between ABP4, exogenous auxin, Ca^{2+}, and ZCAX3 during growth of etiolated maize mesocotyl [480]. In the redefined TAA1-YUC auxin biosynthetic pathway, TAA1/TARs are required for the production of indole-3-pyruvic acid (IPyA) from Trp, whereas YUCs are likely to function downstream. These results strongly suggest that the enzymatic reactions involved in IAA production via IPyA are different from those that were postulated [185]. We also identified an Arabidopsis pyridoxal-phosphate-dependent aminotransferase, VAS1, whose loss-of-function simultaneously increases amounts of the phytohormone auxin and the ethylene precursor 1-aminocyclopropane-1-carboxylate [439]. Further, we demonstrated that oxIAA is a major primary IAA catabolite formed in *A. thaliana* root tissues. We propose that oxIAA is an important element in the regulation of output from auxin gradients and, therefore, in the regulation of auxin homeostasis and response mechanisms [402]. In addition, we showed that these three GH3 genes are required for fine-tuning adventitious root initiation in the *A. thaliana* hypocotyl, and we demonstrate that they act by modulating jasmonic acid homeostasis [241]. Endogenous auxins were investigated in floral and fruit tissues of the Christmas rose (*Helleborus niger* L.). Free IAA, indole-3-ethanol (IEt), and seven amino acid conjugates were afforded by LC-MS/MS. Novel IAA conjugates with Val, Gly, and Phe were identified and quantified [221].

7) We generated transgenic *A. thaliana* and tobacco (*Nicotiana tabacum*, L.) plants with enhanced root-specific degradation of the hormone cytokinin, a negative regulator of root growth. We demonstrated that a single dominant gene (cytokinin oxidase/dehydrogenase, CKX) could regulate a complex trait, root growth in a largely organ-autonomous fashion [97]. In the following paper we showed that enzymes CKX3 and CKX5 regulate the activity of the reproductive meristems of *Arabidopsis thaliana*. CKX3 is expressed in the central WUSCHEL (WUS) domain, while CKX5 shows a broader meristematic expression [111]. Responses to drought, heat, and combined stress were compared in tobacco (*N. tabacum* L.) plants ectopically expressing the CKX1 gene of *A. thaliana* L. under the control of either the predominantly root-expressed WRKY6 promoter or the constitutive 35S promoter, and in the wild type. The results indicate that modulation of cytokinin levels may positively affect plant responses to abiotic stress through a variety of physiological mechanisms [388]. We also analysed the CKX7 gene. 35S:CKX7-expressing plants developed short, early terminating primary roots with smaller apical meristems, contrasting with plants overexpressing other CKX genes. We hypothesized that the pool of cytosolic cytokinins is particularly relevant in the root procambium where it mediates the differentiation of vascular tissues through CRE1/AHK4 [481]. R50 (sym16) is a pea nodulation mutant that accumulates cytokinin (CK) in its vegetative organs. The total CK content increases as the plant ages because of the low activity of CKX responsible for CK degradation [278]. We also unravelled the function of the previously described reticulated EMS-mutant dov1 (differential development of vascular associated cells 1) [308]. This study looked into the question of whether cytokinins in moss derive exclusively from tRNA. Targeted gene knockout of *ipt1* along with localization studies revealed that the chloroplast-bound IPT1 was almost exclusively responsible for the A(37) prenylation of tRNA in Physcomitrella. The data provide evidence for an additional and unexpected tRNA-independent cytokinin biosynthetic pathway in moss [494]. We also provided a comprehensive characterization of the nucleoside N-ribohydrolase (NRH) family in two model plants, *Physcomitrella patens* (PpNRH) and maize (*Zea mays*; ZmNRH), using *in vitro* and in planta approaches. We identified two NRH subclasses in the plant kingdom, solved their crystal structures and prepared knock-outs of single NRH genes in *P. patens*. All PpNRH knockout plants displayed elevated levels of certain purine and pyrimidine ribosides and cytokinins [381]. The putative role of cytokinins in the reproductive development of oilseed rape (*Brassica napus* L. var. oleifera, cv. Górczański) was also investigated in the shoot apices of vegetative and vernalized plants. The results suggest cZ cytokinins are involved in the reproductive development of *B. napus* [324].

8) In contrast to the well-defined polar transport of auxins, the molecular basis of cytokinin transport is poorly understood. We showed that an ATP-binding cassette transporter in Arabidopsis, AtABCG14, is essential for the acropetal (root to shoot) translocation of the root-synthesized cytokinins. Knocking out AtABCG14 strongly impairs the translocation of tZ-type cytokinins from roots to shoots. For this reason, AtABCG14 is a transporter likely involved in the long-distance translocation of cytokinins [564].

9) Auxin and cytokinin are both critical for division and patterning but it is unknown how these hormones converge upon tissue development. We identified a genetic network that reinforces an early embryonic bias in auxin distribution to create a local, nonresponding cytokinin source within the root vascular tissue. We further demonstrated that the auxin-cytokinin interaction acts as a spatial incoherent feed-forward loop which is essential to generate distinct hormonal response zones, thus establishing a stable pattern within a growing vascular tissue [458].

Research projects: 2, 3, 92–96, 100–102, 104, 106, 107, 110, 112-116

Laboratory of Hormonal Regulations in Plants

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Research at the Laboratory of Hormonal Regulations in Plants concentrates predominantly on two groups of plant signalling compounds (phytohormones) – *auxins* and *cytokinins*, and their interactions with other phytohormones, e.g. abscisic acid and ethylene. The focus is on both quantitative and qualitative aspects of mechanisms involved in establishing and modulating their homeostasis (i.e. metabolism and transport) as well as their signalling and control of physiological processes (i.e. stress reactions).

In the picture (from the left):
Ing. Milada Čovanová, Ph.D. / Postdoctoral Fellow, RNDr. Daniela Seifertová, Ph.D. / Postdoctoral Fellow (until 2013), Ing. Petr Skůpa, Ph.D. / Postdoctoral Fellow/Researcher, Innu Kottanal Baby, M.Sc. /PhD Student (maternity leave, until 2015), prof. RNDr. Eva Zažímalová, CSc. / Head of Laboratory, Ing. Mária Čarná, Ph.D. / PhD Student (until 2014), Ing. Karel Müller, Ph.D. / Researcher, RNDr. Adriana Jelínková, Ph.D. / Postdoctoral Fellow, RNDr. Radomíra Vaňková, CSc. /Researcher, Bc. Vojtěch Knirsch / Technician, Ing. Václav Motyka, CSc. /Researcher, Mgr. Sylva Přerostová /PhD Student, Mgr. Markéta Fílová /Research Assistant, Mgr. Zdeněk Cit / PhD Student (until 2014), Ing. Jozef Lacek /PhD Student, Ing. Klára Hoyerová, Ph.D. /Researcher, Ing. Petre Dobrev, CSc. / Researcher, Marie Korecká /Technician, RNDr. Alena Gaudinová /Research Assistant, RNDr. Jan Petrášek, Ph.D. /Researcher, Mgr. Petr Klíma, Ph.D. /Postdoctoral Fellow

Not in the picture:
Mgr. Nikola Drážná /Technician, Mgr. Eva Ge /PhD Student (until 2013), Mgr. Matouš Glanc /PhD Student, Ing. Petr Hošek /PhD Student, Ing. Miroslav Kamínek, CSc. /Researcher, RNDr. Martina Laňková, Ph.D. /Postdoctoral Fellow, Ing. Kateřina Malínská, Ph.D. /Researcher, Mgr. Roman Skokan /Diploma Student/PhD Student, Ing. Eva Žižková, Ph.D. /PhD Student/Postdoctoral Fellow, Mgr. Jana Dobrá, Ph.D. / PhD Student (until 2011), Mgr. Silvia Gajdošová, Ph.D. /PhD Student/Postdoctoral Fellow (until 2012), RNDr. Marie Havlová, Ph.D. /PhD Student (until 2011), Mgr. Andrej Hurný /Diploma Student (until 2012), Mgr. Pavel Křeček, Ph.D. /PhD Student/Postdoctoral Fellow (until 2012), RNDr. Martin Kubeš, Ph.D. /PhD Student/Postdoctoral Fellow (until 30.6.2015), RNDr. Jiří Libus, Ph.D. /Postdoctoral Fellow (until 2014), Karolína Müllerová /Technician (until 2015), Mgr. Sibu Simon, Ph.D. /PhD Student/Postdoctoral Fellow (until 2011), Ing. Jana Stýblová /Technician (until 2014)

Apropos auxins, the main interest was to characterize **mechanisms of action of auxin transporters** residing on plasma membrane and endomembranes (Fig. 1 and 2), as well as to reveal related **auxin-metabolizing processes**. In this regard the Laboratory has:

1. contributed significantly to the discovery of the, until then, unknown PILS (PIN-LIKES) family of putative auxin transporters that, like the putative auxin carrier PIN5, localize to endoplasmic reticulum (ER). Changes in their expression result in changes in the spectrum of auxin metabolites in cells, thus determining the accessibility of free auxin to the nuclear auxin-signalling pathway [211]. However, not only PIN5 and PILSes are found on endomembranes. PIN8, which is expressed in the male gametophyte of *Arabidopsis thaliana*,

plays a crucial role in pollen development and its functionality. PIN8 co-localizes with PIN5 on the ER and is also involved in the control of auxin homeostasis and metabolism [231].

2. participated in characterizing the plasma membrane (PM)-localized auxin transporter *At*ABCB4 from the superfamily of ABC transporters, and in revealing its unique function: depending on intracellular auxin level, ABCB4 is able to transport auxin into and out of cells. This is the first finding of a bi-directional, 'substrate'-concentration-dependent transport of a low-molecular compound across the PM in plants [269]. The paper cited also provides a likely explanation for the herbicidal activity of synthetic auxin 2,4-dichlorophenoxyacetic acid (2,4-D).

3. contributed fundamentally to revealing the, until then, unknown activity to facilitate auxin uptake into cells of the nitrate 'transceptor' NRT1.1. This PM-protein possesses two unique characteristics: it serves as both sensor and transporter for nitrate. As it is able to transport auxin as well, it connects the availability of a crucial mineral nutrient with auxin-controlled root development. This is the first observation of a direct hormonal regulation via nutrient availability driven by one particular protein species in plants [42]. The work on characterization of kinetic properties of NRT1.1 is on-going, e.g. in evaluation of the activities of phosphorylated and non-phosphorylated forms of NRT1.1 at amino acid residue T101 that differ significantly in both signalling and transport functions.

4. has collaborated in revealing the, until then, unknown interaction between auxin efflux carriers PIN1 and PIN2 and dynamin-related proteins at the cell plate that is necessary for proper polar PIN positioning in interphase cells and, concomitantly, for auxin-mediated development [159], and on characterization of reversible ubiquitylation of the auxin efflux carrier PIN2 that is important for PIN2 endocytosis and its delivery into the cell's lytic compartment. Such ubiquitylation, however, does not interfere with PIN2 auxin efflux activity at the PM [276].

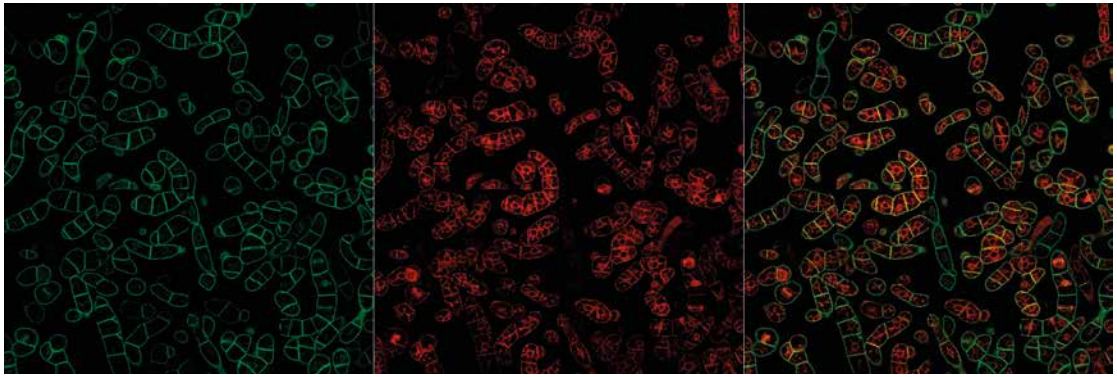

Figure 1: Tobacco BY-2 (*Nicotiana tabacum* L., cv. Bright Yellow-2) cell line overexpressing the influx carrier AUX1 for plant hormone auxin fused with yellow fluorescence protein (YFP) together with red fluorescence protein (RFP) under the auxin-responsive promoter DR5. Left panel: YFP signal depicting AUX1 on the plasma membrane. Middle panel: RFP signal in cell interior showing sites of response to auxin. Right panel: merged (Laňková *et al.*, unpublished).

On a metabolic level, the Laboratory contributed significantly to characterization of the role of major auxin degradation product, 2-oxindole-3-acetic acid (oxIAA), in control of auxin homeostasis [402], and to better understanding of the mode of action of some auxin transport inhibitors [47, 562].

In *Arabidopsis thaliana* (ecotype Landsberg erecta) suspension-cultured cells (LE line) the Laboratory characterized carrier-mediated uptake (influx) and efflux for native auxin indole-3-acetic acid (IAA) and synthetic auxins, naphthalene-1-acetic acid (NAA) and 2,4-D. In contrast to tobacco cells, only a small proportion of NAA is metabolized in LE cells. This makes the LE line favourable for measurements of auxin transport kinetics on a single cell level, distinct from well-established tobacco BY-2 cells [535].

Using a single-cell-based tobacco system, it is possible to track the course of auxin accumulation inside the cells and thus describe the activity of auxin influx and efflux carriers as well as contribution of auxin diffusion and metabolism. Based on this data, the Laboratory designed and experimentally verified the first mathematical model of transport processes involved in auxin accumulation at a single cell level thus providing estimates of key transport parameters for 2,4-D. Such specified and quantified auxin transport parameters represent unique data necessary for precise characterization of auxin transport at tissue level [249].

The Laboratory investigated the then unknown **relationship(s) between non-transcriptional auxin signalling and cellular auxin efflux**:

Auxin was shown to inhibit its own efflux from cells via inhibition of endocytosis of some PM proteins. In a direct follow up, the Laboratory contributed significantly to revealing the underlying mechanism: auxin, after interaction with the putative auxin receptor ABP1,

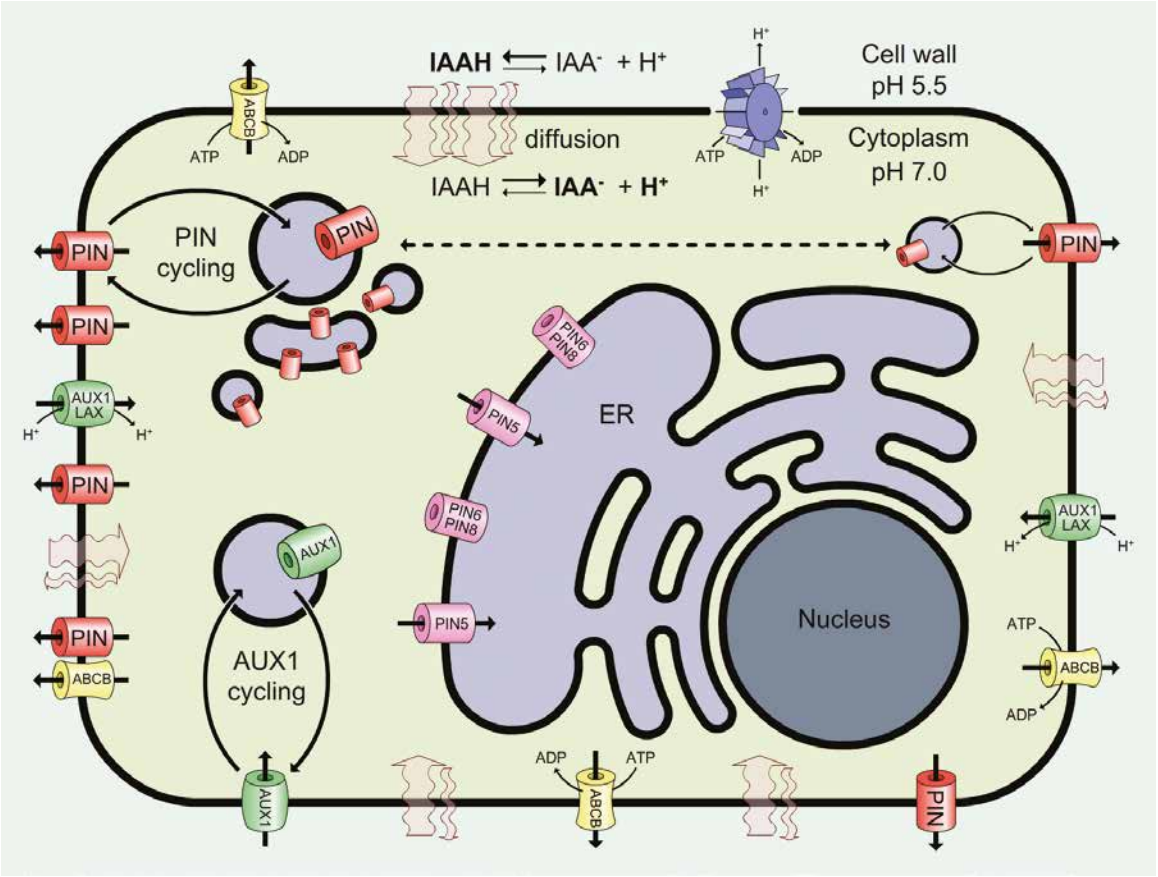

Figure 2: Scheme of auxin transport on cellular level and major proteins involved. PIN efflux carrier proteins depicted in red represent "long" PINs (PIN1, 2, 3, 4, and 7), whereas PINs marked in pink represent "short" PINs (PIN5, 6, and 8). ER marks endoplasmic reticulum, pale grey structures represent ER and endosomes, curved bold full arrows show constitutive protein cycling, and dashed arrows symbolize the process of transcytosis. Blue, mill-like symbol represents plasma-membrane H^+ ATP-ase. Possible collaboration between ABCBs and PINs is suggested by placing the symbols close to each other (from Zažímalová at al., Cold Spring Harb Perspect Biol 2010;2:a001552)

inhibits the clathrin-mediated internalization of PINs via non-transcriptional mechanism [69]. The Laboratory then characterized further the link between the activity of ABP1 in regulating the dynamics of proteins in the PM and the activity of PIN auxin transporters [349].

Using a number of auxin analogues, the Laboratory determined their physiological activity, and investigated their modes of action. The results demonstrated similar but not identical structure-activity relationships, and highlighted some synthetic auxin analogues that display non-canonical behaviour. Such compounds can serve as useful tools for studies of distinct mechanisms involved in the auxin mode of action [421].

In the field of cytokinins, the Laboratory has performed and published the as yet most comprehensive characterization of a specific class of *cis*-zeatin-type cytokinins [126]. It demonstrated their abundance throughout the plant kingdom and their biological activities in cytokinin bioassays as well as specification of their uptake, accumulation and metabolic pathways in plants. In addition, the Laboratory has participated in demonstration of *cis*-zeatin-type cytokinins as the predominant cytokinin forms in dry and/or imbibed seeds of various plant species [315, 316]. The Laboratory has also shown the involvement of *cis*-zeatin-type cytokinins in plant responses to fungal infection [213] as well as to abiotic stresses [11, 262, 388]. Using potato and centaury plants constitutively overexpressing the cytokinin oxidase/dehydrogenase (CKX) gene from *Arabidopsis thaliana* and grown *in vitro*, the Laboratory showed diminished growth and/or reduced morphogenic potential in association with *cis*-zeatin-type cytokinins that were considerably lower than *trans*-zeatin-type cytokinins [303, 430]. These findings formed the basis for advancing the hypothesis that the function

of *cis*-zeatin-type cytokinins is as delicate regulators of cytokinin responses in plants under growth-limiting conditions.

The Laboratory contributed to description of the molecular function of the *Pseudomonas syringae* pv. *tomato* effector HopQ1 that activates cytokinin signalling and enhances concentrations of bioactive cytokinin forms by stimulation of the LOG (*lonely guy*) biosynthetic pathway and demonstrated the importance of cytokinins in plant-microbe interactions [468]. We also characterized two tomato cytokinin biosynthetic genes, *SlIPT3* and *SlIPT4*, in homologous as well as heterologous systems and determined their different spatio-temporal expression patterns during tomato plant development, *in vitro* enzymatic activity and regulation of both genes

Figure 3: Effect of salt stress on tomato wild-type (WT) plants and tomato transformants overexpressing cytokinin biosynthetic gene isopentenyltransferase under constitutive promoter (*35S::SlIPT3*). Superior above-ground growth was apparent in transgenic plants grown 4 weeks on the 100 mM NaCl in comparison to WT.

under salt stress conditions. Moreover, improved tolerance of tomato plants to salinity was found resulting from *SlIPT3* overexpression (Fig. 3). The Laboratory has also been involved in the identification and functional characterization of the first tomato repressor-type zinc finger transcription factor, SlZF2, demonstrating its important role in control of plant development and salinity response. We showed that the involvement of SlZF2 in delayed senescence and improved salt tolerance of tomato plants correlates with maintaining photosynthesis, increasing polyamine and abscisic acid biosynthesis/signalling and modifying the ratio between *trans*- and *cis*-zeatin-type cytokinins [469].

The Laboratory has confirmed the positive effect of enhanced expression of the cytokinin biosynthetic gene under senescence-inducible promoter (*SAG12:IPT*) on suppression of leaf senescence and enhanced drought-tolerance of cassava plants (which provides a source of dietary carbohydrate for over 600 million people) [104]. The previous findings on wheat that grain formation strategy in cereals is based on fast translocation of metabolites to developing grains after pollination, was extended to and confirmed in rice [532].

Part of the activities of the Laboratory was devoted to elucidating the **functions of phytohormones in responses to abiotic stresses**, predominantly drought, heat and cold:

The Laboratory evaluated the role of osmolyte proline by comparing the drought and/or heat stress responses in tobacco plants with constitutively elevated proline content [11]. Hormonal profiles during the early heat stress response (cytokinin up-regulation and abscisic acid down-regulation) showed that stimulation of transpiration is crucial to maintaining leaf temperature lower than the environment, at least until defence mechanisms are activated. Determination of the expression profiles of two proline biosynthetic and three proline degradation genes revealed the key role of *NtP5CSA* in stress and *NtPDH2* during rehydration, as well as the differential regulation of proline content in shoots and roots [118]. Polyamine changes in the proline over-expressor and wild-type were described in our contribution [227, 345].

