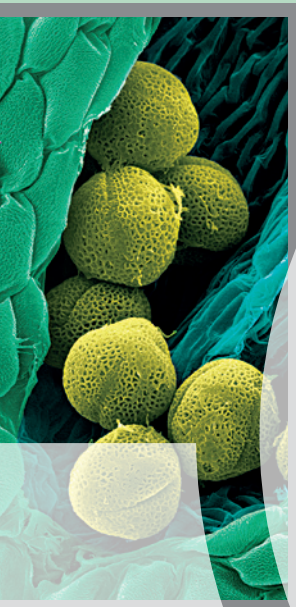
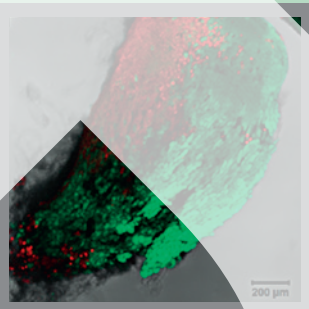
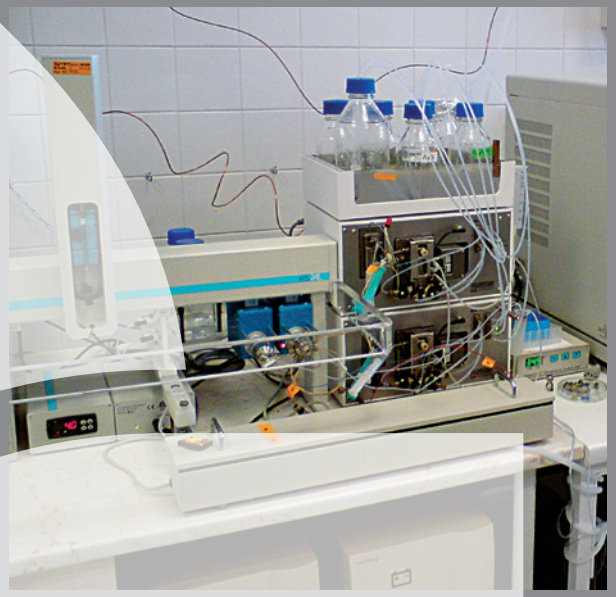
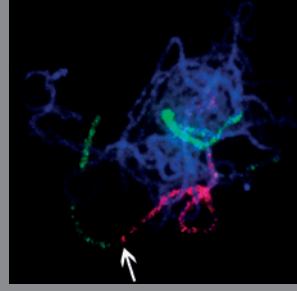
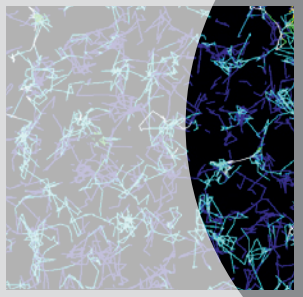
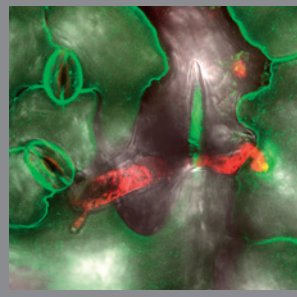
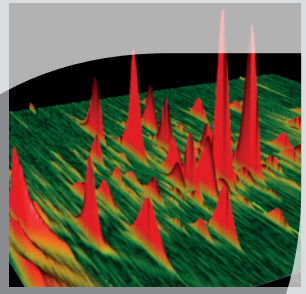
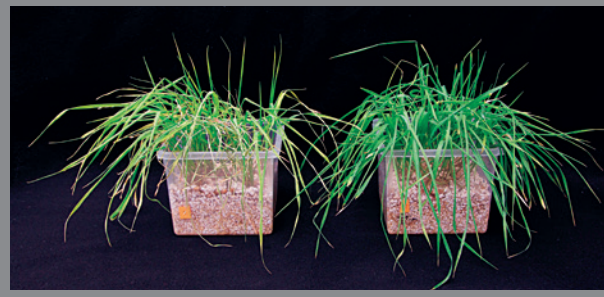
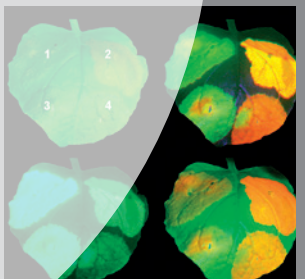
Institute of Experimental Botany
of the Czech Academy of Sciences