The impact of cytokinin down-regulation, both constitutive and root-targeted, on drought and/or heat stress tolerance was characterized in tobacco [388]. Apart from hormonal responses, stress tolerance was evaluated by expression levels of dehydration marker genes *ERD1* and *P5CSA*. The results suggested that the high stress tolerance of *35S:AtCKX1* transformant is due predominantly to morphological changes (suppressed growth rate of dwarf shoots, enhanced root system). Thorough analysis of antioxidant enzymes (ascorbate peroxidase, catalase and superoxide dismutase) revealed that expression of cytosol isoforms is stimulated by stress conditions, when chloroplast isoenzymes are suppressed (along with photosynthesis) [495].

Complex phytohormone analysis allowed the Laboratory to characterize hormonal cross-talk during individual phases of the response to cold stress (e.g., in alarm phase or acclimation) in leaves and crowns of winter and spring wheat genotypes [262]. The cold response of the proteome was described in detail [382]. The up-regulation of active cytokinin content at the onset of transition from vegetative to generative developmental phase indicated the decisive role of cytokinins in this process [556].

Participation of jasmonic acid, a hormone generally associated with defence against herbivore and necrotroph attack was demonstrated during severe dehydration of the resurrection plant *Haberlea rhodopensis* [351].

The Laboratory also contributed to evaluation of cytokinin regulatory roles in drought, salt and abscisic acid responses, and its biosynthesis [162], to understanding the metabolic reorganisation prior to early drought responses in lupine [168], to complex analysis of soybean response to drought stress [274], to characterization of hormonal changes underlying improved performance of somaclonal finger millet line [301], to study of cytokinin functions in grapevine berry initiation [225], to elucidation of the effects of abscisic acid on nuclear genes encoding chloroplast-localized proteins in the basal and apical segments of wheat leaves [436], and to identification of the new role of ascorbate peroxidase 6 in germination control and seed stress tolerance in relation to hormonal cross-talk [472].

We have also contributed to understanding **phytohormone co-action in the control of some developmental processes:** e.g. floral formation (gibberellins, auxin and mutual changes in contents of *cis*- and *trans*-zeatin [529]), apical hook development (auxin and ethylene [91, 106]), organogenesis (cytokinins and auxin [153]), and in response of plants to shading [108].

The Laboratory has also published several (mostly invited) **reviews** on state-of-the-art topics in Laboratory expertise:

- **On auxins in general**: We discussed what an auxin is [180] and its possible applications [580]. Members of the Laboratory were invited to edit a monograph summarizing current knowledge on auxins and their role in plant development with leading scientists in the field contributing particular chapters [586].
- **On auxin transport and transporters**: The present state-of-the-art in auxin transporters research was not only summarized but the fundamental question of "why there are so many different types of auxin transporters in plants" was examined from both functional and evolutionary points of view [102, 576].
- **On subcellular compartments and processes related to auxin action**: PM [152] and methods used for studying endocytosis were summarized [574].
- **On cytokinins and their role(s) in stress responses** [242, 378, 585].
- **On abscisic acid**, particularly its signalling [584].

Finally yet importantly, our research team has **optimized some existing methods and designed new ones**:

After acquisition of a high performance liquid chromatograph coupled with mass spectrometer (LCMS) in 2009, The Laboratory has optimized the extraction of plant samples and HPLC/MS analytical procedure, so that now it is possible to reduce sample quantities to tens to a few hundred mg of fresh weight and to simplify extraction and purification procedures using fewer steps; utilizing micro-volumes of elution solvents allowing us to process larger sample numbers. The Laboratory can perform simultaneous and highly reliable determinations of multiple cytokinin forms together with other plant hormones and their metabolites (auxins, abscisic acid, jasmonates, salicylic acid, gibberellins) in a single sample [351, 567]. Based on this expertise, the Laboratory has been involved in studies of metabolic fate and dynamics of labelled hormones at a cellular level [211, 421, 535] as well as hormonal metabolite identification and transport dynamics [249].

We participated on designing a new method for detecting carrier-driven activities, based on the transient, single-cell-based system. Relative changes in signalling output of the auxin responsive promoter element DR5 were used to indirectly visualize auxin carrier activity. This single-cell-based system will be useful in investigating other hormonal (e.g. cytokinin – via TCS) signalling and transport pathways [338].

The Laboratory has uncovered unknown and unexpected effects of the FM (Fei Mao) styryl dyes. Until then, FM dyes had been considered reliable tools for tracking plant endocytosis. However, the routinely used concentrations of FM 4-64 and FM 5-95 were shown to trigger transient re-localization of PIN and ABCB proteins and FM 1-43 was found to affect their activity. These results emphasize the need for circumspection apropos *in vivo* studies of membrane proteins performed using simultaneous labelling with FM dyes [31].

The Laboratory stimulated and participated in development of methods for *in vivo* measurement of pH in microscopic biological samples of µm or µl size. The methods are based on self-referenced ratiometric fluorescence intensity measurements using pH-sensitive transducer immobilised on the tip of optical fibres. They were successfully used for *in vivo* determination of pH in plant cells and xylem exudates [33, 373].

The Laboratory optimized some cell culture and auxin homeostasis-related methodologies, and described them in invited book chapters in the two volume Series "Methods in Molecular Biology", by Springer Science+Business Media, Totowa:Humana Press [575, 578, 579].

The Laboratory has also participated in preparation of the nomenclature for elements of the two-component pathway in plants involved e.g. in cytokinin signaling [362].

The Laboratory is involved in **broad international collaboration**, e.g. with:

- Prof. Jiří Friml a Dr. Eva Benková (VIB, Univ. Ghent, Belgium and IST Austria, Klosterneuburg, Austria): Transport of auxin and its role in plant development; shared experimental material and joint papers [69, 91, 106, 231, 349, 421, 586].
- Prof. Angus Murphy a Dr. Wendy Peer (Purdue Univ., Indiana, USA, from 2013 Univ. of Maryland, Maryland, USA): Mechanism of auxin transport; shared experimental material, joint papers [102, 269].
- Prof. Christian Luschnig (BOKU, Vienna, Austria): Transport of auxin and its role in plant development; shared experimental material and joint papers [69, 276].
- Prof. Alain Gojon and Dr. Philippe Nacry (Institut de Biologie Intégrative des Plantes, CNRS/INRA, Montpellier, France): Nitrate transporter NRT1.1 and its role in auxin transport; shared experimental material and joint papers [42].
- Dr. Jürgen Kleine-Vehn, (VIB, Univ. Ghent, Belgium and Univ. BOKU, Vienna, Austria): Transport of auxin and its mechanisms; shared experimental material and joint papers [31, 69, 204, 211, 338].
- Prof. Dr. Thomas Schmülling (Freie Universität Berlin, Dahlem Centre of Plant Sciences, Institute of Biology/Applied Genetics, Berlin, Germany): Stress tolerance of tobacco plants over-expressing cytokinin oxidase/dehydrogenase gene under different promoters (35S or WRKY6) [388].
- Prof. Stanley Lutts, Dr. Imène Hichri and Dr. Muriel Quinet (Earth and Life Institute, Université catholique de Louvain, Louvain-la-Neuve, Belgium): Molecular mechanisms involved in hormonal control of plant development and salinity response; joint projects, shared experimental material and joint papers [469, 529]; and several others.

We also closely collaborate with prof. Martin Hof and his team (J. Heyrovský Institute of Physical Chemistry CAS, Prague): Advanced fluorescence microscopy (raster image correlation spectroscopy (RICS), cross correlation Number & Brightness Analysis, FLIM/FRET).

Research projects: 2–20

Laboratory of Mass Spectrometry
Service Department

Head of Laboratory: **Ing. Jiří Malbeck, CSc.**
Phone: +420 225 106 407; E-Mail: malbeck@ueb.cas.cz

The main task of the service laboratory is to provide chemical analyses both to other research groups at the home institute, and collaborate with other research institutions and universities as well. Currently, we also provide analytical services to other entities in the Czech Republic and abroad.

In the picture (from the left): Ing. Jiří Malbeck, CSc. /Head of Laboratory, Ing. Alena Trávníčková /Technician, Ing. Bedřich Pešek /Technician

Figure 1: LC-MS system TSQ Quantum Ultra AM with Rheos 2200 chromatograph and CTC HTS autosampler

The Laboratory of Mass Spectrometry was established in 2007 by separation from the larger research division, in which our team worked as an analytical unit. From the beginning, the laboratory was designated as a service centre performing special instrumental analyses and development of new analytical methods.

We are focused on quantitative analyses of biologically active compounds in plant matrixes using chromatographic methods with mass spectrometric detection. Our analytical results are included in publications of colleagues at our institute, as well as external scientific institutions, whether it is an analysis of cytokinins [11, 108, 142, 160, 213, 260, 303, 442, 532, 566], auxins [47, 91], abscisic acid and its metabolites [262, 442, 511] or phenolic acids [556].

Laboratory instrumentation

The main part of the laboratory equipment consists of two LC-MS systems; one GC-MS system and one HPLC instrument with fraction collector device (see figures). All instruments are equipped with autosamplers.

For the preparation of samples, we use rotary vacuum concentrator Christ Alpha RVC and rotary evaporator Büchi Rotavapor R-200. Analytical Balance Mettler XP26 with a sensitivity of 2 µg is very suitable for the preparation of expensive analytical standards.

2 | 4
3

Figure 2: LC-MS system LCQ with Rheos 2000 chromatograph and CTC HTS autosampler

Figure 3: GC-MS system Polaris Q with Trace GC chromatograph and CTC combi PAL autosampler

Figure 4: HPLC Agilent 1200 with fraction collector Gilson

Research projects: 2, 3

Laboratory of Pathological Plant Physiology

Head of Laboratory: **doc. Ing. Lenka Burketová, CSc.**
Phone: +420 225 106 815; E-Mail: burketova@ueb.cas.cz

The Laboratory of Pathological Plant Physiology has been studying plant–microbe interactions for many years. Our main interest is signalling pathways implicated in defence responses and induced resistance against pathogens. Besides academic collaboration, we endeavour to transfer our results for application via collaboration with institutes of applied research. Our research focuses on: (1) Hormonal signalling pathways in plant defence against pathogens, (2) Phospholipid signalling in biotic stress and (3) Induced resistance to plant pathogens.
(1)) We have discovered signalling events distinct from biotrophs and necrotrophs using interaction of *Brassica napus* with the hemibiotrophic ascomycete *Leptosphaeria maculans* and necrotroph *Sclerotinia sclerotiorum*. Another research topic was determining the role of ROS in plant interaction of a hemibiotrophic pathogen *L. maculans* with *B. napus*. We found that the virulence of *L. maculans* is limited in the presence of ROS scavenger.
(2) We have focused on the role of phosphatidylinositol 4-kinases (PI4Ks) and showed the interconnection between the SA pathway, actin cytoskeleton and phospholipid signalling.
(3) We demonstrated that β-aminobutyric acid protected *B. napus* plants against *L. maculans* and had in addition to its assumed priming activity a direct antifungal activity comparable with that of fungicide. We found that elicitors isolated from *L. maculans* mycelium and antimicrobial peptide anoplin induce resistance in plants to pathogens.

In the picture (from the left):
Standing: Ing. Martin Janda / PhD Student, Ing. Barbora Jindřichová, Ph.D. / Postdoctoral Fellow, Myrta Pařízková / Technician, doc. Ing. Lenka Burketová, CSc. / Head of Laboratory
Sitting: Mgr. Lucie Trdá, Ph.D. /Postdoctoral Fellow, Mgr. Hana Krutinová /PhD Student, Ing. Miroslava Nováková /PhD Student

Not in the picture: Ing. Vladimír Šašek, Ph.D. /Postdoctoral Fellow (until 2013)

Hormonal signalling pathways involved in plant defence against pathogens

Despite huge effort to elucidate hormonal regulations of plant defence in recent years, only limited data are available on signalling pathways implicated in resistance to hemibiotrophic pathogens. Our laboratory has contributed significantly to the field, revealing signalling events distinct from biotrophs and necrotrophs [322]. Regarding the interaction of *Brassica napus* with the hemibiotrophic ascomycete *Leptosphaeria maculans*, we clearly showed that resistance to this pathogen is mediated by salicylic acid (SA) signalling in combination with ethylene (ET). This

was confirmed both by expression study of SA-associated (I*CS1*, *WRKY70*, *PR-1*) and ET-associated (*ASC2a*, *HEL*, *CHI*) genes, hormone quantification in infected tissues, as well as pharmacological experiments. We ascribe this unusual cooperation of SA and ET signalling to the hemibiotrophic nature of *L. maculans*. An additional value of this work lies in that it was performed within a natural pathosystem, where we demonstrated profound difference between the natural host *B. napus* and the model plant *Arabidopsis* in their response to *L. maculans* infection.

Another study carried out in our laboratory changed the current understanding of defence signalling during plant interaction with a necrotroph [516]. On interaction of *Sclerotinia sclerotiorum* with *B. napus*, we demonstrated that hormonal regulation of plant resistance to this necrotroph is more complex than had previously been shown in the model plant Arabidopsis. In addition to jasmonic acid (JA) and ethylene, both SA and abscisic acid (ABA) play roles. Moreover, a gene for putative chorismate mutase (*SS1G_14320*) was identified and found to be highly expressed during *S. sclerotiorum* infection. This finding indicates pathogen manipulation of the SA level.

Another research topic was determining the role of reactive oxygen species (ROS) in plant interaction of a hemibiotrophic pathogen *L. maculans* with *B. napus*. ROS serve as a defence compound and important signalling molecule during plant interactions with biotrophs but their role in the interaction with hemibiotrophs has not yet been fully explained. Our study demonstrates that *L. maculans* behaves like a necrotroph during the early stages of infection [136].

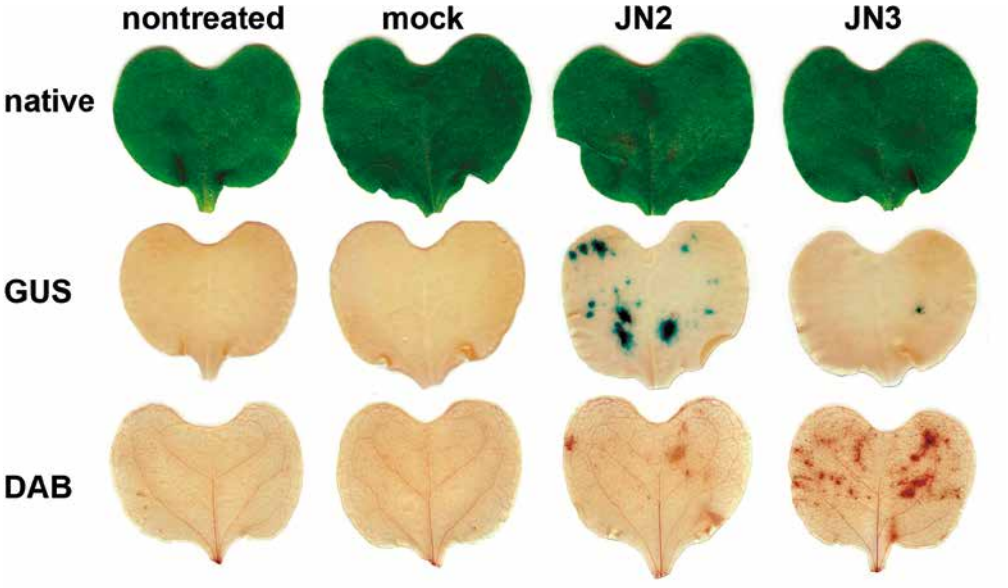

Figure 1: Cotyledons of *Brassica napus* cv. 'Columbus' infected with *Leptosphaeria maculans* virulent isolate JN2 and avirulent isolate JN3. Visualization of fungal mycelium by β-glucuronidase (GUS) and hydrogen peroxide by diaminobenzidine (DAB) *in situ* eight days after inoculation [322]

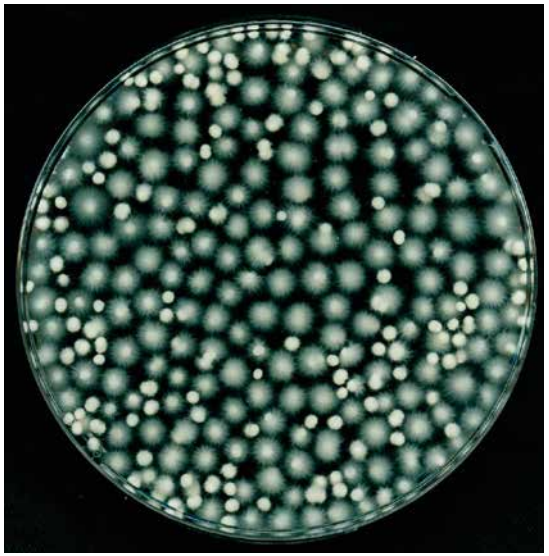

Figure 2: *Leptosphaeria maculans* grown *in vitro*

Phospholipid signalling in biotic stress

This research is based on long-term collaboration with the laboratory of Dr. Eric Ruelland from Université Paris Est-Créteil (UPEC) and prof. Olga Valentová (UCT Prague). Our earlier work revealed an interconnection between the SA signalling pathway and a phospholipid signalling system. Recently, we have focused upon the role of phosphatidylinositol 4-kinases (PI4Ks). We

investigated the mechanisms responsible for the dwarf rosette phenotype of *Arabidopsis thaliana* double mutant in two type III phosphatidylinositol-4-kinases (PI4Ks), *pi4kIIIβ1β2*, which contains high levels of SA and constitutively expresses *PR-1* (Figure 4). Our study revealed that PI4Kβ1 and PI4Kβ2 are negative regulators of SA biosynthesis and act upstream of EDS1 [549, 571]. The team also participated in a study showing interconnection between the SA pathway, actin cytoskeleton and phospholipid signalling [504]. We demonstrated that the pharmacological actin depolymerization induced specifically, the salicylic acid pathway in *A. thaliana* plants and treatment with phosphatidic acid abolished this effect. This work was done in cooperation with UCT Prague and the Laboratory of Signal Transduction, IEB CAS.

Induced resistance to plant pathogens

β-aminobutyric acid (BABA) is generally seen to be a resistance-inducing and priming compound and it is widely utilized experimentally. In our paper [321], we demonstrated that BABA protected *B. napus* plants against *L. maculans* and, importantly, the BABA had in addition to its priming activity, a direct antifungal activity comparable with that of fungicide. This activity had heretofore been overlooked. The cited paper also discusses this compound's mode of antifungal action. This finding is of substantial importance to colleagues using BABA in their experiments. A search for compounds inducing resistance in plants against pathogens has resulted in two publications, prepared in collaboration with UCT Prague. The first demonstrates induction of resistance in *B. napus* against *L. maculans* by elicitors isolated from *L. maculans* mycelium and describes a new trisaccharide fungal pathogen-associated molecular pattern [377]. In the second study, the antimicrobial peptide anoplin revealed an unknown antifungal activity and ability to induce resistance in plants [478].

Collaboration with applied research

Long-time collaboration with the Institute of Oilseed Crops (OSEVA Pro. Ltd.), OSEVA Development and Research Ltd., and the Institute of Plant Production Prague has led to three patent applications which were submitted to the Industrial Property Office of the Czech Republic in 2011 (Nos. PV 2011-670, PV 2011-774, and PV 2011-842), one utility model (No. 24517, recognized on 12 November 2012), and one certified methodology (No. SRS 028110/2013, recognized on 27 May 2013). The subjects of these applications are bio-based resistance-inducing compounds/molecules utilizable as active substances in potential crop-protecting preparations. The results of our laboratory tests were validated in field experiments by our collaborators. The source material for inducer preparations originated in TBU Zlín (protein inducers) or prepared in collaboration with UCT Prague (mycelial elicitors).

International collaboration

International collaboration is of a great importance for the laboratory. Research on phospholipid signalling has been proceeding in close collaboration with

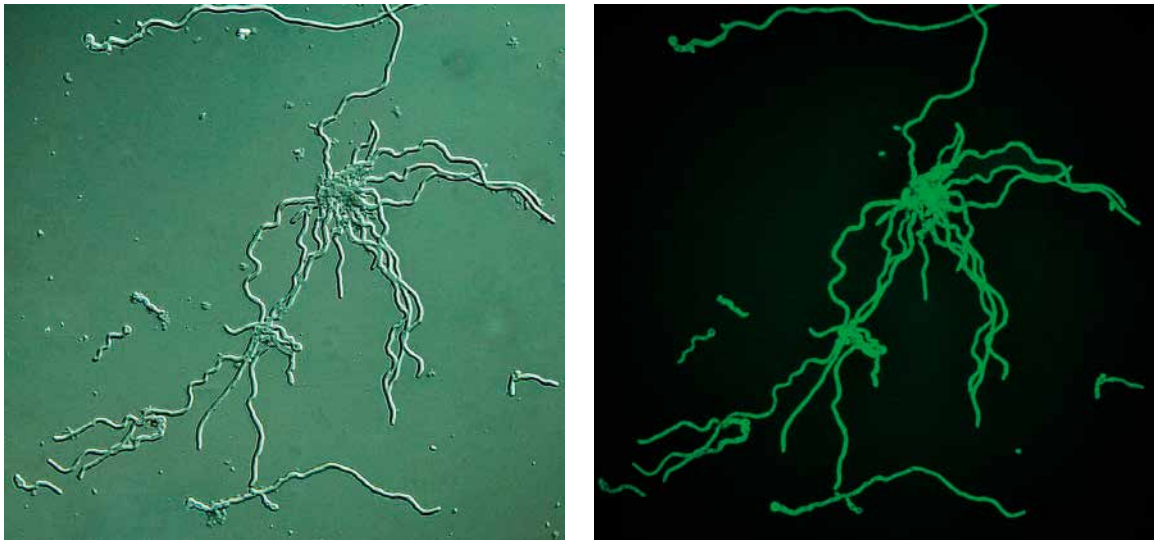

Figure 3: GFP-transformed isolate of *Leptosphaeria maculans* grown in an axenic culture observed by a differential interference contrast (left) and a fluorescent microscopy (right)

Dr. Eric Ruelland from the Université Paris Est-Créteil (UPEC), as shown by joint publications [367, 549]. Another close collaboration has been with the Plant Protection Institute of the Hungarian Academy of Sciences in Budapest (Dr. Joszka Fódor) and Eötvös Loránd University in Budapest, Hungary (Dr. Károly Bóka). Collective work relates to ROS signalling [136] and electron microscopy [322, 549]. The work involving *L. maculans* has been carried out in collaboration with the laboratory of Dr. Thiery Rouxel, INRA, Centre de recherche de Versailles-Grignon, France. New collaborations have been set up on SA signalling and growth trade-offs with Dr. Kenichi Tsuda, which emerged from Martin Janda's 2014 fellowship at Max Plank Institute in Köln, Germany, and on fungal effectors with Dr. Peter Solomon from The Australian National University, Canberra, Australia.