Scientific Report
2018–2020

Contents

Discovering the World of Plants

Introduction

The years 2018–2020 were another extremely successful period for the Institute of Experimental Botany. This scientific report presents a profile of our institute, its organisational structure, and the main research results from this period. And because our staff deserves credit for all these achievements, you will also find their team photos here. Many thanks to them.

The covid-19 pandemic during the last year was a stress test for the institute, comparable to the impact of the catastrophic flood at our Moravian facilities in 1997. Research inside laboratories was limited, and scientists stayed isolated in their homes for some time. However, as our results show, the work did not stop even under these conditions. On the premises of the institute, we set strict rules to prevent virus transmission. However, infection often occurred within families and in public spaces – more than fifty colleagues contracted covid-19. I am very glad that none of these cases were fatal and that everybody is already back at work. Now, in June 2021, the worst is perhaps behind us: most employees have been vaccinated, the number of new cases in the country has fallen rapidly, and we are conducting regular PCR screening at the institute.

In the years 2018–2020, we were awarded two projects from the Operational Programme Research, Development and Education. This significantly increased the amount of research funding available to us. For the first time in the institute's history, nearly all teams had secured financing for the next several years. We also managed to further replenish the institute's instrumentation, including expensive top-notch equipment which is necessary to maintain our competitiveness.

If I wrote in the previous report that 2015–2017 was our most successful period in terms of publication output, then the last three years were even better. In 2018–2020, we had 520 articles in journals with an impact factor. Moreover, the quality increased along with the quantity. In the record-breaking year of 2020, we published 196 such articles, almost 30% of them in journals belonging to the best decile in the field according to the Article Influence Score.

In line with the mission of the Czech Academy of Sciences, our priority is basic research. However, some of our results can immediately be used in practice. After their facilities were thoroughly modernised, the Station of Apple Breeding for Disease Resistance started using more efficient breeding technologies. They produced several new and promising apple varieties and were also very successful in selling licence agreements for their varieties.

We continued an intensive cooperation with universities; our scientists now teach at ten of them. Many students work on their bachelor's, master's, and Ph.D. theses in our laboratories. A great example of close cooperation is the Laboratory of Growth Regulators, which has been a joint facility of the IEB and Palacký University in Olomouc for a quarter of a century.

For more than fifty years, the institute has published two scientific journals, *Biologia Plantarum* and *Photosynthetica*. In accordance with modern trends, both magazines have been published in an open-access, online-only format since 2019. They are among the best scientific journals based in the Czech Republic, and their impact factors are gradually increasing.

In closing, I would like to thank my colleagues, who have created the superb international reputation of the institute through their excellent work, scientific enthusiasm, brilliant ideas, and relentless diligence. I also thank them for maintaining a wonderful, friendly atmosphere in the workplace, which is often a crucial element in attracting promising scientists from abroad. And as my second term is slowly coming to an end, I wish the institute much success in the future.

Martin Vágner, Director of the IEB

Photo: Dylan Lowe

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DEPUTY DIRECTOR:

RNDr. Jan Martinec, CSc.