Research projects: 120–123, 126, 130, 135, 138

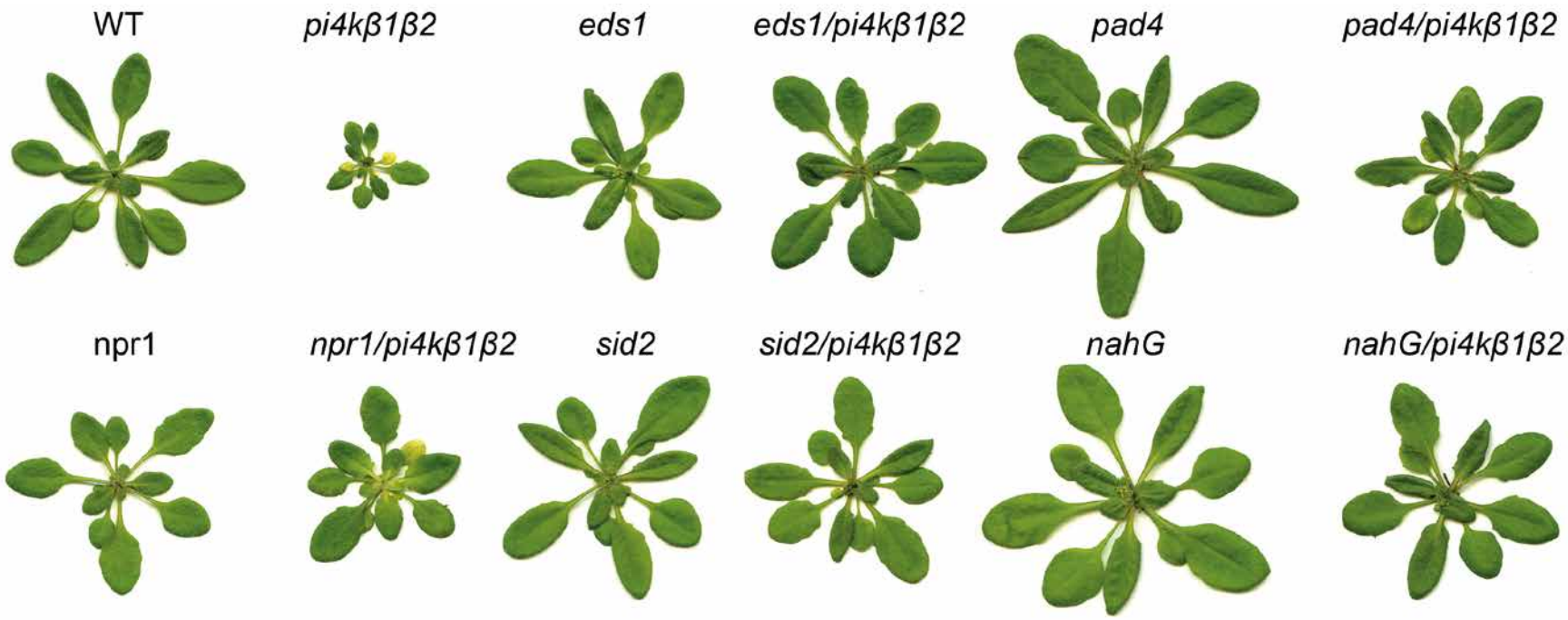

***Figure 4: Arabidopsis thaliana* mutants demonstrating the link between phosphatidylinositol 4-kinases (PI4Ks) β1 and β2 and salicylic acid (SA) signalling.** An *Arabidopsis thaliana* double mutant in two type III PI4Ks, *pi4kIIIβ1β2*, displays a stunted rosette growth. The dwarf phenotype of rosettes is suppressed in all triple mutants. *eds1 pi4kIIIβ1β2*, *sid2 pi4kIIIβ1β2* and *nahG pi4kIIIβ1β2* had similar levels of SA to the wild-type (WT) but *npr1 pi4kIIIβ1β2* had more SA than *pi4kIIIβ1β2* despite being less dwarfed. This indicates that PI4KIIIβ1 and PI4KIIIβ2 are genetically upstream of EDS1 and need functional SA biosynthesis and perception through NPR1 to express the dwarf phenotype. The slow root growth phenotype of *pi4kIIIβ1β2* was not suppressed in any of the triple mutants. The *pi4kIIIβ1β2* mutations together cause the constitutive activation of SA signalling that is responsible for the dwarf rosette phenotype but not for the short root phenotype [549].

Laboratory of Plant Biotechnologies

Head of Laboratory: **RNDr. Mgr. Tomáš Vaněk, CSc.**
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In 2010–2014 our research has been focused predominantly on plant–xenobiotic interactions and plant secondary metabolites. The work was funded by altogether 35 projects from different grant agencies.
Our "traditional" approach has been expanded in two directions:
(1) More detailed study of plant metabolism and plant stress responses, enabled by our success in OPPK grants which provided us with the possibility of acquiring the most sophisticated equipment – 2D GC-MS and LC-MS/MS. Additionally, proteomic and transcriptomic methods have become widely used in our Laboratory.
(2) Our comprehensive results on the utilization of plants for environmental protection (phytoremediation) gave us the ability to extend our efforts to semi-real and real conditions, in order to contribute to resolving environmental problems not only in the Czech Republic.
We were able to continue and extend our international cooperations by means of joint projects, mainly with the USA, China and other countries. We also succeeded in getting 16 COST projects, which gave us wide opportunity to cooperate with scientists from European and other COST countries. These cooperations led, among others, to election of Tomáš Vaněk as a Board member of the European Plant Science Organization (EPSO).

In the picture (from the left):
Zdenka Hornychová /Technician, Ing. Kateřina Moťková /PhD Student, Ing. Přemysl Landa, Ph.D. /Researcher, Ing. Jan Rezek, Ph.D. /Researcher, Ing. Miroslav Šíša, Ph.D. /Researcher, RNDr. Radka Podlipná, CSc. /Researcher, Mgr. Petr Maršík, Ph.D. /Researcher, RNDr. Mgr. Tomáš Vaněk, CSc. /Head of Laboratory, RNDr. ThMgr. Petr Soudek, Ph.D. / Researcher, RNDr. Marcela Dvořáková, Ph.D. /Postdoctoral Fellow, Ing. Šárka Petrová, Ph.D. /Researcher, Ing. Lenka Langhansová, Ph.D. /Researcher

Not in the picture:
Alexandra Solodovniková /Bc Student, Jekaterina Ten /Bc Student, Markéta Kleinová /Bc Student, František Pavlík / Diploma Student, Barbora Kadlecová /Diploma Student, Lenka Matějková /Diploma Student, Mgr. Lukáš Zappe /PhD Student, Ing. Jan Tauchen /PhD Student, RNDr. Marie Kvasnicová, Ph.D. /Postdoctoral Fellow (maternity leave)

In the area of **plant–xenobiotic** interactions, *Helianthus* was found to be superior for phytoremediation of soils heavily polluted with lead and zinc. Fortification of the antioxidant system with glutathione supplementation significantly increased plant fitness and enhanced the plant accumulation potential. Improved metal accumulation capacity was also achieved by addition chelating agents. We also tested uranium, radium and thorium accumulation in plants. Plants can also substantially diminish other types of pollutants from the environment, e.g. dust particles. We analysed the up-take and transformation of organic xenobiotics (TNT) and pharmaceuticals (pain relieving drugs, drugs against

parasitic worms) and evaluated the potential effect of nanoparticles (nZnO, FS, $nTiO_2$) on gene expression and generally on plant metabolism.

Secondary metabolites are of plant origin and could become starting compounds for the development of new drugs. We compared two widely used pharmacophore modelling and screening software programmes for prediction of the most effective compounds, as the activities of plant secondary metabolites can be improved by suitable chemical modification. We also focused on characterization of natural products with anti-inflammatory, anti-proliferative, anti-cancer and anti-microbial properties, which could be used as natural substitutes for synthetic pharmaceuticals. We optimized the biotransformation of turpentine to different monoterpenes. The efficacy of the anti-cancer drug, paclitaxel was increased by its conjugation with specific targeting compound. We performed labelling of physiologically active compounds with fluorescent dye for the visualization of the compound localization *in vivo*.

Plants and the Environment

The main focus of the Laboratory research is study of the mechanisms of plant–xenobiotic responses. This may enable the use of plants in **phytoremediation**.

The toxicity of cadmium, cobalt, copper, zinc, nickel, lead, chromium and arsenic (in wide concentration) was compared in 23 *Linum usitatissimum* cultivars [75]. We found that the most toxic element was arsenic. Substantial differences among individual flax cultivars indicated the need to select a suitable cultivar in case of contaminated soils. In order to find a suitable plant for phytoremediation of soils heavily polluted with Cd, Cr, Cu, Pb or Zn, we compared *Zea mays* and *Helianthus annuus* responses [77]. *Helianthus* was found to be superior in case of Pb and Zn. Taking into account relatively heavy soil contamination from uranium ore in former mines, along roads and in former processing factories in former Czechoslovakia, we tested uranium uptake by *Zea mays* plants [184], by hairy root cultures of *Armoracia rusticana* [183], by *Nicotiana tabacum* plants cultivated hydroponically [542]. In the case of maize and tobacco, phosphate deficiency substantially enhanced uranium uptake. The reason may be up-regulation of ion transporters. Also tartaric acid and low pH (3.5) had positive effects. Apart from uranium, radium [76] and thorium [422] accumulation was also monitored.

Plants can also substantially diminish other types of pollutants, e.g. dust particles which are a major environmental problem in urban areas [312].

Apart from heavy metals, serious soil and water contamination is caused by organic xenobiotics, for example explosives (in former military areas). We characterized the impact of 2,4,6-trinitrotoluen (TNT) on gene expression in *Arabidopsis thaliana* rosettes and roots using microarrays [46]. The up-regulated genes included nitrate reductase, several glycosyltransferases and ABC transporters. The uptake and transformation of nitroglycerine and ethylene glycol dinitrate from wastewater were optimized for *Juncus inflexus* and *Phragmites australis* plants [64].

Wide use of pharmaceuticals is a serious, and increasing source of contamination. After being excreted these substances may persist in the environment and impact non-target organisms. This assumption is especially true for pain relieving drugs (diclofenac, ibuprofen and acetaminophen). We tested *Armoracia rusticana* hairy root culture, *Linum usitatissimum* cell culture and *Lupinus albus*, *Hordeum vulgaris* and *Phragmites australis* plants [38]. Similar effects can be found in case of benzimidazole anthelmintics, drugs against parasitic worms, widely used in human as well as veterinary medicine [409]. These compounds were completely metabolized in reed cell cultures. Taking into account increasing use of **nanoparticles** for multiple purposes and their uncontrolled release into the environment, we evaluated the potential effect of zinc oxide (nZnO), fullerene soot (FS) and titanium dioxide ($nTiO_2$) nanoparticles on gene expression in *Arabidopsis thaliana* roots using microarrays [272]. The resuts indicate that in the case of the use of specific nanoparticles, great attention should be paid to their impact on the environment. Further research in this area is in progress.

Our extensive knowledge on phytoremediation methodology was summarized in book chapters [583, 582].

Plant metabolites

Secondary metabolites, including many **pharmaceuticals**, are **of plant origin**. They could become the starting compounds for development of new drugs. Pharmacophore modelling has become an integrated tool in drug discovery. We compared two widely used pharmacophore modelling and screening software programmes and found that they yielded vastly different hit lists but both predicted active compounds [552]. Twenty-three quinone compounds of plant origin were tested *in vitro* for their potential anti-flammatory effects [384]. The screening was complemented with *in silico* molecular docking to crystal structure of selected lipoxygenase. Cudraflavone B, a prenylated flavonoid from *Morus alba* roots, was identified as a potent inhibitor of several inflammatory mediators [130]. Anti-proliferative (anti-cancer) and anti-inflammatory effects detected in extracts from *Vaccinium bracteatum* leaves and fruits indicated that

this material can be a useful source of biologically active compounds [491]. We found a strong anti-proliferative effect of *Myrica rubra* essential oil. [492]. The anti-inflammatory activity of ten anthraquinone, nine naphthoquinone, and five benzoquinone compounds of natural origin was compared with the function of five synthetic naphthoquinones [271]. Red wine as a complex mixture was found to be a powerful inhibitor of a number of pro inflammatory enzymes [489]. Wine also contains phenolic compounds with antimicrobial activity [401]. The activity was especially true for pterostilbene, resveratrol and luteolin.

The activities of plant secondary metabolites can be improved by suitable chemical modification. However, the active compounds occur in nature in the form of several stereoisomers which can have significantly different biological activity. Chemical synthesis may thus be difficult. In this case **biotransformation** of a specific isomer could offer an advantage. We optimized the biotransformation of turpentine to different monoterpenes, in particular, *trans*-verbenol and *trans*-pinocarveol, in *Picea abies* cells [120]. Stereospecific biotransformation of (1S)-2-carene and (1S)-3-carene by *Picea abies* suspension has also been described [122].

Synthesis of the conjugate of cytostatic paclitaxel with an analogue of the gonadotropin-releasing hormone (as a targeting moiety) allowed us increase the antiproliferative effect of paclitaxel substantially [171]. The non-hydrolyzable alkylcarbonate analogues of O-acetyl-ADP-ribose were synthesized to obtain effective inhibitors of sirtuins, histone deacetylases, which are required for gene silencing [354]. The effective synthesis of biologically active compounds requires suitable methodology. Mechanisms of the migration of methyloxycarbonyl group from secondary to primary hydroxyl in furanosides were elucidated [234]. Fluorescent labelling of the brassinosteroid receptor enabled us to follow the dynamics of its subcellular distribution and regulation of brassinosteroid signal transduction [251]. This compound enabled the first visualisation of brassinosteroid-receptor complex in plants.

Within project "LD14127 Synthesis of strigolactone derivatives" we prepared 9 analogues of strigolactones, some of these will be **patented**.

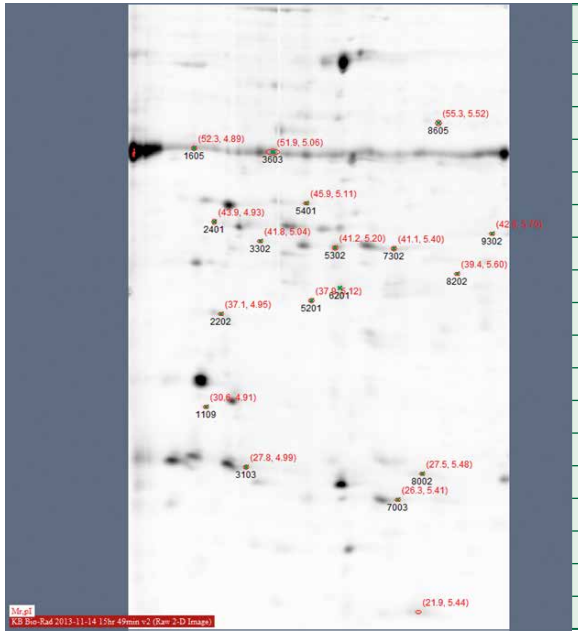
A number of the above mentioned results can be utilized as the first step in the preparation of new pharmaceuticals, e.g. synthesis of paclitaxel analogues. A range of conjugates was synthetized in 2013–2014. They have been confirmed in tests of anti-proliferative activity and a **patent** is pending.

A further example can be new anti-inflammatory compounds derived from plant products. Some of these were synthetized in 2013–2014, being currently tested.

Education

More than **40 students** been trained in our Laboratory, at Bachelor, Masters and Doctoral levels in the area of plant–xenobiotic interaction and plant bioactive compounds. A number of Laboratory staff lecture, especially at the Faculty of Science of the Charles University in Prague.

Research projects: 55–90



SSP	Mr (kD)	pI	control	nTiO$_2$
1109	30.6	4.91	618858	276843
1605	52.3	4.89	807184	2917164
2202	37.1	4.95	1300282	0
2401	43.9	4.93	184357	460126
3103	27.8	4.99	2202015	98177
3302	41.8	5.04	894660	304348
3603	51.9	5.06	10432978	2960532
3703	60.9	5.00	455596	1131233
5201	37.9	5.12	385784	948716
5302	41.2	5.20	4059419	1664738
5401	45.9	5.11	1360573	546646
6201	38.7	5.23	1231299	2744794
7003	26.3	5.41	2416893	1120131
7302	41.1	5.40	114499	723591
8002	27.5	5.48	1937875	952162
8202	39.4	5.60	284074	1038349
8605	55.3	5.52	538627	191232
9302	42.6	5.70	734982	331720

Figure: *Arabidopsis thaliana* proteome stress response to TiO$_2$ nanoparticles

Laboratory of Plant Reproduction

Head of Laboratory: **RNDr. Helena Štorchová, CSc.**
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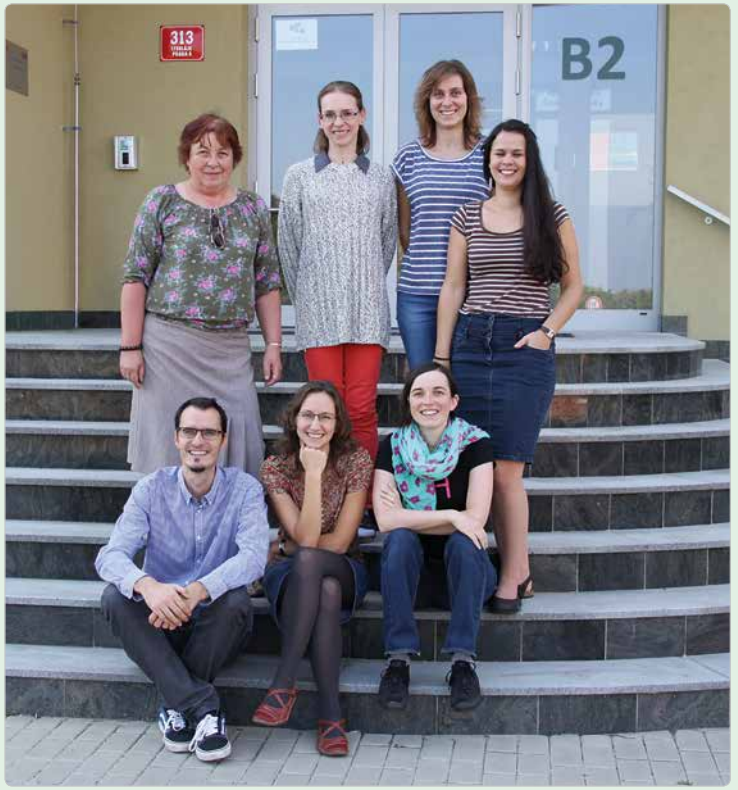
The Laboratory of Plant Reproduction was established in 2007. It represents a young team also considering the average age of lab members. The lab is working on two main topics using advanced approaches of molecular biology and bioinformatics. The first field of interest is the genomics and transcriptomics of plant mitochondria and mitochondrial–nuclear interactions. We found an extreme variation among mitochondrial (mt) genomes in *Silene vulgaris* [311]. We revealed the presence of chimeric genes in mt genomes, most likely associated with cytoplasmic male sterility (CMS). We performed the detailed study of *atp1* transcription [397] and demonstrated that expression of mt genes was influenced by the nuclear background.

Another research topic is the study of flowering in the genus *Chenopodium* and the evolution of flowering-related genes. We found that the *CrFTL1* gene was the main floral activator in *Chenopodium rubrum* [462]. Unlike other short day plants, which express the floral inducer at night, the *CrFTL1* expression peaks in the middle of day in *C. rubrum*. The duplicated gene *CrFTL2* is the ortholog of *BvFT1*, floral repressor in sugar beet. However, it is not involved in the control of flowering in *C. rubrum*. It underwent an accelerated evolution and obtained a novel, so far unknown function in this species. The *FTL* genes were used as phylogenetic markers which helped to reveal the origin of quinoa, an important crop of South America.



In the picture (from the left):
Standing: RNDr. Helena Štorchová, CSc. /Head of Laboratory, Ing. Kateřina Haškovcová /Research Assistant, Mgr. Helena Mašterová /PhD Student, Ing. Pavla Koloušková /PhD Student
Sitting: Mgr. Petr Vít, Ph.D. /Postdoctoral Fellow–Guest, Mgr. Lucie Černá /Research Assistant, Ing. Jana Drabešová, Ph.D. /Postdoctoral Fellow

Genomics and transcriptomics of plant mitochondria and mitochondrial–nuclear interactions CMS

Plant and animal mitochondrial genomes are very distinct, despite of sharing a common eubacterial ancestor and a similar set of genes. Whereas animal mt genomes are short, compact and conserved in structure, plant mt genomes are large and highly rearranged.

We selected *S. vulgaris* (bladder campion or maiden's tear) as a study species to understand plant mt genome structure and evolution, because it represented a model for the study of gynodioecy, a plant reproduction system characterized by the co-occurrence of females and hermaphrodites, and controlled by the interaction of mitochondrial and nuclear genes. Gynodioecy is frequent among angiosperms (about 10% of species). CMS is exploited in agriculture to ensure the production of hybrid seed.

Initially, we revealed an extreme polymorphism in mtDNA in Central European populations of *S. vulgaris*.