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RNDr. Martin Vágner, CSc. – IEB CAS
prof. RNDr. Olga Valentová, CSc. – UCT, Prague

Secretary:

Dr.rer.nat. Ing. Helena Plchová – IEB CAS

Abbreviations

Institutions of the Czech Academy of Sciences (CAS):

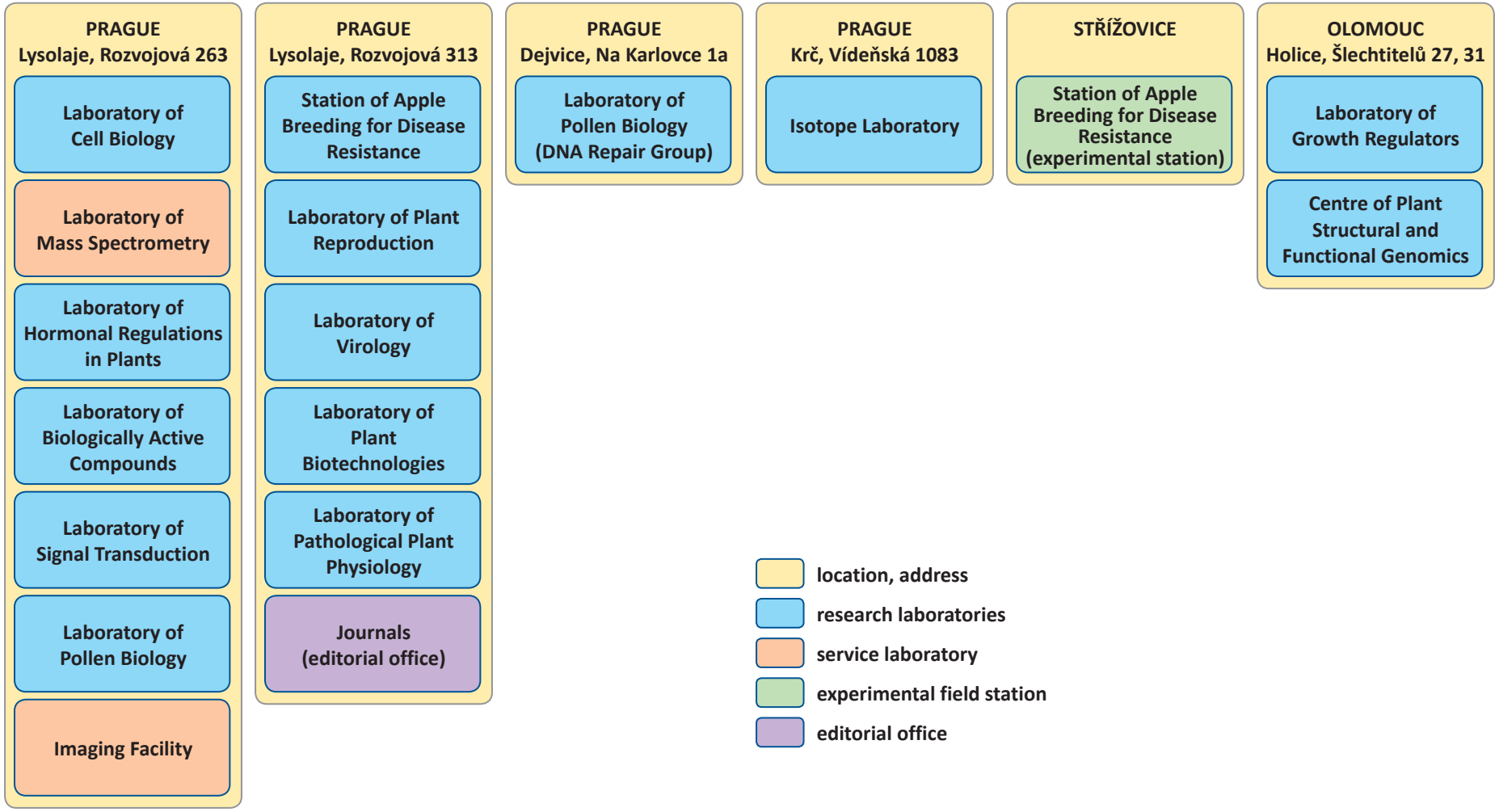
IBT – Institute of Biotechnology
IEB – Institute of Experimental Botany
IOCB – Institute of Organic Chemistry and Biochemistry

Others:

CRI – Crop Research Institute
FS CU – Faculty of Science, Charles University
MENDELU – Mendel University
RIFC Ltd. – Research Institute for Fodder Crops Ltd.
UCT – University of Chemistry and Technology