Indeed, the mt genome changes so rapidly, that differences arise between not only among full siblings, but even among the branches of the same individual. We also found that specific mtDNA haplotypes were associated with specific transcripts of the genes *atp1* and *cox1* [15]. To further investigate the cause of this remarkable within-species transcript size variation, we analyzed in detail the transcription of the *atp1* gene. We found that the sequences upstream from this gene, including putative regulatory motifs, varied among mt haplotypes. We examined the *atp1* transcript in the KOV mt genome by means of RNA circularization and discovered three 5' ends, created by the combination of transcription initiation and RNA processing. Surprisingly, the utilization of a particular transcription start site depended on the nuclear background, which suggested the involvement of nuclear genes in transcription initiation in plant mitochondria [397].

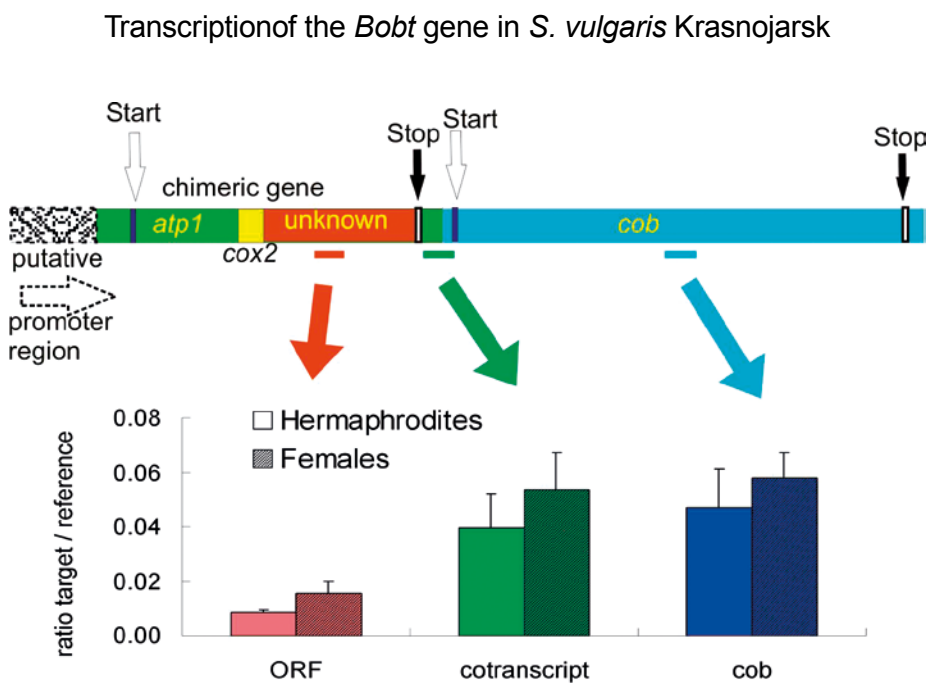
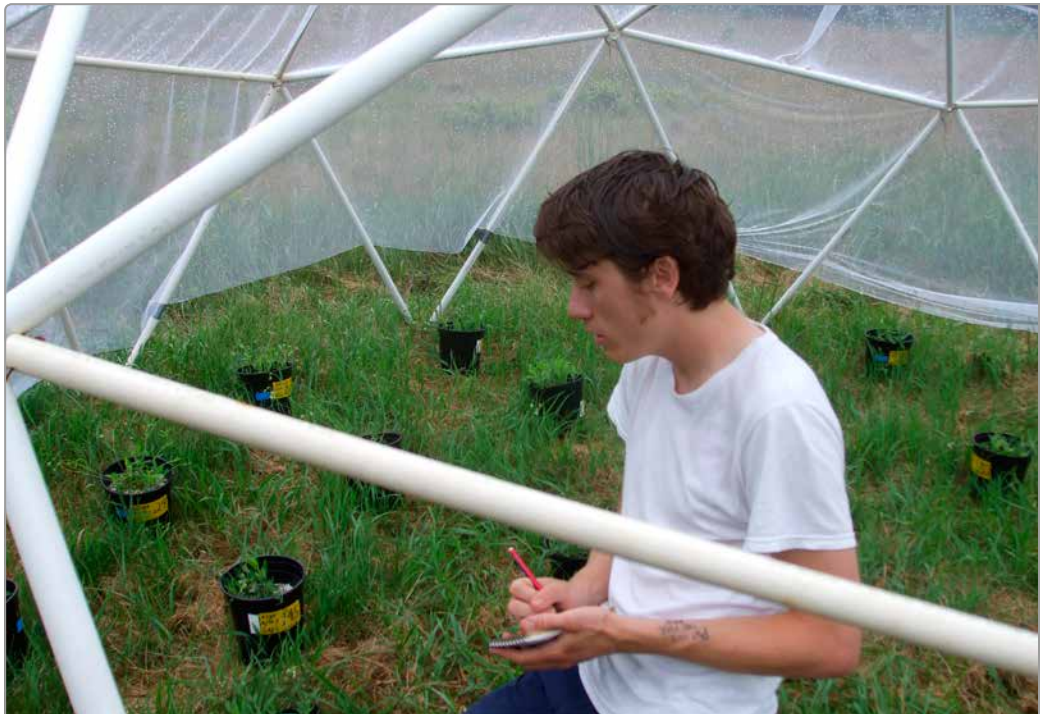


Figure 1: The *Bobt* gene is a candidate Cytoplasmic Male Sterility gene in *S. vulgaris*. Its transcript level is higher in females than in hermaphrodites which may cause mitochondrial dysfunction and pollen abortion in hermaphrodites. The *Bobt* gene is located just upstream of *cob*, an essential gene encoding cytochrome b, which does not have its own promoter and has to rely on the co-transcription with *Bobt*. The *Bobt* promoter cannot be therefore switched off. The *cob* gene was used as "a hostage" to ensure the transcription of the Cytoplasmic Male Sterility gene, which is an example of selfish gene.

We documented prominent differences in mt genomes at the within-species level in *S. vulgaris* together with D.R. Taylor (Univ. Virginia, USA) and D.B. Sloan (now Colorado State Univ., USA) using the tools of comparative genomics. We also contributed Southern hybridizations confirming intramolecular mt genomic recombinations in *Silene latifolia* in the assembly of the first completely sequenced mt genome in the genus *Silene* [74]. We generated complete sequences of four mt genomes of *S. vulgaris* and revealed an extreme level of mt genomic rearrangements affecting not only gene order, but also gene content. This within-species mtDNA variation is by far the highest so far described. We performed Southern hybridization which confirmed an autonomous physical structure of the smallest subgenome predicted by bioinformatics [311].

A closer inspection of mt genomic sequences found several open reading frames (ORFs), composed of the pieces of known mt genes and putatively encoding highly hydrophobic proteins putatively associated with CMS. The ORF discovered in the MTV genome was identical with the previously described *Bobt* gene exhibiting a significantly higher expression in females than in hermaphrodites which is characteristic for CMS genes [323]. Some mt genomes harbored two or three CMS candidates, in contrast to KOV which contained none, despite a clear indication of CMS. In conclusion, *S. vulgaris* represents an ideal plant to study mitochondrial–nuclear interactions owing to its enormous variation in mt genomes associated with gene losses, rearrangements and with the origin of novel genes. Whether or not such mt diversity is mirrored by nuclear genomes is a topic of current research.

With five distinct completely sequenced mt genomes of *S. vulgaris* available, we are now adopting a transcriptomic approach to analyze global transcript



2 3
4

Figure 2: *Silene vulgaris* – the detailed view
Figure 3: Dachstein: Ancient populations of *Silene vulgaris* grow in the Alps, above the timberline, in gravel scree below Dachstein peak

Figure 4: James D. Stone (Guest postdoctoral fellow in the Laboratory of Plant Reproduction) investigates pollination of *Silene vulgaris* in the field

profiles and editing events (conversion of C to U in RNA) in male sterile and male fertile plants. We study modes of gene expression across entire mt genomes and their modifications in distinct nuclear backgrounds. Finally, we aim to understand the control of mt transcription in various tissues and genders and the roles of nuclear genes involved in male fertility.

The floral induction and the evolution of flowering-related genes in *Chenopodium* (goosefoot)

C. rubrum has been a traditional model plant in our institute for decades and detailed experimental protocols of its floral induction have been elaborated. *C. rubrum* is a short-day weedy plant which may be induced to flowering by a single period of darkness at seedling stage with two cotyledons and no true leaves. This feature makes possible to achieve synchronous growth and to study the regulatory genes participating in a signaling pathway, which is less complex than in other models such as *Arabidopsis* or rice.

The proper timing of flowering is an essential requirement for plant survival and adaptation. It is triggered by the *FLOWERING LOCUS T LIKE1* (*CrFTL1*) gene in *C. rubrum*, the homolog of the *FT* gene of *Arabidopsis*. We confirmed the florigenic function of *CrFTL1* by the complementation of *ft* mutants in *Arabidopsis*. The *CrFTL1* gene is expressed during the day. A dark–light transition following a permissive period of darkness is necessary for its activation. This requirement is unique among investigated short-day plants, which express *FT* homolog at night and do not need a dark–light transition for its activation [462].

FTL genes serving as key inducers of flowering have been so far discovered in each angiosperm species under study. They underwent frequent duplications and the paralogous copies often obtained a novel function. For example, the *BvFT1* paralog is a floral inhibitor in sugar beet, which belongs to the same family Amaranthaceae as *Chenopodium*. We discovered the second copy of *FTL* in *C. rubrum*, homologous to the sugar beet *BvFT1* gene. It arose by the duplication of *FT* gene before or in the course of the origin of the family Amaranthaceae. The function of *CrFTL2* is so far unknown. It is not a pseudogene, because its transcript level is high. *CrFTL2* shows an accelerated evolution rate and its expression pattern as well as overexpression in *Arabidopsis* are not consistent with any function in the process of flower induction.

We found that the third intron of the *FTL1* and *FTL2* genes was a sensitive genetic marker capable of resolving complicated phylogenetic relationships among closely related *Chenopodium* species. We used this marker to solve the origin of quinoa (*C. quinoa*), an important crop of South America. Quinoa is allotetraploid, but only one parent (related to recent American *Chenopodium* diploids) was known. We found (in collaboration with Brigham Young University in Provo, USA) that the second parent of quinoa was related to *C. suecicum* or *C. ficifolium*, which are recently distributed in Europe and Asia. Most likely, their relative grew in America in the past. We apply the *FTL* markers in a broad taxonomic survey of *Chenopodium* in collaboration with the Institute of Botany CAS in Pruhonice.

During the last three years we have constructed the reference transcriptome of *C. rubrum* based on 454 sequencing and Illumina HiSeq. We adopted bioinformatic tools in transcriptomic assembly, most recently the Evigene pipeline. We analyze differential gene expression to identify additional genes involved in floral induction in *C. rubrum*.

Figure 5: *Chenopodium rubrum* is a variable plant – its size, branching pattern and leaf shape depend on external conditions, e.g. on the photoperiod

Collaborative research

Our laboratory supports other teams at IEB to adopt the methods of molecular biology in plant research. We collaborated with Dr. R. Vaňková (Laboratory of Hormonal Regulations in Plants) and designed novel RT qPCR essays to estimate the expression of cytokinin-related genes [118, 388]. We also helped to adapt qPCR for the study of mycorrhiza in the Institute of Botany CAS in Pruhonice [266, 370]. Recently, lab members introduced transcriptomic approach at the University of South Bohemia in České Budějovice in the course of collaborative research on aquatic rootless plant *Utricularia vulgaris*.

Research projects: 29–35

Laboratory of Pollen Biology

Head of Laboratory: **doc. RNDr. David Honys, Ph.D.**
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The Laboratory of Pollen Biology IEB has continuously dedicated its activities to the fundamental research of plant reproductive development, sexual plant reproduction and genome stability. In this area, the laboratory has performed research leading to several pioneering and highly cited publications, namely the priority results on pollen developmental transcriptomics (in a broader sense the first study of effectively single-cell global gene expression profiling and its developmental dynamics in plants). These results also contributed to the establishment of the current paradigm in male gametophyte research towards asking and answering specific gene-oriented questions. Moreover, novel strategies to manipulate the gametophyte development and function are of current interest in agriculture and breeding. This is related to the introduction of new model species like *Physcomitrella*, hops and tomato.

The former Laboratory of Molecular Farming and DNA Repair joined in 2013 the Laboratory of Pollen Biology as a self-reliant Group of DNA Repair. The group continued on developing new approaches to study DNA damage and cell response to it as DNA repair of afflicted DNA lesions and possible consequences like induced mutations. Laboratory of Pollen Biology consists of three groups that are closely interconnected as documented by joint participation on grants and publications. In the years 2010–2014 we extended our previous activities and our research was focused mainly on several aspects of pollen development, pollen communication with fiale tissues and genome stability.

In the picture (from the left):
Front row: Ing. Lucia Mašinská /Research Assistant, Ing. Jana Feciková /Research Assistant, Mgr. Antónia Gibalová / PhD Student, Bc. Alena Náprstková /Diploma Student, RNDr. Lenka Steinbachová, Ph.D. /Postdoctoral Fellow, Ing. Tereza Bazgerová /PhD Student, Ing. Iveta Jelínková /Research Assistant
Rear row: Peter Darivčák /Diploma Student, Mgr. Jan Fíla /PhD Student, Said Hafidh, Ph.D. /Researcher, RNDr. Karel J. Angelis, CSc. /Senior Researcher, doc. RNDr. David Honys, Ph.D. /Head of Laboratory, Shailesh Kumar, Ph.D. / Postdoctoral Fellow, Mgr. Pavel Bokvaj /PhD Student, Bc. Filip Linhart /Diploma Student, RNDr. Nikoleta Dupľáková, Ph.D. /Researcher

Not in the picture:
RNDr. David Reňák, Ph.D. /Postdoctoral Fellow, Mgr. Katarína Kulichová /PhD student (honeymoon, diving in Indonesia), Mgr. Katarzyna Šolcová /PhD Student (maternity leave), Mgr. Marcela Holá /PhD Student, RNDr. Zuzana Gadiou, Ph.D. / Research Assistant, Bc. Radka Vágnerová /Diploma Student, Petra Rožnovská /Technician

Regulation of *Arabidopsis* pollen development

Screen and functional analyses of male gametophytic transcription factors

Male gametophyte development leading to the formation of a mature pollen is precisely controlled at various levels, including transcriptional, post-transcriptional and posttranslational. We focused on the identification of **pollen-expressed transcription factors** (TF) involved in the regulation of pollen development by screening of 74 T-DNA insertion lines representing 49 genes

of 21 TF families active in either early or late pollen development. Twenty nine screened lines showed strong phenotypic changes (i.e., ≥ 25% aberrant pollen) including four lines that produced a remarkably high proportion (70–100%) of disturbed pollen. Our results served as a basal information resource for future functional characterization of specific TFs in male gametophyte development [304] This phenotype screen was partly enabled by the optimization of our previously published protocol for large-scale separation of developing spores (Dupľáková, Reňák and Honys – resubmitted to Nature Protocols).

The expertise in transcriptomics and molecular techniques was exploited jointly with O. Lapčík (University of Chemistry an Technology, Prague) to study the biosynthesis and distribution of **plant secondary metabolites, isoflavonoids** [406] One of the selected TF was early male gametophytic gene ***AtREN1***, a close homolog of *HSFA5* gene, a member of the **heat shock transcription factor** (HSF) gene family. The *atren1* mutation causes multiple defects in male gametophyte development in both structure and function including defective pollen heat stress response, pollen phenotype abnormalities and pollen germination defects associated with the limited transmission via male gametophyte. We localized the AtREN1 protein specifically to the nucleolus that suggests its likely involvement in ribosomal RNA biogenesis therefore linking heat stress response with translation [531]. We have further functionally analysed the **regulatory network of bZIP transcription factors** in long-term collaboration with D. Twell, University of Leicester, UK. That extended our previous study of AtbZIP34 by the inclusion of its interactors AtbZIP18, AtbZIP52 (Gibalová, Honys *et al.*, manuscript in preparation).

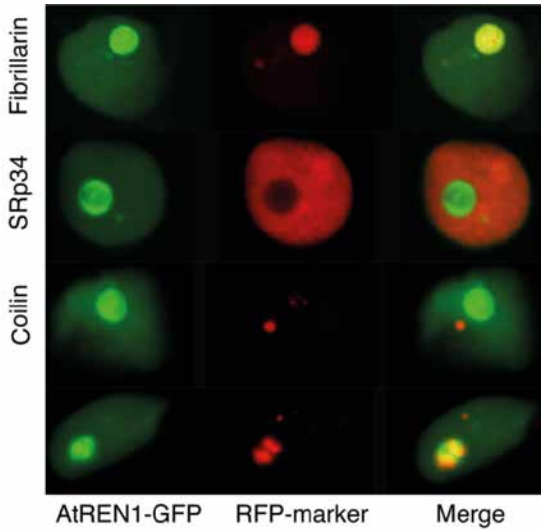

Figure 1: Co-localization of AtREN1-GFP with fibrillarin (nucleolus), SRp34 (nucleoplasm) and coilin (Cajal body). AtREN1 is specifically targeted into the nucleolus and accessory nuclear bodies, not into the general nucleoplasm [531].

The role of auxin in pollen development

Auxin is a key coordinative signal required for many aspects of plant development and its levels are controlled by auxin metabolism and intercellular auxin transport. Within the multilateral network lead by J. Friml (IST Austria), we found that the non-canonical member of PIN auxin transporter family, **PIN8** was active in *Arabidopsis* pollen and played a crucial role **in pollen development** and function by **regulating auxin homoeostasis and metabolism**. Our results revealed a role of the auxin transport in male gametophyte development in which the distinct actions of ER-localized PIN transporters maintained the auxin levels optimal for pollen development and pollen tube growth [231]. Our results of double mutant functional tests were also the first indication of the possible antagonistic role of PIN8 and PIN5 on the ER.

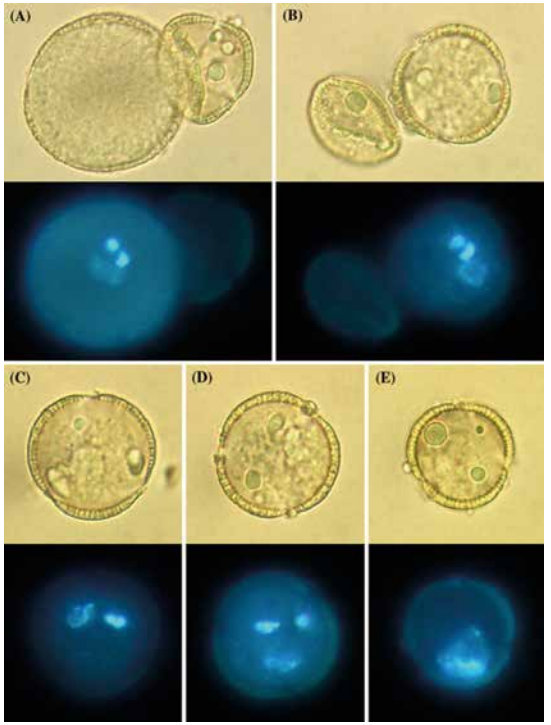

Figure 2: Phenotypic defects in *atbzip34* pollen. Bright field and fluorescence images after DAPI-staining are shown, (A) wild type and *atbzip34* collapsed pollen, (B–E) *atbzip34* pollen.

Tobacco pollen as a bicellular model for -omic studies

Tobacco pollen developmental transcriptomics and translatomics

The majority of flowering plants produce bicellular pollen. The two cells of the pollen grain are destined for separate fates in the male gametophyte, which

provides a unique opportunity to study genetic interactions that govern guided single-cell polar expansion of the growing pollen tube and the coordinated control of germ cell division and sperm cell fate specification.

We performed the first comprehensive **developmental transcriptomic analysis of the tobacco male gametophyte** representing the first plant species shedding bicellular pollen [244, 568]. These transcriptomic data sets presented a benchmark for future functional studies using developing pollen as a model. In addition, a comparative study of the *Arabidopsis* root-hair trichoblast transcriptome evaluated genetic factors and common genes and regulatory pathways involved in polarized cell-tip expansion. Reverse genetic analysis of selected candidates demonstrated that Cu/Zn superoxide dismutase 1 (CSD1), a WD-40 containing protein (BP130384), and Replication factor C1 (NtRFC1) were among the central regulators of pollen-tube tip growth. In addition, we highlighted the molecular dynamics of core cell-cycle regulators in the male gametophyte and postulated the first genetic model to account for the differential timing of spermatogenesis among angiosperms and its coordination with female gametogenesis. [244]. We further showed the **complexity of tobacco male gametophyte transcriptome** over long period of **progamic phase** – 24 h of pollen tube growth. We demonstrated the ongoing transcription activity and specific transcript accumulation in post-pollen mitosis II pollen tubes cultivated *in vitro*. In all, we have identified 320 genes that were newly transcribed as late as at least after 4h of pollen tube cultivation *in vitro*. This represented the first evidence for such late transcriptional activity in pollen tubes [568]. Comparison with tobacco pollen tube proteome even revealed that most of these transcripts were not translated (joint effort with Z. Zdráhal, CEITEC MU Brno,) that highlighted them as the likely candidates for **paternal complement** to postfertilization events. As pollen tube growth and competition in female pistil is a race of the fittest, there is an apparent evolutionary trend among higher plants to store large material reserves and nutrients during pollen maturation utilized predominantly for its rapid elongation in the pistil. Previous transcriptomic data from *Arabidopsis* showed massive expression of genes encoding proteins forming both ribosomal subunits that were accumulated in developing pollen, whereas their expression was not detectable in growing pollen tubes. We observed a similar phenomenon also in less-advanced bicellular tobacco pollen.

Recently, we have initiated completely new direction of our research, tobacco **pollen translatomics**. It has been well established that both transcription and translation play an important role in global and specific gene expression patterns during pollen maturation. On the contrary, germination of many pollen species has been shown to be largely independent of transcription but vitally dependent on translation of stored mRNAs. We demonstrated that **large ribonucleoprotein particles (EPP granules)** were formed in immature pollen where they contained translationally silent mRNAs and then served as a **long-term storage of mRNA** transported along with the translational machinery to the tip region where the translation took place. Such an organization is extremely useful in fast tip-growing pollen tube. Moreover, the asymmetric mRNA distribution is the determinant of protein gradient influencing cell polarity, cell fate and overall patterning during development. We proposed a model outlining the network

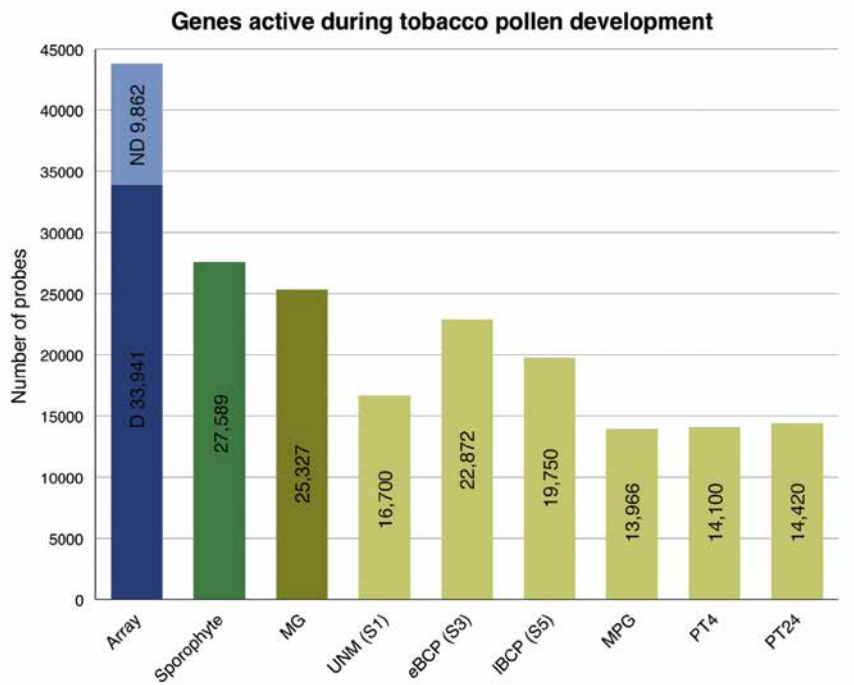

Figure 3:
Quantification of genes expressed in sporophyte and during tobacco male gametophyte development. The first column shows the total number of probes represented on the Agilent 44K Tobacco Genome Array indicating probes that gave positive signal in at least one sample ("D") and those that showed no expression in any sample ("ND"). MG – male gametophyte; UNM (S1) – uninucleate microspore (Stage 1); eBCP (S3) – early bicellular pollen (Stage 3); lBCP (S5) – late bicellular pollen (Stage 5); MPG – mature pollen grain; PT4 – 4-hr cultivated pollen tube; PT24 – 24-hr cultivated pollen tube.

of posttranscriptional control with a focus on the role of stored RNPs [565, 569] and started the functional characterization of RNA-binding proteins (collaboration with C. Bousquet-Antonelli, INRA Perpignan, France) We have extended our transcriptomic and proteomic analyses to cover three cytoplasmic subfractions containing mRNAs at different translational status and to demonstrate their developmental dynamics: 1) actively translated transcripts associated with **polysomes** (PS – termed **translatome**), 2) pollen mRNAs bound to pollen **stored ribonucleoprotein particles** (stored mRNPs/ free mRNPs – termed **mRNPome**) and 3) long-term stored transcripts on **EPP granules** (EPPs – termed **sequestrome** (Hafidh, Fíla, Honys *et al.*, manuscript in preparation).

Tobacco pollen developmental phosphoproteomics

Rapid changes of protein phosphorylation play a crucial role in the regulation of many cellular processes. Being post-translationally modified, phosphoproteins are often present in low abundance and tend to co-exist with their unphosphorylated isoforms within the cell.

Therefore we first developed the **protein extraction protocol** suitable for subsequent phosphoprotein enrichment from tough tobacco pollen tissue [123] and selected the appropriate **phosphopeptide enrichment procedure** (MOAC, metal oxide/hydroxide affinity chromatography) including the general review of phosphoprotein and phosphopeptide enrichment protocols [236]. We used the mOAC protocol to describe a population of differentially (de)phosphorylated phosphoprotein candidates from both mature and *in vitro* activated tobacco pollen grains. We identified and validated a set of 139 phosphoprotein candidates including the detection of 52 phosphorylation sites. As a joint effort with Dr. H.-P. Mock's (IPK Gatersleben) and Dr. R. Zahedi's (ISAS Dortmund) groups, we showed for the first time the **dynamics of protein phosphorylation and dephosphorylation** associated with early stages of pollen germination [237].

We finely extended this analysis to three time points – mature pollen, 5-min and 30-min-activated pollen. We identified 471 phosphopeptides (301 phosphoproteins) carrying 432 phosphorylation sites, position of which was exactly matched by mass spectrometry. The quantitative data highlighted the regulatory trends; we showed that several phosphopeptides representing the same phosphoprotein underwent different regulation, which pinpointed the **complexity and dynamics of protein phosphorylation** at the initiation of the **progamic phase**. Collectively, we showed the first phosphoproteomics data on activated pollen where the position of the respective phosphorylation sites was clearly demonstrated. (Fíla *et al.* – manuscript in revision in Mol Cell Proteomics;)

The published dataset was later used for the comparative study with the *Arabidopsis* mature pollen phosphoproteome (published by Mayank *et al.* 2012, Plant J 72: 89–101). The representation of the O-phosphorylated amino acids and the phosphorylation sites common for both *Arabidopsis* and tobacco phosphoproteins were listed as well as the phosphorylation motifs identified [464].

Tobacco secretomics

Some of the stored mRNAs encode for secreted proteins required for male-female signalling during pollen tube guidance. To understand the spectrum of translational regulation and mRNA storage, we studied **pollen tube secretomics** as "bottom-up" approach to link with our sequestrome transcriptome. As a novel approach, we have improvised a modified SIV **(semi-*in vivo*) technique**, SIV-PS (SIV pollen tube secretome) in collaboration with M. Johnson, Brown University, USA and R. Palanivelu, Univ. of Arizona, USA. As a joint effort with Z. Zdráhal's group (CEITEC MU, Brno), we performed gel-free LC-MS/MS for highthroughput analysis of pollen-tube-secreted proteins. Our approach has led to the identification of over 341 protein groups on average (801 accessions). Among them are **pollen tube-secreted ligands and receptor proteins** representing potential male components in perceiving ovule-emitted cues for guidance [467]. Primarily proteins of ≤ 30 kDa (60%) of which 40% were ≤ 20 kDa dominated the pollen tube secretome. They included Plant defensin subfamily, Cysteine-rich, LORELEI-like GPI-anchored 3 (LLG3), Thionin-like protein, RNAses, lipid transfer proteins (LTPs), pollen Ole-e-allergen, arabinogalactants, pectinases and invertases. The pollen tube secretome comprised vastly of non-classical type of secreted proteins. Intriguingly, we discovered that TCTP1, a **non-classically-secreted protein hijacked the classical secretory pathway** and co-localized with nanovesicles exosome marker Ole-e-1. This follow-up study has uncovered novel pistil-dependent pollen tube-secreted proteins critical for establishing **male-female signalling** interaction map for successful sperm cells delivery and fertilization and as means to overcome interspecies pre-zygotic barriers (Hafidh *et al.*, manuscript in revision in Genome Biology). The link between pollen tube sequestrome with the secretome is currently evaluated.

DNA repair and chromosome maintenance

The Group of DNA Repair is world-wide renowned for developing and use of microscopic based electrophoretic analysis of single cell genomic DNA damage –

"**Comet assay**" in plants with modifications enabling **detection of specific DNA lesions** as single (SSB) and double (DSB) strand breaks, DNA–DNA and DNA–protein crosslinks and specific base modifications as oxidative damage or formation of UV photoproducts CPDs.

This methodological advantage of direct measurement of DNA damage enabled to established picture of overall two phase DSB repair kinetic with extremely rapid (so far unrecognized) first phase, which depends on Structure Maintenance of Chromosome (SMC) proteins particularly on complex SMC5/6. SMC protein complexes form heteroduplexes that can bind sister chromatid for various purposes as SMC1/3 – chromosome cohesion or SMC2/4 chromosome condensation. Our first observation and description of novel DSB repair pathway

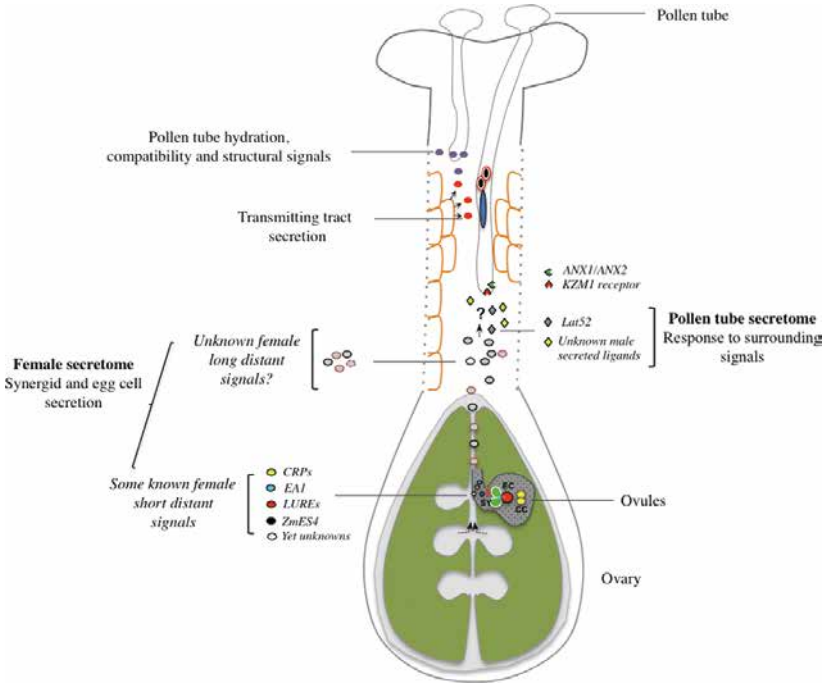

Figure 4: Sketch of pollen tube growth through the pistil exemplifying secreted peptides known to be involved in pollen tube perception, with the majority being those identified from the female reproductive tissues [467].

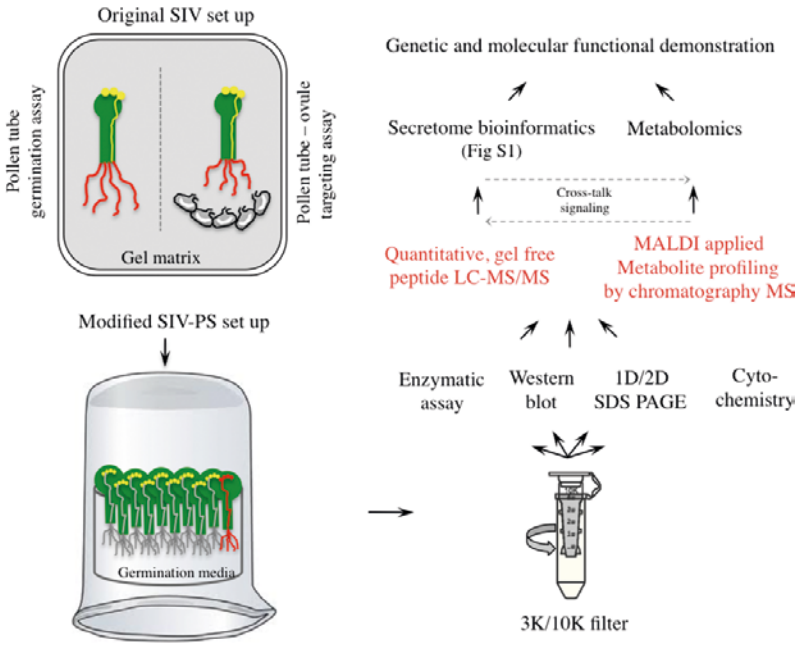

Figure 5: Stepwise guidance on capturing and identification of pollen-tube-secreted proteins and metabolites in the semi-*in vivo* setup [467].

in *Arabidopsis* and the important role of SMC5/6 was further investigated during 2010–2014 period.

We scouted for new genes thought to be potentially involved in DSB repair to prove their participation by affecting kinetic profile. Firstly in cooperation with G. Böhmdorfer of GMI, Vienna, we studied and described for the first time involvement of **SMCHD** (**proteins** containing "Hinge" region of SMC proteins) protein GMI1 in recombination and DSB repair [113]. In cooperation with J. da Costa-Nunes, Univ. Of Lisboa we continued on deciphering the role of **RAD21 kleisins of SMC1/3 complex** and found out the sequential circularization of cohesin SMC1/3 complex firstly by RAD21.1 followed by induced RAD21.3, which return after completion of DSB repair to quiescence RAD21.1 circularization [456]. To ascertain the mechanism of procession of uneven DSB ends we investigated possible role of POLΛ in partial filling of gaps in cooperation with T. Furukawa and A.B. Britt, UC Davis (currently reviewed in Frontiers in Plant Science, section Plant Physiology for publication).

The hurdles of using *Arabidopsis* model plant for DNA damage and repair study led us to acquire moss ***Physcomitrella patens*** we **used for the production of recombinant antibodies** (ID 371127). Physcomitrella besides uniquely high homologous recombination rates pose other advantages as haploid gametophyte growing in early stages in filaments [85]. This enables by shearing to initiate culture of filament fragments 3–5 cells long, where up to 50% of apical cells are dividing.

When compared to older culture one can distinguish processes in dividing vs. Differentiated tissue. We described this approach when we in cooperation with A. Cuming, CPS, Univ. of Leeds, F. Nogue, INRA Versailles and D. Scheafer, Univ. de Neuchâtel studied moss mutants of essential DSB repair MRN (MRE11, RAD50 and NBS1) complex [257]. Our group took advantage of haploid state and thus easy selection of mutants to study mutagenesis by positive selection of adenineribosidephosphotransferase (APT) mutants rendering resistance to 2-fluoroadenine (2FA). By combining comet and mutagenesis assays in moss enabled us to show that sensitivity of *ppmre11* and *pprad50* mutants to DSB induction is not due to defect of their capacity to repair them, but rather due to unrestricted high, though error-prone DSB repair leading to **unsupervised mutagenesis** largely representing as deletions of various sizes. This draws a picture of blocked participation of error-free homologous recombination and shifting equilibrium toward error-prone non-homologous end joining (NHEJ) pathway inducing mutations and inactivation of essential genes, thus expressing sensitive phenotype.

We explored this Physcomitrella-based combined approach to further study the role PpLIG4 [364]) and collected extensive mutagenesis data in various Physcomitrella repair background lines induced by genotoxins potentially representing various environmental stresses. Finally, in collaboration with J. Fajkus, Z. Zdráhal (CEITEC MU, Brno) and E. Sýkorová (Institute of Biophysics CAS, Brno) we are investigating the role of **plant telomerase and telomerase-associated proteins** in telomeres maintenance in Physcomitrella, Algea, Arabidiopsis and tobacco. We found in Physcomitrella that telomere phenotypes are absent and DSB repair kinetics is not affected in mutants for DSB factors involved in non-homologous end joining (NHEJ). This is compliant with the overal dominance of homologous recombination over NHEJ pathways in the moss, contrary to the inverse situation in flowering plants (Fojtová *et al.*, Plant Mol Biol 2015 87:591–601) and that algea strains *Zygnema* sp. 436 and *Zygnema circumcatinatum* TEL 181 are not responsive to DSB induction and repair at all.

Brief list of national and international collaborators (sorted alphabetically)

Dr. B. Banović, University of Belgrade, Serbia; Dr. G. Böhmdorfer, Gregor Mendel Institute, Vienna, Austria; Dr. C. Bousquet-Antonelli, INRA Perpignan, France; Dr. Sofija Božinović, Zemun Polje Maize Research Institute, Serbia; Prof. A.B. Britt and Dr. T. Furukawa, UC Davis, CA, USA; Dr. J. da Costa-Nunes, University of Lisboa, Portugal; Dr. A. Cuming, CPS, University of Leeds, UK; Dr. P. Doerner, University of Edinburgh, UK; Prof. T. Dresselhaus, University of Regensburg, Germany; Prof. J. Fajkus, Assoc. Prof. Z. Zdráhal, Dr. M. Fojtová, CEITEC MU, Brno, Czech Republic; Dr. N. Firon, Volcano Center, Bet Dagan, Israel; Prof. J. Friml, IST Austria, Austria; Prof. M. Johnson, Brown University, USA; Prof. O. Lapčík, University of Chemistry and Technology, Prague, Czech Republic; Dr. J. Matoušek, Biological Center, České Budějovice, Czech Republic; Dr. H.-P. Mock and Dr. A. Matros, IPK Gatersleben, Germany; Dr. F. Nogue, INRA Versailles, France; Prof. Ravi Palanivelu, University of Arizona, Tucson, AZ, USA; Dr. R. Peyman-Zahedi, ISAS Dortmund, Germany; D. Scheafer, University de Neuchâtel, Switzerland; Prof. Enrico Schleiff, Dr. Klaus-Dieter Scharf, Goethe University Frankfurt a/Main, Germany; Dr. E. Sýkorová, IBP CAS, Brno, Czech Republic; Prof. D. Twell, University of Leicester, UK; doc. Dr. Zbyněk Zdráhal, CEITEC Brno

Research projects: 29, 40–54

Laboratory of Signal Transduction

Head of Laboratory: **RNDr. Jan Martinec, CSc.**
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The Laboratory of Signal Transduction conducts research on phospholipid signalling. Currently, it is mainly investigating the role of non-specific phospholipase C (NPC) in plant development and stress responses.

In the picture (from the left): Ing. Přemysl Pejchar, Ph.D. /Researcher, Ing. Jitka Brouzdová /PhD Student, Kateřina Vltavská /Technician, Ing. Zuzana Krčková /PhD Student, Mgr. Michal Daněk /PhD Student, Ing. Vladimíra Hajná /PhD Student, RNDr. Jan Martinec, CSc. /Head of Laboratory

Not in the picture: Ing. Daniela Kocourková, Ph.D. */Research Assistant*

Non-specific phospholipase C (NPC) catalyses the hydrolysis of phosphatidylcholine (PC) to generate phosphocholine and diacylglycerol (DAG). NPC has a long tradition in animal signal transduction (where it is called PC-PLC) to generate DAG as a secondary messenger in addition to the well-known phosphatidylinositol splitting phospholipase C (PI-PLC). Until 2005, however, there was no information on the role of NPC in plants at the genome level.

Since 2010, we have published a series of articles on the functional analysis of NPCs. In collaboration with a research group from Hannover, we studied the role of NPCs in plant development and hormone signalling [98]. We showed for the first time that two members of the *Arabidopsis* NPC protein family, NPC3 and NPC4, are important in auxin as well as brassinolide-mediated signalling in relation to root growth. We hypothesized that at least one NPC is a plant signalling enzyme in brassinolide signal transduction.

In following articles, we reported on the role of NPC in the response of plants to aluminium toxicity. Aluminium ions (Al) are an acknowledged major toxin in crop production in acidic soils. For this reason, aluminium plant interaction is now widely studied. However, the exact molecular mechanism and time sequence of individual changes following Al exposure remains unclear. In the first of our articles [60], we showed biochemically that a significant decrease in DAG in cells treated with $AlCl_3$ was caused by an inhibition of NPC activity. In the next article, we focused on a plasma membrane-bound isoform of NPC, NPC4. We examined the impact of Al on the expression, activity, and function of NPC4. The growth of tobacco pollen tubes rapidly arrested by Al was partially rescued by the overexpression of AtNPC4 while *Arabidopsis* npc4 knockout lines were found to be more sensitive to Al stress during long-term exposure to Al under conditions of low phosphate. Our observations suggested that NPC4 plays a role in both early and long-term responses to Al stress.

Salt stress was another environmental effect that was studied in connection with *Arabidopsis* NPCs in our laboratory [143]. Expression of *NPC4* was highly induced by NaCl. Results from histochemical analysis of PNPC4:GUS plants showed localization of salt-induced expression in root tips. On the biochemical level, increased NPC enzyme activity, as indicated by accumulation of DAG, was observed after salt treatment of *Arabidopsis* seedlings. Phenotype analysis of *NPC4* knockout plants showed increased sensitivity to salinity compared to wild-type plants. Expression levels of abscisic acid-related genes *ABI1*, *ABI2*, *RAB18*, *PP2CA*, and *SOT12* were substantially reduced in salt-treated *npc4* plants. These observations demonstrated a role for NPC4 in the response of *Arabidopsis* to salt stress.

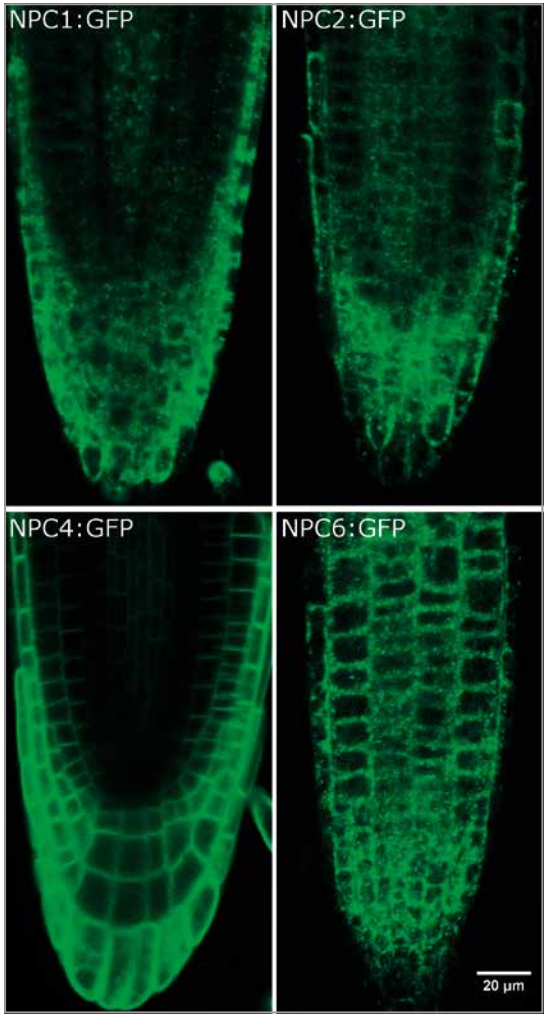


Figure 1: Individual non-specific phospholipase C isoforms exhibit distinct subcellular localization in *Arabidopsis* seedling roots.