Organizational Structure of the Institute

INSTITUTE OF EXPERIMENTAL BOTANY, CZECH ACADEMY OF SCIENCES



Buildings of IEB

Rozvojová 263, Prague 6 – Lysolaje (7 laboratories)

Šlechtitelů 31, Olomouc (Centre of Plant Structural and Functional Genomics)

Rozvojová 313, Prague 6 – Lysolaje (5 laboratories)

Šlechtitelů 31, Olomouc (Centre of Plant Structural and Functional Genomics)

Šlechtitelů 27, Olomouc (Laboratory of Growth Regulators)

Střížovice 20, Pěnčín u Liberce (Station of Apple Breeding for Disease Resistance)

Others:

Vídeňská 1083, Prague 4 – Krč
(Isotope Laboratory)

Na Karlovce 1a, Prague 6 – Dejvice
(Laboratory of Pollen Biology,
Group of DNA Repair)

Centre of Plant Structural and Functional Genomics

Head of the laboratory:

prof. Ing. Jaroslav Doležel, DrSc.

Phone: +420 585 238 703
E-mail: dolezel@ueb.cas.cz

Our research focuses on the organization of the nuclear genome, its evolution, and its function. This fundamental research unravels the molecular mechanisms of inheritance and the way the plant phenotype is determined, and delivers the knowledge and concepts to support crop breeding. Most of our work is concentrated on agronomically important species, with an emphasis on polyploids and, in particular, those which originated by interspecific hybridization. The majority of our research involved cereals from the tribe Triticeae, forage and amenity grasses, and also the banana. Although initially considered intractable due to their complex genomes, some of these species are gradually being established as models for studying the role of polyploidy and interspecific hybridization in plant genome evolution and speciation. Recently, we have complemented our experimental models by including a small-genome plant, *Arabidopsis*, to help in uncovering the role of chromatin components in spatial nuclear genome organization and function.

In the picture (from the left):
Front row: Bc. Jitka Weiserová / technician, Mgr. Miroslava Karafiátová, Ph.D. / postdoctoral fellow, Mgr. Anna Katarzyna Nowicka, Ph.D. / researcher, Ritu Dixit, Ph.D. / postdoctoral fellow, Fen Yang / Ph.D. student, Mgr. Lucie Bílková / assistant, Mgr. Miroslav Valárik, Ph.D. / researcher, Helena Tvardíková / technician, Mgr. Lucie Šimková / Ph.D. student, Mgr. Veronika Kapustová / Ph.D. student, Mgr. Beáta Strejčková / Ph.D. student, Mgr. Martina Bednářová / Ph.D. student.
Second row: Mgr. Zuzana Tulpová, Ph.D. / postdoctoral fellow, Mgr. Jana Čížková, Ph.D. / postdoctoral fellow, Mgr. Alžběta Němečková / Ph.D. student, Pranav Sahu, Ph.D. / postdoctoral fellow, Jovanka Vladejić / Ph.D. student, Mgr. Veronika Koláčková, Ph.D. / postdoctoral fellow, Mgr. Kateřina Perničková / Ph.D. student, Mgr. Pavla Navrátilová, Ph.D. / researcher, Mahmoud Said, Ph.D. / research assistant, prof. Ing. Jaroslav Doležel, DrSc. / head of the centre, Mgr. Denisa Šimoníková / Ph.D. student, Mgr. Klára Procházková / Ph.D. student, Mgr. Kateřina Lahnerová / Ph.D. student, Mgr. Hana Jeřábková, Ph.D. / postdoctoral fellow, Dr.habil. Aleš Pečinka, Ph.D. / researcher, Ing. Zbyněk Milec, Ph.D. / researcher.
Third row: Mgr. Eva Hřibová, Ph.D. / researcher, István Molnár, Ph.D. / researcher, Ing. Petra Neplechová / accounting officer, Romana Šperková / technician, Eliška Čamková / secretary, Mgr. Tereza Vojtková / assistant, Eva Jahnová / technician, Mgr. Marek Glombik / Ph.D. student, Ing. Radoslava Kvasničková / programme manager, Mgr. Radim Svačina / Ph.D. student, Ing. Marie Seifertová / technician, Ing. Hana Šimková, CSc. / researcher, RNDr. David Kopecký, Ph.D. / researcher, Mgr. Martin Kovačik / Ph.D. student, Mgr. Jan Bartoš, Ph.D. / deputy head, Mgr. Pavel Solanský / assistant.
Top row: RNDr. Jan Šafář, Ph.D. / researcher.