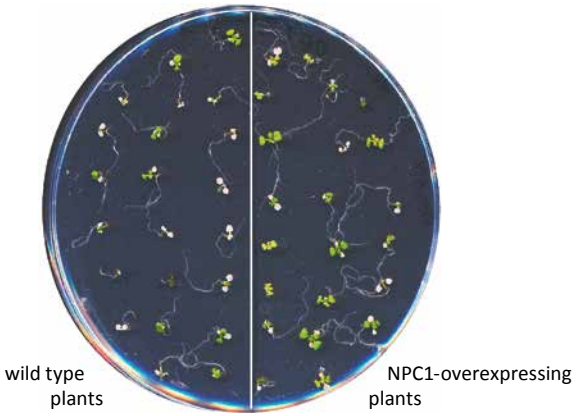
Currently, three more articles on with NPC are in preparation. First, we found that manipulation with *NPC1* expression leads to altered heat sensitivity in *Arabidopsis*. Second, we demonstrated that the level of *NPC2* transcripts decreased during PAMP (pathogen-associated molecular patterns)-triggered immunity as well as during effector-triggered immunity. Third, we analysed the NPC protein family in tobacco.

In 2013, we also published a review on non-specific phospholipase C in plants. This review for the first time summarized current data on this relatively new plant protein family while focusing on its sequence analysis, biochemical properties, cellular and tissue distribution and physiological functions. Possible modes of action were also discussed [410]. It should be noted as well that out of 11 articles on plant NPC currently included in the WOS database, 5 are from the Laboratory of Signal Transduction.

In addition to work on NPC, we participate in a number of other research projects via collaboration with other research teams, both within the Institute of Experimental Botany and from other institutes and universities in the Czech Republic. Within the Institute of Experimental Botany, we have long collaboration with the Laboratory of Pathological Plant Physiology [367, 504]. Further, we cooperate with the Laboratory of Cell Biology [60, 63, 167, 295, 298, 410, 525, 577] and with the Laboratory of Hormonal Regulations in Plants [31]. We have a long-enduring collaboration with the Institute of Chemical Technology Prague [60, 63, 132, 143, 367, 504] and with Charles University in Prague [60, 267].

On an international level, we work with the research group led by Dr. Günter Scherer from Leibniz Universität Hannover already mentioned. From 2010–2014, two joint publications were published [98, 143]. Another fruitful collaboration is with Dr. Eric Ruelland from Université Paris Est-Créteil (UPEC), formerly from UPMC Paris. We published two reviews as a result. One was on the role of phosphoglycerolipids in plant hormone signal transduction [367] (together with the Laboratory of Pathological Plant Physiology) and another was on NPC [410]. A joint article is currently under revision (regarding NPC1 and heat stress, see above). We also have a long-term collaboration with the group of Dr. Volodymyr Kravets from the Institute of Bioorganic Chemistry and Petrochemistry, National Academy of Sciences of Ukraine [261, 410].

Figure 2: Overexpression of *NPC1* led to higher resistence to heat stress in *Arabidopsis*. Wild type and NPC1-overexpressing seedlings were grown on agar plates at 22 °C for seven days. The plates were exposed to heat (42 °C, 45 min), then returned to control conditions. The picture was taken seven days after heat stress.



Research projects: 3, 117, 127, 128, 131–133, 139

Laboratory of Stress Physiology

Head of Laboratory: **RNDr. Naďa Wilhelmová, CSc.**
Phone: +420 225 106 814; E-Mail: wilhelmova@ueb.cas.cz

The Laboratory of Stress Physiology focuses on two major areas of research: nitrosative and oxidative stress and, antioxidant defence during ageing and/or under stress. In the first area of investigation, we carried out a study on nitric oxide and reactive nitrogen species metabolism during natural and stress induced leaf senescence.

The effect of cytokinins (CK) was included in these studies. Increased CK in tobacco leaves led to improved Zinc tolerance according to photosynthetic and transpiration rates and also to accumulation of free amino acids. CK boosted Zn tolerance was not associated with lower Zn accumulation in leaves. The Zn tolerance of CK transformants was associated with maintenance of the accumulation of free amino acids that play a role in stress adaptation i.e. methionine and γ-aminobutyrate. Conversely, asparagine, a major compound associated with senescence, was maintained at lower levels in leaves with enhanced CK. The Nitric Oxide (NO) content and nitrate reductase activity decreased with leaf age, independently of CK content. On the other hand, significant increase in nitrated protein tyrosine was observed with leaf ageing, indicating elevated nitrosative stress which CK mitigated. Higher activity of nitrosoglutathione reductase was able to prevent NO production from nitrosoglutathione. DNA damage was detected during both natural and stress induced senescence. Zn promoted DNA damage predominantly in roots. We also studied stress tolerance in tobacco with different inserted CKX genes and different promoters, resulting in lower CK content in leaves. Such plants were more tolerant to stress. No significantly better antioxidant protection was found. Only transgenic tobacco with introduced CKX2 under the control of the 35S promoter had a more effective antioxidant system and aged more slowly than WT. We also devoted attention to explaining the variable tolerance of maize genotypes to drought stress. More tolerant genotypes allowed photosynthesis to proceed and synthesise protecting proteins, including antioxidative enzymes.

In the picture (from the left):
Front line: RNDr. Naďa Wilhelmová, CSc. /Head of Laboratory, Mgr. Renáta Schnablová Ph.D. /Postdoctoral Fellow
Upper line: Mgr. Daniel Haisel, Ph.D. /Researcher, Lenka Kolčabová /Technician, RNDr. Helena Synková, CSc. /Researcher

Research project: 38

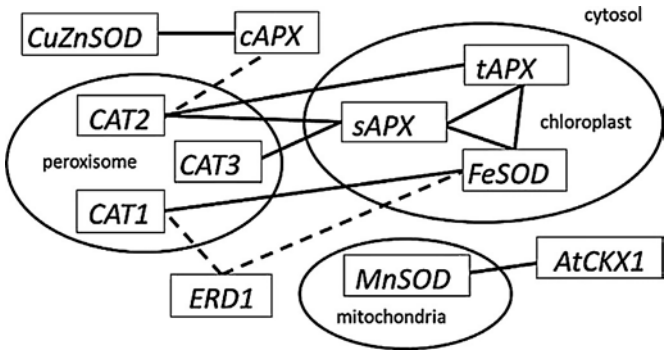


Figure: Schematic representation of the relationships among the expression profiles of individual antioxidant enzymes in tobacco. Solid and dashed lines represent positive and negative correlations, respectively, with coefficient > |0.5|. (1) Chloroplastic transcripts, sAPX, tAPX and FeSOD, were correlated. (2) Transcript profiles of antioxidant enzymes in chloroplasts and peroxisomes followed similar trends. (3) CAT transcript levels were not interrelated, (4) Cytosolic CuZnSOD correlated with another stress protective enzyme, cAPX. (5) MnSOD exhibited positive correlation with AtCKX1 expression. [495]

Laboratory of Virology

Head of Laboratory: **doc. RNDr. Noemi Čeřovská, CSc.**
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The Laboratory of Virology has contributed to the understanding and management of plant viral diseases and to the development of new and innovative ways to control their incidence. For this purpose, we have generated specific antibodies against plant viruses using various recombinant viral proteins and transgenic potato cultivar with increased resistance to PLRV has been developed. Our main focus is on the biotechnological use of plant viruses in particular on transient expression of proteins with therapeutic importance. Our laboratory has successfully expressed different antigens of HPV-16 fused to PVX CP using PVX-based vector in plants, where the antigens were presented on the surface of PVX particles. We have also started with the improvement of expression system for antigen presentation in putative surface exposed loops within PVX CP. In collaboration with Danforth Plant Science Center and USDA, St Louis USA, we have developed a novel virus vector-derived expression platform based on in planta encapsidation of defective plant virus by coat protein expressed in trans and another system for controlled and tissues specific protein expression in soybean seed.

In the picture (from the left): Karolina Müllerová /Technician, Renata Hadámková /Technician, Mgr. Tomáš Moravec, Ph.D. /Researcher, doc. RNDr. Noemi Čeřovská, CSc. /Head of Laboratory, Dr.rer.nat. Ing. Helena Plchová /Researcher, Mgr. Petr Vaculík /PhD Student, Glenn van Haesendonck /Hosting Student (Belgium)

Not in the picture: Dagmar Cibochová /Technician († 2013), Ing. Jan Fousek, Ph.D. /Technician, Mgr. Hana Hoffmeisterová, Ph.D. /Postdoctoral Fellow (maternity leave), RNDr. Oldřich Navrátil, CSc. /Research Assistant, Bc. Lucie Dlabalová-Kešnerová /Diploma Student (until 2014), Mgr. Jitka Folwarczna /PhD Student (until 2012), Ondřej Lidický /Diploma Student (until 2010)

The Laboratory of Virology has reported the strategy for production of polyclonal antibodies against both structural and non-structural recombinant proteins of potato-infecting viruses. Recombinant viral proteins expressed in bacteria showed interesting potential as an alternative source of antigens for raising specific antibodies to plant viruses, which can be produced in large quantities adapted for specific applications. The obtained polyclonal antibodies can be used not only for virus detection but also for the study of viral replication cycle [8, 170, 224]. In collaboration with the Potato Breeding Institute in Havlickuv Brod we have developed transgenic potato cultivars with increased resistance to Potato Leafroll Virus (PLRV) and set of primers for quantitative detection of viral load in infected materials (industrial designs (2012): CZ 23383 and CZ 23384).

Biosafe and efficient transient gene expression in plants could give a fast, flexible and reproducible technique for large quantity production of useful proteins. Our laboratory is focused on the expression of the heterologous proteins in plant host cells at quantities sufficient for practical use. Particularly we have explored possibility to transiently express epitopes of *Human papillomavirus* type 16 (HPV-16) to prepare experimental vaccine against HPV-16. The HPV-16 along with other high risk papillomaviruses are responsible for approximately half a million new cervical cancer cases every year. Current vaccines provide limited cross-protection between various HPV types and could only be used as prophylactic treatment prior to the HPV infection. Experimental vaccines are being developed to address either one or both of these issues.

For the transient expression of HPV-16 antigens we used viral vector based on *Potato virus X* (PVX). It has been shown that coat protein (CP) of plant viruses represents an ideal, highly ordered, multivalent scaffold

to be used for the display of immunogenic epitopes. So far the PVX based vector has been utilized in two ways – (a) for the production of non-fused full-length proteins/peptides or (b) for proteins/peptides fused to the N-terminus of PVX-CP and their presentation on the surface of viral particles. We have used both well-established means for epitope presentation as well as novel strategies developed in our team.

We have successfully expressed $L2_{108–120}$-epitope derived from minor capsid protein HPV-16 L2 fused to the N-terminus of PVX CP in plants. The PVX chimeric particles displaying immunoreactive epitopes moved systemically in experimental plants and achieved high yields [223].

We have also used C-terminus of PVX CP for peptide presentation for the first time. Mutagenized E7 oncoprotein (E7ggg) from HPV-16 fused to the C-terminus of PVX CP was successfully expressed in plants [169]. The same approach was used for the expression of HPV-16 $L2_{108–120}$-epitope on the C-terminus of PVX CP [223, 248]. To display another HPV-16 antigens on PVX particles mutagenized oncoprotein E6 (E6GT) was transiently expressed as the C-terminal fusion with PVX CP using the same system previously designed for E7ggg. The chimeric protein accumulated in inoculated leaves of *N. benthamiana* plants and successfully formed viral particles [343].

In addition, we are developing a more reliable system for antigens presentation on the surface of viral particles for experimental vaccine production. We have started with the expression system improvement by searching for new fusion positions located within PVX CP. Based on spatial structure model of the PVX CP subunit in a virion we have inserted HPV E7 epitope (aa 44–60) together with 6xHis or StrepII tag into different putative surface exposed loops [Vaculik *et al.*, PCTOC, in press].

Furthermore, we are investigating whether PVX induces DNA damage in nuclei and mutations in leaves using comet and somatic mutation assays respectively in PVX inoculated tobacco leaves [451].

We have also developed a novel viral vector based expression platform that can be used in plant molecular farming. The system is based on in planta encapsidation of defective plant virus by coat protein expressed in trans. It has the advantage that the production in plants can be efficiently inoculated without the use of *Agrobacterium* and simultaneously inhibit virus transmission by secondary infection. This system has been forwarded for patent application CZ201100843-A3 in the Czech Republic.

In cooperation with the scientists at the Danforth Plant Science Center and USDA, St. Louis USA we have successfully developed a system for controlled and tissues specific protein expression in soybean seed [72].

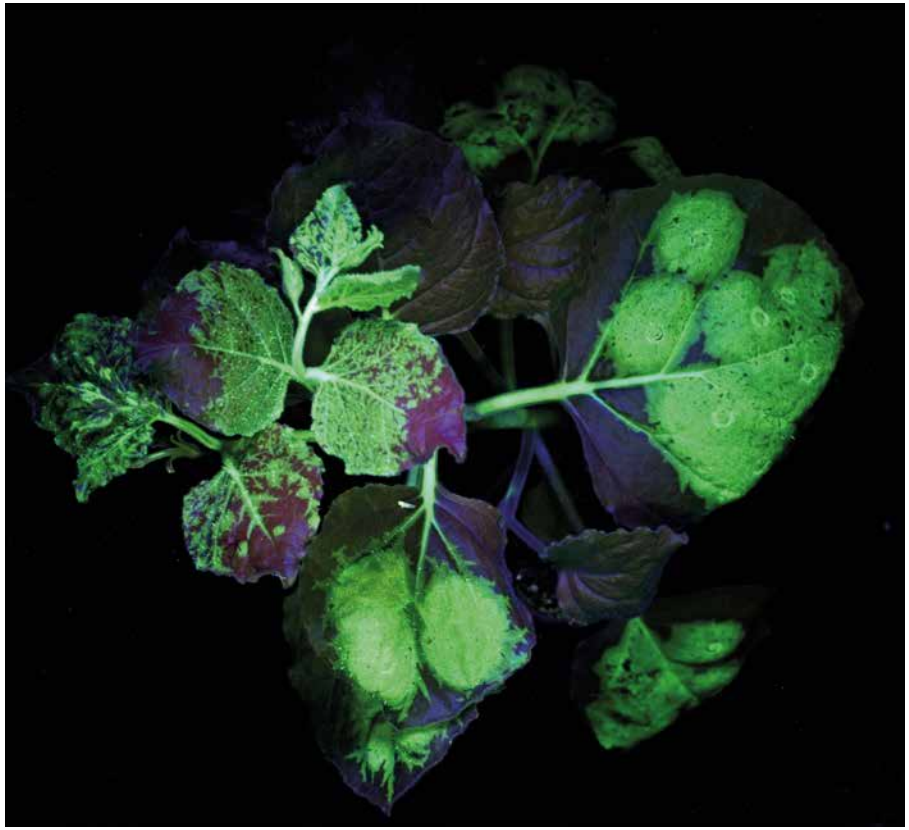

Figure: *N. benthamiana* plant infected with plant virus that expresses jellyfish green fluorescent protein (GFP). Scientists use fluorescent protein so that they can visualize the spread of the viral infection through the plant. Ten days after innoculation the virus translocates from the point of infection to the plant vascular tissues and moves to the young growing leaves. Virus infection can also reach the flowers, however most of plant viruses cannot access the seed, thus the new plant generation will be healthy and virus free.

Research projects: 2, 36, 37, 39

Station of Apple Breeding for Disease Resistance

Head of Laboratory:
Ing. Jaroslav Tupý, DrSc.

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In the picture (from the left):
Standing: RNDr. Ludmila Říhová /Research Assistant, Ing. Jan Zima /Research Assistant, Dagmar Švestková /Technician, Ing. Miloslav Juříček, CSc. /Researcher, Jarmila Veverková /Secretary, Ing. Radek Černý /PhD Student, Ing. Jaroslav Tupý, DrSc. /Head of Laboratory, Ing. Otto Louda /Research Assistant, Naděžda Nováková /Guest, Květoslava Rabochová /Technician
Sitting: Zdeněk Mikula /Technician, Zdeněk Haleš /Dipl. Technician

This is a continuation of a long-term project on breeding high quality apple varieties resistant to scab caused by *Venturia inaequalis*, the most widespread and harmful apple disease.

The first source of resistance against scab used in breeding was *Malus floribunda* bearing the resistance gene *Vf*. The gene can be transferred to the progeny simply by crossing and the presence of the gene in plants is evidenced using specific molecular markers. A resistance hybrid has commercial potential only when the growth/bearing characteristics and fruit qualities fulfil the requirements of the grower and the market. To achieve this, there are usually several progeny generations needed. At present in most, resistant varieties, scab resistance is encoded monogenetically by the gen *Vf*.

Currently, this type of monogenic resistance has been overcome in some localities by new races of the fungus. This motivated us to focus on new sources of scab resistance. Our ongoing research is on improving the commercial qualities of resistant varieties and on a combination of *Vf* resistance with tolerance against scab encoded polygenetically in order to render scab resistance more durable. Efficient use of polygenic resistance in apple breeding will require us to develop molecular markers to identify the genes involved.

The results were incorporated into practice by conclusion of License Agreements predominantly with producers of propagation plant material and/or apples of protected varieties. The royalties are paid to the Institute of Experimental Botany CAS, v. v. i., as licensor. The number of the trees sold depends mainly on

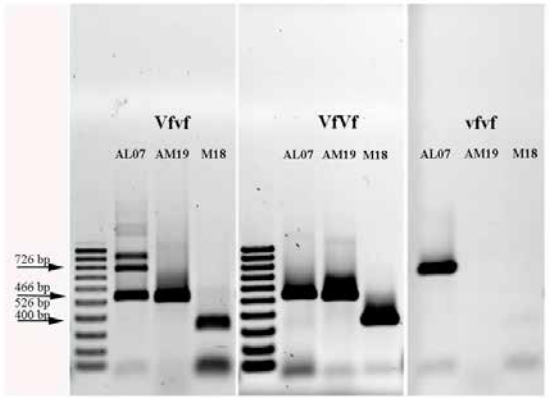


Figure 1: Multi-PCR detection of dominant and recessive alleles *Rvi6* (*Vf*) in the new scab resistant varieties of apple trees

the quality of the variety, marketing and fruit selling organizations. Of the License Agreements concluded before 2010, the most successful were the varieties Topaz with its red mutation Red Topaz. Topaz is the most planted scab resistant variety in Europe. Topaz is very popular in organic fruit growers. More than 400 000 trees a year were planted on a total surface of 1000 ha in the year 2014.

Figure 2: Topaz in supermarkets in Germany

Very popular, mainly in the USA and Chile is the variety UEB 32642 known under the Trademark Opal which is registered in more than 40 countries. In Europe the international society fruit.select was established by 5 members of plant nurseries.

In the USA, the independent society Perishables Group rated Opal as the highest grade “excellent” based on large scale testing by 936 consumers. The variety is protected by a Plant Patent in the USA and by Community Plant variety Right in EU and later applied for UPOV protection in a number of countries (Australia, Brazil, Chile, South Africa, Canada, Morocco, Mexico and New Zealand).

In the USA, Opal trees are grown at the farm of Ralph Broetje, Washington State and the Opal apples are exclusively sold by the society First Fruits a portion of all sales of Opal apples being awarded for charitable purposes. In 2015, the estimated donation was 150 000 US$. In the years 2010 to 2014 the total number of Opal trees sold exceeded 1.3 million.

In the years 2010 to 2014, 16 Licensee Agreements were concluded for varieties with scab resistance *Vf* newly released for commercialization. Of particular importance, is the contract with an American society for varieties with compact columnar growth habit for the territory of the whole world. Columnar varieties released were protected in the EU and in the USA. This type of tree is sold for home gardens. In the years 2010 to 2014 about 300 000 trees were sold in the Netherlands, Germany, the USA, Switzerland and the Czech Republic.

The total number of trees of UEB varieties sold was more than 1.2 million per year. The yearly income of royalties from licensed varieties increased from 4.47 million CZK in 2010 to 8.06 million CZK in 2014.

Figure 3: Opal® in supermarkets in the USA

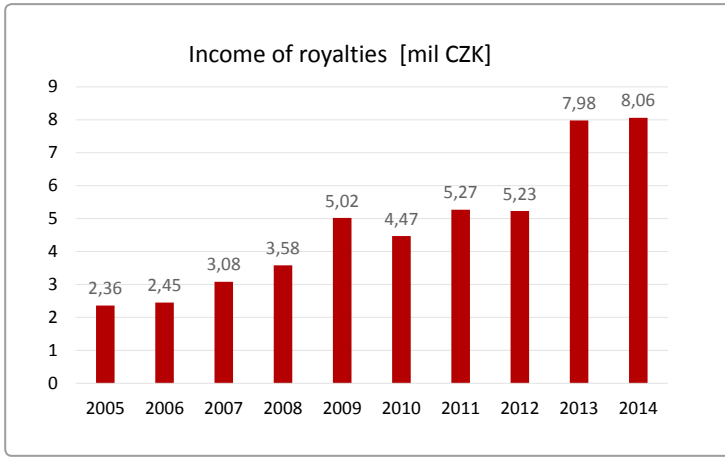


Figure 4: Income from royalties for licensed varieties of apple trees

Research project: 1

Research Projects 2010–2014

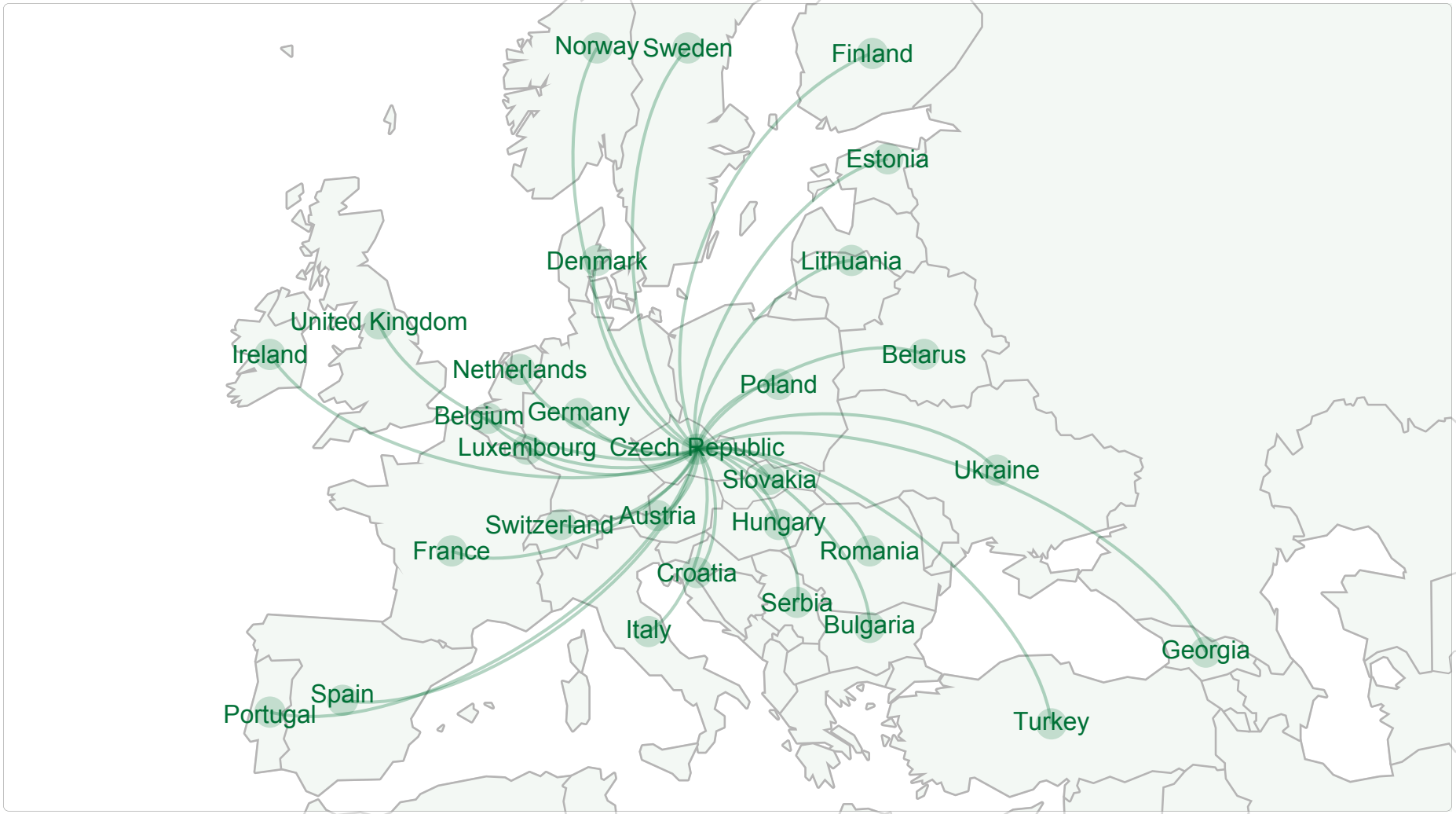
1. ME10038, Chromatin regulation of Phaseolin transcription
2. 1M06030, Functional genomics and proteomics for crop improvement
3. LC06034, Regulation of morphogenesis of plant cells and organs
4. IAA600380701, Alternative ways regulating intra- and extracellular concentrations and activities of isoprenoid cytokinins in plants
5. IAA600380805, Metabolic regulations of root to shoot hormonal signaling in plants
6. QH82231, Production of strawberries in organic system of growing
7. KJB600380904, Transcriptional regulation of PIN genes
8. GA206/09/2062, The role of cytokinins and polyamines in heat stress response and thermotolerance in tobacco and Arabidopsis plants
9. GA522/09/2058, Dynamics of plant hormones and proteome during the cold acclimation in winter and spring wheat and selected recombinants
10. MEB040924, Changes in the plant hormone metabolism during abiotic stress processes
11. MEB040925, Dissection on physiological and molecular levels of the effects of climate extremities on plants
12. OC09084, Characterization of stress hormone levels in strawberry
13. GAP506/11/0774, Integrating proteomic and genomic tools to contribute evolutionary processes across the plant kingdom with emphasis to the family of cytokinins
14. GAP305/11/2476, Auxin transport and cytoskeleton in the morphogenesis of plant cells
15. GAP305/11/0797, Molecular mechanisms controlling homeostasis of plant growth regulatory compound auxin
16. TA01011802, Auxinic herbicides: Design of herbicides with modified effectiveness and/or species selectivity
17. GPP305/11/P797, Cytoskeletal proteins mediating targeted deposition of auxin transporters
18. LD11073, The role of plant hormones in the response to salt stress – comparison of Arabidopsis and Thellungiella
19. GPP501/12/P951, The role of auxin binding protein 1-mediated signaling in the control of vesicle trafficking in plant cells
20. LD14120, The impact of phosphorus nutrition on strigolactone, cytokinin and auxin cross-talk
21. KJB600380802, Transcriptome of the exo70A1 mutant and cellular roles of EXO70A1, a putative subunit of the exocyst complex, in Arabidopsis thaliana
22. IAA601110916, Phosphatidic acid and diacylglycerol-mediated signalling in the polar growth of plant cells
23. GP522/09/P299, Characterisation of NADPH oxidase from tobacco pollen and its role in regulation of polar cell expansion
24. GAP305/10/0433, Characterization of selected representatives of novel plant Class II and Class III formin families
25. GAP501/10/2081, The role of the exocyst complex in the plant-pathogen interaction
26. GAP305/11/1629, Functions of the plant exocyst tethering complex in exocytosis, cell division and cell wall biogenesis
27. GPP501/11/P853, The exocyst, secretory vesicles tethering complex, in auxin transport polarization
28. GA13-19073S, Multiscale analysis of signalling phospholipids and their interaction protein partners in the regulation of plant tip growth
29. LC06004, Integration of research activities to study the plant genome

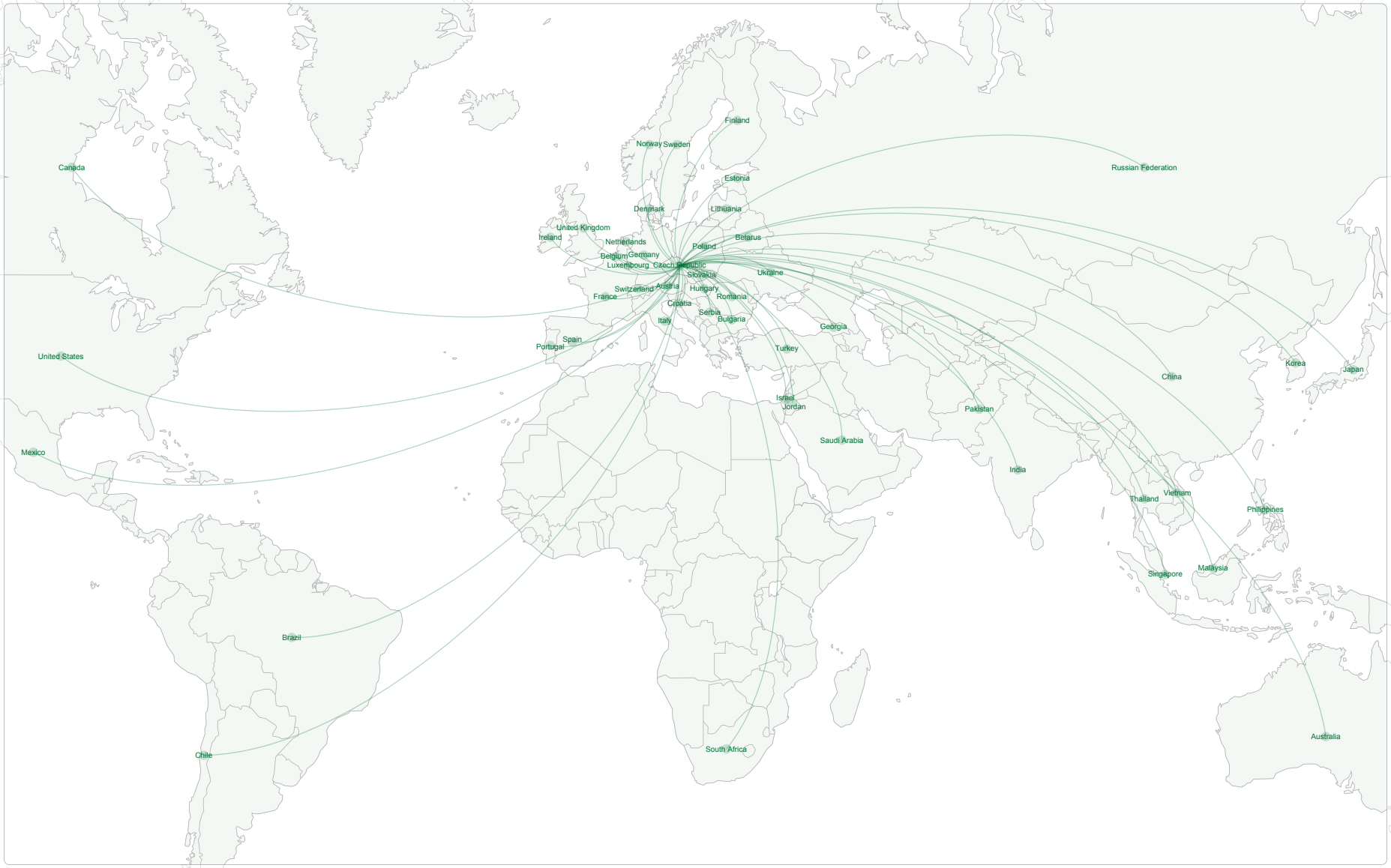
30. GA521/09/0261, Dynamic changes of mitochondrial DNA and transcription profiles in Silene vulgaris
31. GA526/09/0838, Coexistence of native and inoculated arbuscular mycorrhizal fungi in the roots of host plants
32. ME09035, The molecular genetic analysis of the candidate genes responsible for cytoplasmic male sterility in Silene vulgaris
33. GAP504/11/0783, Hunters or gardeners? Probing plant-microbe interactions in rootless carnivorous Utricularia from a transcriptomic perspective
34. GAP506/12/1359, The control of flowering in Chenopodium investigated by the transcriptomic approach
35. GA13-02290S, The role of hybridization and polyploidization on the evolution in Chenopodium album aggregate: From biosystematics to gene expression
36. QH71123, Variability of Potato leafroll luteovirus (PLRV), improved reliability of its detection and utilization of transgenic resistance
37. GA521/09/1525, Biosafe plant virus expression system for transient production of human papillomavirus oncoproteins and their use for therapeutic vaccine development
38. GAP501/11/1239, Nitrosative stress during natural and zinc induced senescence
39. GAP501/12/1761, Impact of different topology of heterologous antigenic determinants in PVX-based plant viral vector on their expression level and immunogenicity
40. 1M0505, Center of targeted therapeutic drugs
41. OC08011, Importance of nucleoprotein complexes for the regulation of the male gametophyte development
42. GA525/09/0994, Chemotaxonomy of isoflavonoids
43. GA522/09/0858, Integrative analysis of the role of bZIP transcription factors in pollen maturation
44. OC10054, Transcriptional regulation of male gametophyte development – synthesis of pollen cell wall
45. GPP501/11/P321, Depicting a functional model of NTP303 mRNA translational repression during tobacco pollen maturation
46. GAP501/11/1462, Functional characterisation of pollen unique storage ribonucleoprotein particles
47. GAP305/12/2611, The role of bZIP proteins in the control of lipid metabolism and transport during male gametophyte development
48. GA13-06595S, Telomeres and genome stability in lower plants
49. GA13-06943S, Structural and functional components of plant telomeres
50. GP13-41444P, The role of auxin and auxin-amino acid conjugate hydrolases during male gametophyte development of Arabidopsis thaliana
51. LD13006, Molecular basis of plant response to UV-B radiation
52. LD13049, Localisation of translation of cell wall components in growing pollen tube, an effectively single-cell model system
53. GA14-32292S, Widespread translation repression and function of paternally stored transcripts nurturing early stages of embryonic patterning
54. LD14109, Role of microRNAs in the regulation of cell wall biosynthesis - implications for the fertility of crop plants
55. 2B06187, The use of genomics and genetic engineering for identification and development of plant genotypes suitable for environment bioremediation
56. ME08070, Biotechnological production of Vaccinium bracteatum and evaluation of its biological activity
57. 2B08058, Utilization of energy plants for phytoremediation
58. SP/1B7/129/08, Green technologies for environment protection
59. GP525/09/P528, Anti-inflammatory activity of plant quinines
60. OC09082, Study of plant response to heavy metal stress and production of stress protective compounds
61. OC10028, Halofytes for phytoremediation
62. OC10026, Biorefineries as a source of “green chemicals”
63. ME10037, Determinants of host specificity of potential biocontrol agents
64. CZ.2.16/3.1.00/24014, Crucial improvement of the equipment necessary for research of plants as a source
65. MEB051026, Evaluation of suitability of various plant-based platforms for the production of target compounds
66. TA01020573, Biotechnology system for agricultural wastewaters cleaning and reuse
67. TA01020744, Biodegradable polymers in waste management
68. MEB061112, Discovery and analysis of new redox-based inhibitors for cyclooxygenase and lipoxygenase
69. FR-TI3/778, Wastewaters reclamation in integrated biotechnology system
70. LH11047, Plants and nanoparticles – friends or foes?
71. LH11048, Study and utilization of plant metabolism for organic xenobiotics degradation
72. LD11005, Exploration of grapevine diversity in production of health promoting compounds
73. LH12162, Immobilization of heavy metals and metalloids in contaminated sites
74. LH12165, Study on Isolation and identification of the possible bioactive compounds from leaves of Myrica rubra
75. LH12164, Production of Dendrobium candidum biomass *in vitro* and study its biological activity
76. 7AMB13AT008, Identification of cyclooxygenase and lipoxygenase inhibitors from vine grapes
77. LD13013, Production of anticancer polyacetylenes by elicited ginseng cultures
78. LD13026, Suspension culture as the model for study of physiological response to heavy metal stress
79. LD13028, Ecotoxicity of novel flame retardants and their degradation products
80. LD13029, The utilization of charcoal for immobilization of heavy metals

81. GA14-22593S, Metabolism of selected non-steroidal anti-inflammatory drugs in plants and its environmental consequences
82. LD14078, Metabolic interactions between ash tree and its new invasive fungal patogen Hymenoscyphus pseudoalbidus
83. LD14079, Plant non-wood forest products as a source of biologically active substances
84. LD14125, Phytotoxicity of nanofibres
85. LD14100, The toxicity of nanoparticles for wetland plants
86. LD14128, Synthesis of sirtuin inhibitors
87. LD14127, Synthesis of strigolactone derivatives
88. LD14106, Remediation of urban sites using energy plants
89. LD14107, Remediation of urban browfields using plants
90. CZ.2.16/3.1.00/21519, Modern equipment for plant research
91. 2B06024, Supramolecular materials based on natural phytosterols for application in biology
92. KAN200380801, Immunonanotechnologies for hormone diagnostic
93. GD522/08/H003, Integration of doctoral studies in biochemistry, plant physiology and biophysics
94. GA301/08/1649, Modulation of cell division of normal and cancer cells by cyclin-dependent kinase inhibitors
95. GA522/09/1576, Development of biospecific ligands for affinity chromatography of cytokinin related proteins
96. NS10282, Genomic integrity and instability mechanisms in the pathogenesis and potential personalized targeted treatment of prostate cancer
97. GP522/09/P394, Emissions of volatile chlorinated hydrocarbons in coniferous forest ecosystem
98. 7F09026, Monitoring of chlorine in the forest ecosystem – its cycling and effects
99. OC09039, Enzyme-mediated deracemization of non-natural amino acids and their application in development of supramolecular dendrimer structures
100. QI92A247, Genetic diversity of elm relic populations in ed regions of the CR and their *in vitro* reproduction
101. GA206/09/1284, Cyanobacterial cell factory: Modeling and experimental validation of models of photosynthetic energy conversion, of growth, and of production
102. GAP501/10/1450, Fluorescently labeled cytokinins as the way to understand their action in plants
103. OC10001, Supramolecular systems in chemical biology
104. NT11065, Analysis and targeting of DNA damage signaling and repair mechanisms in glioblastomas and glioblastoma stem cells as a strategy to elucidate pathogenesis and search for individualized targeted treatments combined with standard therapy
105. GAP503/11/0616, Antimycobacterial and antimicrobial agents and plant elicitors inspired by natural products of insect symbionts
106. GAP505/11/1163, Anti-inflammatory activity of extracts isolated from selected Indonesian plants and their effect on opportunistic parasitoses
107. TA01010861, Research, testing and production of targeted growth regulators, new fertilizers and combined formulations for crop production
108. GAP305/12/0783, Evaluation of cyclin-dependent kinase inhibitors in cancer cell lines with specific genetic alterations
109. GA13-11101S, Following elusive low molecular weight organochlorine compounds of natural and anthropogenically affected ecosystems
110. LK21306, Targeted metabolite profiling of plant growth regulators
111. LD13057, Gels produced through supramolecular self-assembly for medicinal chemistry applications
112. GA14-19590S, Modulation od cyclin-dependent kinases in haematological malignancies
113. GA14-34792S, New analytical approaches in phytohormone analysis
114. ED3.1.00/14.0327, New biotechnological products of IEB ASCR
115. TA04020547, Progressive biotechnology based on new synthetic cytokinin derivatives to obtain doubled haploid lines of caraway, linseed and pea
116. LO1204, Sustainable development of research in the Centre of the Region Haná
117. GA522/07/1614, Phosphatidylcholine-specific phospholipase C at the crossing point of stress signalling pathways
118. OC 158, Biochemical and morphological parameters determinig cryotolerance in conifer embryogenic cultures
119. OC 154, Melatonin as a novel antioxidant and radical scavenger: melatonin levels in berry species
120. QH72117, Biostimulators and biological inducers of resistance at cereals and oilseed crops
121. GA522/08/1581, Signalling pathways in defence response of rape seed against serious pathogens
122. QH81201, Biotechnological strategies in improvement of oilseed rape resistance to phoma stem canker
123. QH81284, Genotype diversity and morphological variability of Mycosphaerella graminicola population, identification of wheat resistance genes and study of defence reactions for utilization in control of septoria tritici blotch
124. QH82303, The use of biotechnology methods for the preservation and reproduction of autochtonous populations of hurst ecotype of Norway spruces
125. OC08013, Effects of drought and heat stress on polyamine metabolism in wild type and transgenic tobacco plants
126. GA522/09/1693, The role of antimicrobial peptides in plant defense against pathogenic microorganisms
127. MEB040923, The role of phospholipases in plant basal resistance
128. ME09108, The role of phospholipases in plant basal resistance
129. QI102A256, Improvement of pre-sowing treatments for dormant, European beech seeds
130. GAP501/11/1654, Phospholipid signaling and interaction with microtubule/actin cytoskeleton in biotic stress response of Arabidopsis thaliana

131. GAP501/12/1942, Nonspecific phospholipase C: Molecular, cellular and functional characterisation of novel plant enzyme
132. GPP501/12/P950, The role of diacylglycerol in aluminium toxicity in plants
133. 7AMB12FR018, The role of nonspecific phospholipase C and diacylglycerol kinase in Arabidopsis reactions to stresses. Phenotyping and gene expression studies
134. 7AMB12FR017, Exchange and sharing of methodical know-how used in conifer somatic embryogenesis studies
135. GA13-26798S, Fungal effectors manipulating plant defence system
136. LD13050, Effect of drought and heat stress on polyamine metabolism and contents of phenolics, auxin and abscisic acid in Norway spruce somatic embryos
137. LD13051, Effect of UV-B radiation on polyamine metabolism and accumulation of hydroxycinnamates and flavonoids in Norway spruce
138. LD14056, Mechanism of activation of plant defence against pathogens using protein inducers
139. GA14-09685S, Flotillin: a novel player in plant stress signaling
140. GA204/07/1169, The role of Ran GTPases in microtubule nucleation and spindle organization in acentrosomal higher plant cells
141. IAA600380703, Molecular organization and evolution of the 45S rDNA locus in banana (Musa spp.)
142. QH71267, Development and use of DArT chip technology for breeding of new xFestulolium cultivars
143. OC08025, Construction of physical map of the hexaploid wheat D genome using the chromosome-based approach
144. GA521/08/1629, Construction of BAC DNA libraries specific for chromosome 4AL, and positional cloning of gene for adult plant resistance to powdery mildew in wheat
145. 7E08064, Genomics for Triticeae improvement
146. GP204/09/P155, Aurora kinases and their role in cell division of acentrosomal plant cells
147. KJB500380901, Comparative genome analysis in banana (Musa spp.) using 454 sequencing
148. GAP501/10/1778, Fine mapping and candidate gene analysis of the flowering time gene on wheat
149. GAP501/10/1740, Physical map of the wheat chromosome 4AL and positional cloning of a gene for yield
150. GAP501/11/0504, Genome interactions in interspecific hybrids ×Festulolium
151. QI111A019, New genomic technology for the alogamic cultivated plant breeding for improving utility traits
152. LG12021, Collaboration with Bioversity International on global analysis and conservation of genetic diversity of bananas
153. GAP501/12/2554, Physical map of wheat chromosome arm 7DS and its use to clone a Russian wheat aphid resistance gene
154. GAP506/12/1320, Will orchids reshape our understanding of genome-wide processes? Solving the enigma of progressively partial endoreduplication
155. GAP501/12/2220, Sex chromosome evolution – chromosome-specific genomics in genus Silene
156. GBP501/12/G090, Evolution and function of complex plant genomes
157. GA13-04454S, Foreign genetic material in Elymus repens and other Triticeae grasses: its nature, origin, and evolutionary implications
158. GA13-08786S, Chromosome arm 3DS of bread wheat: its sequence and function in allopolyploid genome
159. LD14105, Development of marker panel for genotyping and molecular characterization of Blumeria graminis f.sp. hordei isolates
160. GA14-07164S, Cloning and molecular characterization of wheat QPm-tut-4A gene conferring seedling and adult plant race nonspecific powdery mildew resistance
161. GA14-28443S, Dark matter in plant cell nuclei – characterization of nuclear proteins
162. ED0007/01/01, Centre of the Region Haná for Biotechnological and Agricultural Research

International Collaboration 2010–2014




Finland
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Russian Federation
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Denmark
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United Kingdom
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Japan
China
Israel
Jordan
Pakistan
Saudi Arabia
Mexico
India
Vietnam
Thailand
Philippines
Singapore
Malaysia
Brazil
South Africa
Australia
Chile