Not pictured:
Ing. Radim Čegan, Ph.D., RNDr. Roman Hobza, Ph.D., Mgr. Pavla Christelová, Ph.D., Ing. Beáta Petrovská, Ph.D. / researchers, Mgr. Iva Ilíková, Ph.D. / research assistant, Mgr. Petr Cápal, Ph.D., Mgr. Eva Dvořák Tomaštíková, Ph.D., Mgr. Kateřina Holušová, Ph.D., Mgr. Helena Toegelová, Ph.D. / postdoctoral fellows, Wojciech Krzysztof Jesionek / assistant, Mgr. Eva Janáková, Mgr. Jana Zwyrtková / Ph.D. students, Zdeňka Dubská, Radomíra Tušková / technicians.

We have continued in pioneering and applying unique experimental approaches, such as chromosome genomics to facilitate the analysis of complex genomes and gene cloning. Our broad expertise made it possible to perform the studies at a wide range of levels of the organization, extending from the DNA sequence level up to the molecular composition of chromosomes and interphase nuclei and spatial organization of their chromatin. By studying genome organization and its dynamics at all complexity levels, we strived to obtain

a comprehensive picture of a plant genome. This work benefited from our long-term experience in genetics, microscopy, molecular cytogenetics and flow cytometry and sorting, the latter enabling the preparation of unique materials for performing the analyses on well-defined samples and at high resolution.

By combining multiple experimental approaches on-site, we occupied a unique position within the international research community and collaborated intensively with many leading groups around the globe. In particular, we were a strategic partner in ambitious projects that delivered genome sequences of important crops, including barley, pea, rye, and wheat.

To facilitate a rapid transfer of the new knowledge and methods into practice, we have established a productive collaboration with applied research institutes and breeding programs both in the Czech Republic and abroad. The collaborative activities have ranged from the characterization of genetic diversity to the identification of genomic loci associated with agronomic traits of interest. We were also active in public engagement and outreach activities, which included events targeted to students and the general public, as well as to political representatives.

Sequencing genomes of important crops

Our largest and most prestigious research project was the sequencing of the enormous and complex genome of hexaploid bread wheat. We were one of the key partners in the global effort managed by the International Wheat Genome Sequencing Consortium, which produced annotated reference sequence of the bread wheat genome (IWGSC 2018). We contributed by dissecting the complex genome into individual chromosomes and chromosome arms, by constructing chromosome arm-specific BAC libraries, and by constructing BAC-based physical maps [118, 295, 360] and optical maps [55] of several chromosomes. Moreover, we contributed to the joint effort of the IWGSC with clone-by-clone sequencing of the short arm of chromosome 7D [295]. Comparison of the size of the bread wheat and other cereal reference genomes with corresponding genome sizes revealed that about 10–15% of the genomes are missing in the assemblies [19]. We demonstrated that DNA repeats organized in large tandem arrays, such as ribosomal RNA multigene loci, contributed to the missing part of the genomes, and demonstrated how the missing information can be added to the genome assembly with the aid of nanopore sequencing of BAC clones and optical mapping [199].