Publications 2010–2014

Impacted Publications

2010

1. Bennettova B, Slaninova J, **Vlasakova V**, Hlavacek J, **Holik J**, Tykva R. Study of oostatic peptide uptake and metabolism in developing ovaries of the flesh fly, Neobellieria bullata. Journal of Insect Science (2010) 10: 48, 1–10.
2. **Beres T**, Zatloukal M, **Voller J**, Niemann P, Gahsche MC, **Tarkowski P**, **Novak O**, Hanus J, **Strnad M**, **Dolezal K**. Tandem mass spectrometry identification and LC-MS quantification of intact cytokinin nucleotides in K-562 human leukemia cells. Analytical and Bioanalytical Chemistry (2010) 398: 2071–2080.
3. Beuchat J, Scacchi E, **Tarkowska D**, Ragni L, **Strnad M**, Hardtke CS. *BRX* promotes *Arabidopsis* shoot growth. New Phytologist (2010) 188: 23–29.
4. Biesaga-Koscielniak J, Koscielniak J, Filek M, Marcinska I, **Krekule J**, **Machackova I**, Kubon M. The effect of plant growth regulators and their interaction with electric current on winter wheat development. Acta Physiologiae Plantarum (2010) 32: 987–995.
5. **Cvikrova M**, Mala J, **Hrubcova M**, **Martincova O**, Cvrckova H, Lipavska H. Defence responses induced in embryogenic cultures of Norway spruce by two fractions of *Gremmeniella abietina* mycelia. Forest Pathology (2010) 40: 467–484.
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Patents 2010–2014

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2. **Doležal K**, **Popa I**, **Holub J**, **Lenobel R**, Werbrouck S, **Strnad M**, **Zatloukal M**. Heterocyclic compound based on N6-substituted adenine, methods of their preparation, their use for preparation of drugs, cosmetic preparations and growth regulators, pharmaceutical preparations, cosmetic preparations and growth regulators containing these compounds. Issue date: 20.01.2010. **Patent No. KR100939147**
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11. **Tupý J**, **Louda O**, **Zima J**. Columnar apple tree named ‘Moonlight’. Issue date: 23.11.2010. **Patent No. US PP21,511**

2011

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15. Zatloukal M, **Lenobel R**, Holub J, **Doležal K**, Werbrouck S, Popa I, **Strnad M**. Heterocyclic compounds based on N6-substituted adenine, methods of their preparation, their use for preparation of drugs, cosmetic preparations and growth regulators, pharmaceutical preparations, cosmetic preparations and growth regulators containing these compounds. Issue date: 01.09.2011. **Patent No. AU2008203838**

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2013

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27. **Szüčová L**, Zatloukal M, **Spíchal L**, **Voller J**, **Doležal K**, **Strnad M**, Massino FJ. 6, 9-disubstituted purine derivatives and their use as cosmetics and cosmetic compositions. Issue date: 05.11.2013. **Patent No. US8575182**

2014

28. **Doležal K**, Zatloukal M, **Strnad M**, **Voller J**, **Szüčová L**, **Spíchal L**, Massino FJ. 6,9-disubstituted purine derivatives and their use as cosmetics and cosmetic compositions. Issue date: 13.02.2014. **Patent No. AU2008345103**
29. **Szüčová L**, Zatloukal M, **Spíchal L**, **Voller J**, **Doležal K**, **Strnad M**, Massino FJ. 6,9-disubstituted purine derivatives and their use as cosmetics and cosmetic compositions. Issue date: 26.02.2014. **Patent No. EP2245031**

Apple Varieties 2010–2014

2010

1. **Tupý J**, **Louda O**, **Zima J**. Variety of Malus domestica Borkh., **GOLDLANE**. Issue date: 31.7.2010. Identification No. CH 10.2230.
   A new and distinct apple variety is provided which exhibits columnar tree type, compact growth, predominant bearing on spurs and *Vf*-resistance against scab. The new variety yields late maturing medium-sized generally globose to obloid yellow colored fruits with firm crispy flesh and very good eating and keeping qualities.

2. **Tupý J**, **Louda O**, **Zima J**. Variety of Malus domestica Borkh., **MOONLIGHT**. Issue date: 31.3.2010. Identification No. CH 10.2216.
   A new and distinct variety of apple characterized by columnar tree type, weakly vigorous compact growth, predominant bearing on spurs, presence of *Vf*-resistance to scab and by late maturing medium-sized globose conical to conical fruits of good storage quality. Fruit color is yellow-green to yellow partly with red to orange blush. The flesh is yellow firm crisp and juicy with a good sweet-sour balance and very good eating quality.

3. **Tupý J**, **Louda O**, **Zima J**. Variety **SHALIMAR**. Issue date: 31.1.2010. Identification No. CH 10.2195.
   A new and distinct very late fruit apple variety with *Vf*-resistance against scab suited for commercial apple growing. The variety is diploid, medium vigorous, is harvested about two weeks after Golden Delicious. The fruits are conic, orangered on greenyellow ground colour, storage excellent. The flesh is characterised by high firmness, distinctive flavour and high sugar and acid content.

2011

4. **Tupý J**, **Louda O**, **Zima J**. Variety **CACTUS**. Issue date: 30.9.2011. Identification No. CH 11.2305.
   A new and distinct, late, apple variety with specific attractive fruit coloration, resistant to scab (*Vf*), tolerant to mildew.

5. **Tupý J**, **Louda O**, **Zima J**. Variety of Malus domestica Borkh., **CACTUS**. Issue date: 23.5.2011. Identification No. EU 30092.
   A new and distinct late variety characterized by columnar tree type, very compact growth, predominant bearing on spurs, globose conical, green to yellow colored fruits and presence of *Vf*-resistance to scab.

6. **Tupý J**, **Louda O**, **Zima J**. Variety of Malus domestica Borkh., **KARNEVAL**. Issue date: 7.1.2011. Identification No. CZ 1/2011.
   A new and distinct late apple variety outstanding in very attractive coloration, *Vf*-resistant to scab and mildew tolerant.

7. **Tupý J**, **Louda O**, **Zima J**. Variety of Malus domestica Borkh., **KARNEVAL**. Issue date: 18.4.2011. Identification No. EU 29620.
   A new and distinct, robust, diploid, late, dessert apple variety, outstanding in very attractive coloration of fruits. It is characterized by medium vigor, high and regular productivity, scab resistance based on *Vf* gene, medium sized, globose to conical fruits, multi-coloured with prominent red stripes on yellow ground color, appears russet free, finely acid with slightly aromatic good flavour. Variety may be of interest especially for Christmas time.

8. **Tupý J**, **Louda O**, **Zima J**. Variety **LUNA**. Issue date: 28.12.2011. Identification No. UA 110599.
   A new and distinct, late, diploid variety of apple that produces fruits having crisp, juicy flesh with a pleasant aroma and harmonic sugar/acid content suitable for use as a dessert fruit. The new variety is a similar to Golden Delicious in tree habit, yellow ground color of fruits, and long fruit stem to Golden Delicious, but exhibits a globose fruit shape, absence of fruit russeting, later fruit maturation, better keeping quality of the fruits, and the presence of *Vf* resistance against scab.

9. **Tupý J**, **Louda O**, **Zima J**. Variety **ORION**. Issue date: 28.12.2011. Identification No. UA 110596.
   A new and distinct, late, dessert apple variety suited mainly for commercial organic apple growing. The variety is triploid, medium to strongly vigorous and exhibits *Vf* resistance against scab. Fruits are large, uniform, broad globose, green-yellow to yellow, occasionally with a slight reddish blush and fine russeting. Fruit flesh is yellowish, medium firm, fine textured, very juicy and is characterized by high sugar content and very good distinctive flavor. Maturation time and keeping quality of fruits are similar to Golden Delicious.

10. **Tupý J**, **Louda O**, **Zima J**. Variety **RED TOPAZ**. Issue date: 28.12.2011. Identification No. UA 110600.
The "Red Topaz" apple tree originated as a spontaneous limb sport mutation discovered on a "Topaz" apple tree. "Red Topaz" is distinguishable from the original Topaz variety by earlier and more intensive red fruit coloration.

11. **Tupý J**, **Louda O**, **Zima J**. Variety **ROZELA**. Issue date: 28.12.2011. Identification No. UA 110598.
A new and distinct, late, diploid fruit apple variety maturing about one week before Golden Delicious. It is characterized by medium vigor and high productivity, scab resistance based on *Vf* gene, medium sized, globose fruits with high amount of dark red over color without russeting, good sweet aromatic flavor and medium time of eating maturity.

12. **Tupý J**, **Louda O**, **Zima J**. Variety **SIRIUS**. Issue date: 28.12.2011. Identification No. UA 110597.
A new and distinct fruit apple variety of the type Golden Delicious. It is characterized by triploidy, strong vigor, scab resistance based on *Vf* gene, medium to large round fruits with yellow grand color, occasionally covered with a slight orange-red blush, maturing about 10 days after Golden Delicious and having good storage quality. The flesh is yellowish, firm, crisp, fine grained, very juicy, with high, well balanced sugar and acid content and aromatic flavor thereby providing an excellent eating quality. The variety is considered mainly for commercial organic apple growing.

2012

13. **Tupý J**, **Louda O**, **Zima J**. Variety of Malus domestica Borkh., **ADMIRAL**. Issue date: 4.1.2012. Identification No. CZ 1/2012.
A new and distinct late, vigorous apple variety of excellent eating qualities, of exceptionally long storability and with *Vf* and polygennic scab resistance, sensitive to bitter pit.

14. **Tupý J**, **Louda O**, **Zima J**. Variety of Malus domestica Borkh., **ADMIRAL**. Issue date: 20.2.2012. Identification No. EU 31550.
A new and distinct late, vigorous apple variety of excellent eating qualities, of exceptionally long storability and with *Vf* and polygennic scab resistance, sensitive to bitter pit.

15. **Tupý J**, **Louda O**, **Zima J**. Variety of Malus domestica Borkh., **JUNO**. Issue date: 4.1.2012. Identification No. CZ 3/2012.
A new and distinct apple variety is provided which exhibits very early ripening and combined *Vf* and polygennic resistance against scab.

16. **Tupý J**, **Louda O**, **Zima J**. Variety of Malus domestica Borkh., **MERKUR**. Issue date: 4.1.2012. Identification No. CZ 2/2012.
A new and distinct apple variety ripening with Gala, characterized with aromatic, sweet taste, bears gene *Vf* for resistance against scab and is only slightly susceptible to mildew.

17. **Tupý J**, **Louda O**, **Zima J**. Variety of Malus domestica Borkh., **MERKUR**. Issue date: 20.2.2012. Identification No. EU 31549.
A new and distinct apple variety ripening with Gala, characterized with aromatic, sweet taste, bears gene *Vf* for resistance against scab and is only slightly susceptible to mildew.

18. **Tupý J**, **Louda O**, **Zima J**. Variety **UEB 32642**. Issue date: 30.6.2012. Identification No. TR 2012/023.
A new and distinct fruit apple variety of the type Golden Delicious. It is characterized by moderately vigor, scab resistance based on *Vf* gene, medium round fruits with yellow grand color, covered with a slight orange-blush, with russeting in stem cavity and having good storage quality. The flesh is yellowish, firm, crisp, fine grained, medium juicy, with high sugar content and aromatic flavor thereby providing an excellent eating quality. The variety prefers sunny, dry, wine growing areas with irrigation.

2013

19. **Tupý J**, **Louda O**, **Zima J**. Variety **REDSPRING**. Issue date: 4.2.2013. Identification No. EU 34099.
A new and distinct late apple variety maturing with Golden Delicious, characterized by columnar tree type, compact growth, globose conical, red colored fruits and presence of *Vf*-resistance to scab. This winter dessert variety is suitable mainly for home gardens.

20. **Tupý J**, **Louda O**, **Zima J**. Variety **REDSPRING**. Issue date: 31.5.2013. Identification No. CH 13.2429.
A new and distinct late apple variety maturing with Golden Delicious, characterized by columnar tree type, compact growth, globose conical, red colored fruits and presence of *Vf*-resistance to scab. This variety is suitable mainly for home gardens.

21. **Tupý J**, **Louda O**, **Zima J**. Variety **REDSPRING**. Issue date: 7.1.2013. Identification No. CZ 3/2013.
A new and distinct late variety maturing with Golden Delicious, characterized by columnar tree type, compact growth, globose conical, red colored fruits and presence of *Vf*-resistance to scab. This variety is suitable mainly for home gardens.

22. **Tupý J**, **Louda O**, **Zima J**. Variety **ROSALIE**. Issue date: 3.6.2013. Identification No. EU 35515.
A new and distinct, ornamental apple variety characterized by compact columnar type with red flowers, greyed-purple young leaves, dark-red fruits with reddish flesh not suitable for fresh eating. The scab resistant variety (*Vf*) is suitable for ornamental purpose mainly for home gardens.

23. **Tupý J**, **Louda O**, **Zima J**. Variety **ROSALIE**. Issue date: 7.1.2013. Identification No. CZ 4/2013.
A new and distinct, ornamental apple variety characterized by compact columnar type with red flowers, greyed-purple young leaves, dark-red fruits with reddish flesh not suitable for fresh eating. The scab resistant variety (*Vf*) is suitable for ornamental purpose mainly for home gardens.

24. **Tupý J**, **Louda O**, **Zima J**. Variety **SOLARIS**. Issue date: 30.6.2013. Identification No. CH 13.2432.
A new and distinct, yellow, late, good dessert apple variety with resistance against scab (*Vf*) and good storage qualities and shelf life. Fruit has medium size, conical shape and appears russet free. Flesh is firm, crisp and juicy.

25. **Tupý J**, **Louda O**, **Zima J**. Variety **SOLARIS**. Issue date: 18.3.2013. Identification No. EU 34437.
A new and distinct, late, yellow, good dessert apple variety with resistance against scab (*Vf*) and good storage qualities and shelf life. Fruit has medium size, conical shape and appears russet free. Flesh is firm, crisp and juicy.

2014

26. **Tupý J**, **Louda O**, **Zima J**. Variety **ADMIRAL**. Issue date: 30.4.2014. Identification No. CH 14.2485.
A new and distinct late, triploid, vigorous apple variety of excellent eating qualities, of exceptionally long storability and with *Vf* and polygennic scab resistance, sensitive to bitter pit.

27. **Tupý J**, **Louda O**, **Zima J**. Variety **ALLEGRO**. Issue date: 12.12.2014. Identification No. CZ 85/2014.
A new and distinct, healthy and friendly, early ripening variety with attractive bicolor appearance, good fruits quality and resistance against scab assumed polygenic basis, variety is suitable for organic production as a home garden.

28. **Tupý J**, **Louda O**, **Zima J**. Variety **DIANA**. Issue date: 30.4.2014. Identification No. CH 14.2484.
A new and distinct, early ripening variety with good fruits quality and resistance against scab (*Vf* and on polygenic basis) and vigorous growth. The variety is suitable for home garden.

29. **Tupý J**, **Louda O**, **Zima J**. Variety **DIANA**. Issue date: 8.1.2014. Identification No. CZ 1/2014.
A new and distinct, early ripening variety with good fruits quality and resistance against scab (*Vf* and on polygenic basis), growth vigour, variety is suitable for home garden.

30. **Tupý J**, **Louda O**, **Zima J**. Variety **JUNO**. Issue date: 30.4.2014. Identification No. CH 14.2483.
A new and distinct apple variety is provided which exhibits very early ripening and combined *Vf* and polygennic resistance against scab.

31. **Tupý J**, **Louda O**, **Zima J**. Variety **KARNEVAL**. Issue date: 30.4.2014. Identification No. CH 14.2486.
A new and distinct, late, apple variety with specific attractive fruit coloration, resistant to scab (*Vf*), tolerant to mildew.

32. **Tupý J**, **Louda O**, **Zima J**. Variety **MINERVA**. Issue date: 8.1.2014. Identification No. CZ 2/2014.
A new and distinct, early to fall ripening apple variety with attractive conical shaped, carmine red colored fruits and resistance against scab (*Vf* and on polygenic basis), suitable especially for organic production and home garden.

33. **Tupý J**, **Louda O**, **Zima J**. Variety **ROMANCE**. Issue date: 19.5.2014. Identification No. EU 38114.
A new and distinct, attractive fall, scab resistance (*Vf*) dessert variety with maturing about 3 weeks before Golden Delicious and eating maturity shortly after harvest.

34. **Tupý J**, **Louda O**, **Zima J**. Variety **UEB 3366/1**. Issue date: 10.2.2014. Identification No. EU 36794.
A new and distinct, smaller sized apple dessert variety with resistant against scab (*Vf*). Fruits are red colored with good and aromatic flavor, eating maturity shortly after harvest.

35. **Tupý J**, **Louda O**, **Zima J**. Variety **UEB 33752**. Issue date: 30.7.2014. Identification No. NZ 30978.
A new and distinct, late, diploid variety of apple that produces fruits having crisp, juicy flesh with a pleasant aroma and harmonic sugar/acid content suitable for use as a dessert fruit. The new variety is similar to Golden Delicious in tree habit, yellow ground color of fruits, and long fruit stem to Golden Delicious, but exhibits a globose fruit shape, absence of fruit russeting, later fruit maturation, better keeping quality of the fruits, and the presence of *Vf* resistance against scab.

Figures: ***1*** – Columnar variety Moonlight (2010); ***2*** – Columnar variety Redspring (2013); ***3*** – Summer variety Allegro (2014); ***4*** – Variety Karneval (2011); ***5*** – Variety Admiral (2012)

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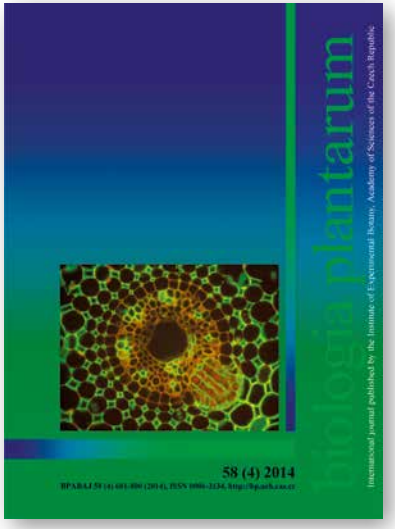
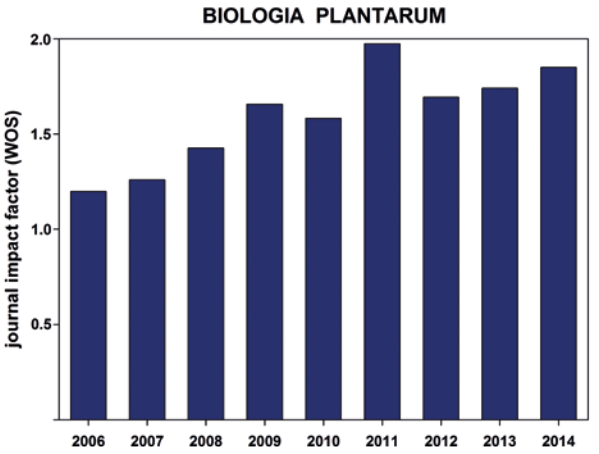
Journals

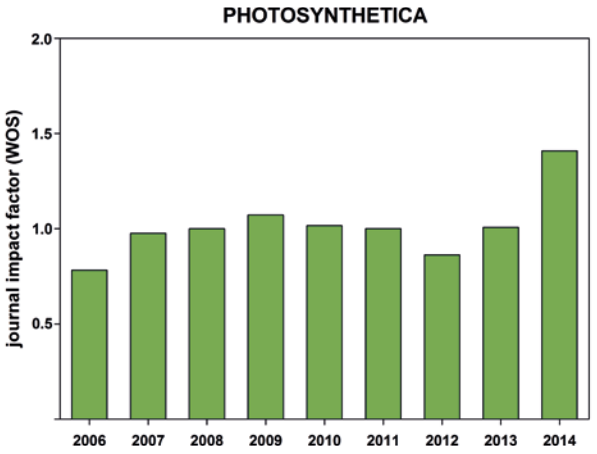
Institute of Experimental Botany publishes two scientific journals, both with impact factor. Springer Distribution Center GmbH Heidelberg, Germany is the distributor of these journals.

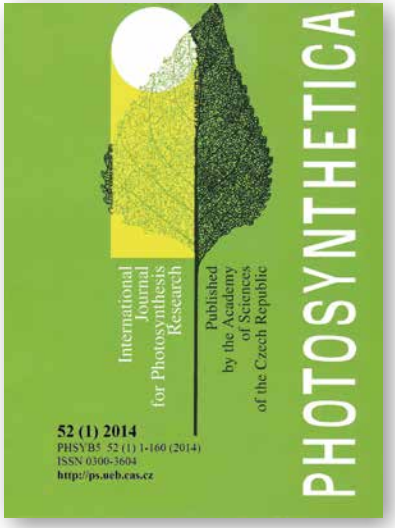
Biologia Plantarum, an international journal of experimental botany, publishes in English original research reports, review articles and brief communications ranging across all fields of plant physiology, molecular biology, biochemistry, biophysics, biotechnology, genetics, structural botany and pathology. The journal also regularly presents reviews of books dealing with topics within the general scope of the journal.

The Editor-in-Chief of Biologia Plantarum is RNDr. Jana Pospíšilová, CSc., Institute of Experimental Botany, the Czech Academy of Sciences, Prague.









Photosynthetica is devoted to the investigation of photosynthesis, combining biochemical, biophysical and ecological approaches to the study of photosynthesis in plants. The journal carries specialized reviews on various aspects of photosynthesis research and presents papers on the structure of the photosynthetic apparatus; chloroplast pigments (both *in vivo* and *in vitro*); biochemical and biophysical mechanisms of photosynthetic reactions; measurements of photosynthesis and photosynthetic production by techniques ranging from laboratory gas-exchange measurements to growth analysis, etc. Photosynthetica is directed by an international editorial board. The articles are written in English. The journal regularly publishes reviews of books dealing with photosynthesis, reports on photosynthetic congresses and symposia, and bibliographic lists of papers on methods and reviews.

The Editor-in-Chief of Photosynthetica is RNDr. Helena Synková, CSc., Institute of Experimental Botany, the Czech Academy of Sciences, Prague.

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