In addition to the wheat genome sequencing project, we participated in two other prestigious international projects that produced reference genomes of pea [212] and rye (Rabanus-Wallace *et al.* 2021, Nature Genet 53: 564–573). Adding to the

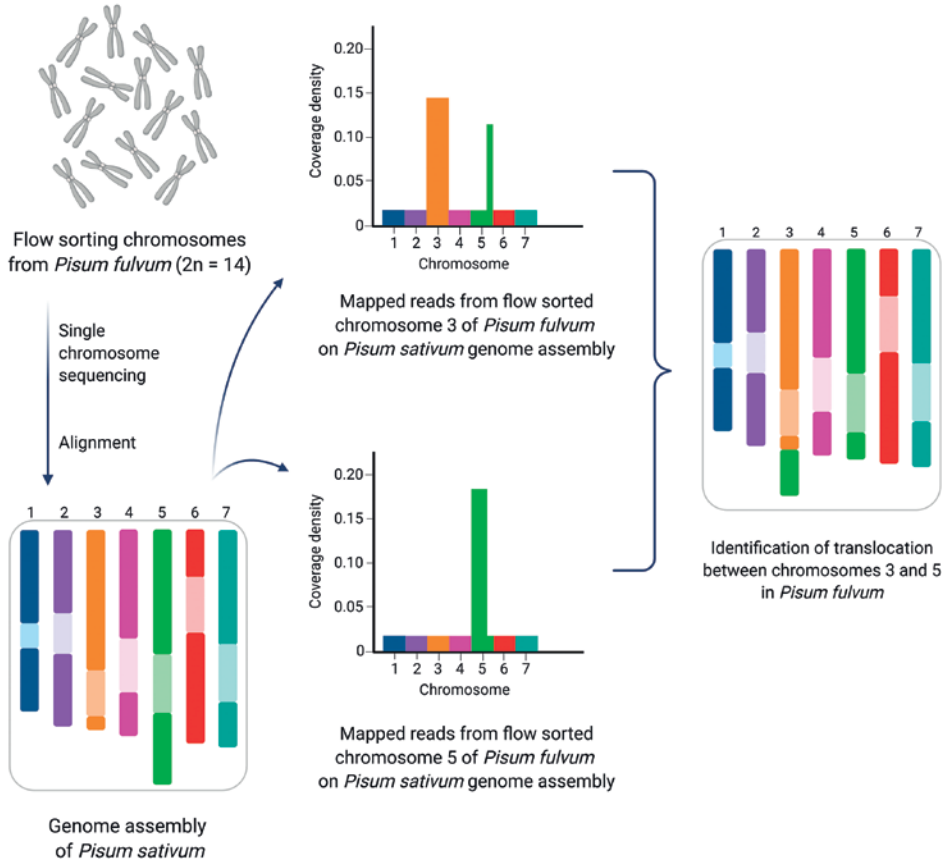


Figure 1. Identification of chromosome translocation discriminating cultivated *Pisum sativum* from its wild relative, *P. fulvum*. DNA amplified from single flow-sorted *P. fulvum* chromosomes was sequenced and the reads were mapped to *P. sativum* pseudomolecules. Reads from a *P. fulvum* chromosome corresponding to *P. sativum* chromosome 3 were mapped on *P. sativum* pseudomolecules of chromosomes 3 and 5. This indicated a translocation between chromosomes 3 and 5 in *P. fulvum* as compared to *P. sativum*. The translocation was confirmed by the lack of mapping reads from *P. fulvum* chromosome corresponding to *P. sativum* chromosome 5 from ~465 Mb to its end. Modified from [212].

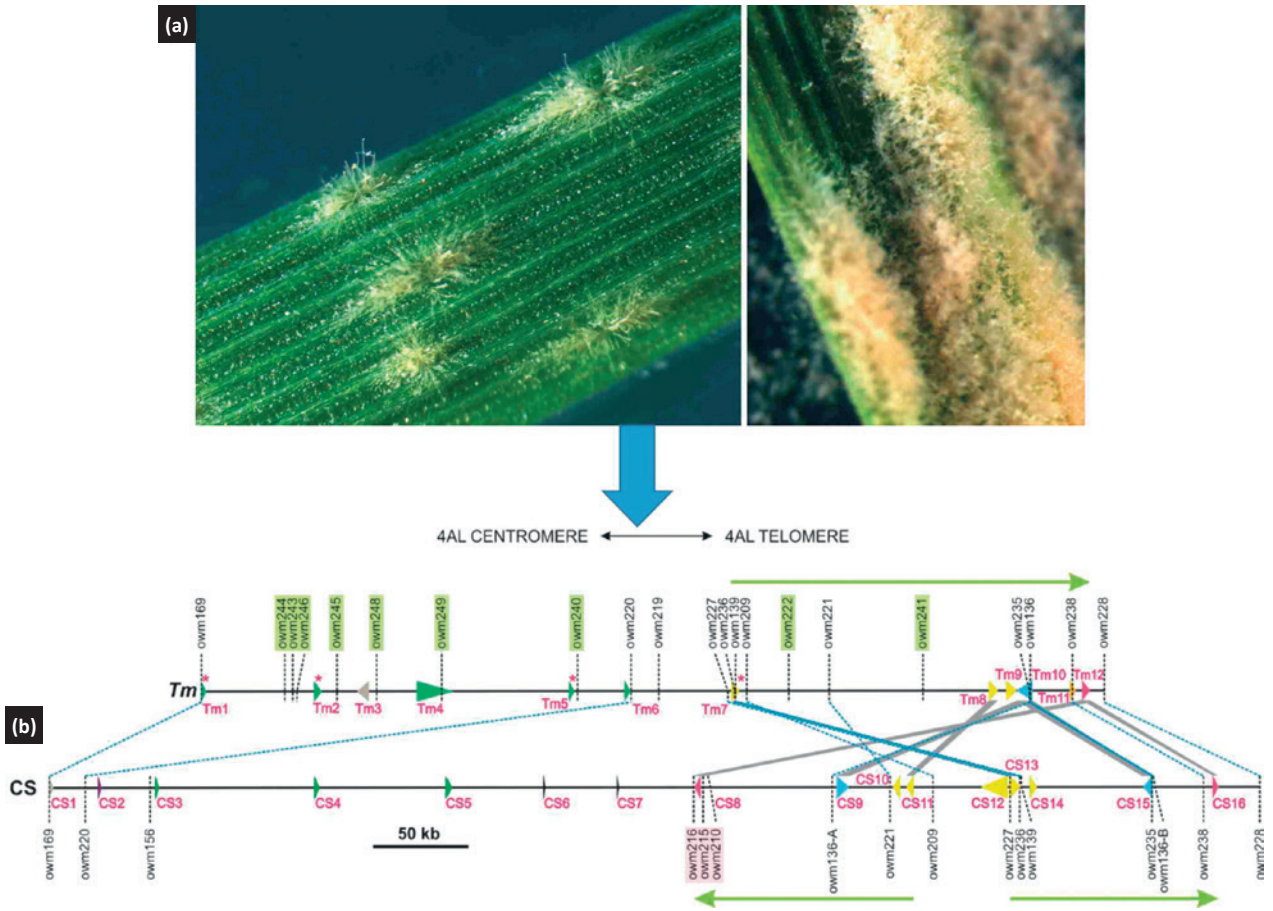


Figure 2. Mapping and cloning of race-nonspecific powdery mildew resistance locus introgressed into bread wheat from *Triticum militinae*. **(a)** The fungus *B. graminis* is a causal agent of the wheat powdery mildew disease. **(b)** Genetic and physical mapping of the resistance locus provided a 480.2 kbp segment inherited from *T. militinae* and the 640.8 kbp segment of wheat chromosome 4AL replaced by the introgression. The introgressed region comprises twelve candidate genes (Tm1–Tm12), including four LRR-like genes (green arrowheads); the wheat replaced region contained sixteen genes (CS1–CS16). The genes are depicted by arrowheads indicating their size and orientation. Syntenic genes are connected by lines. Green arrows indicate duplicated and inverted syntenic regions.

previously produced chromosome survey sequences of rye, we developed optical genome maps as a contribution to both projects. In the case of pea, we also flow-sorted chromosomes whose DNA was sequenced and used to validate the genome assembly. Moreover, sequencing chromosomes flow-sorted from wild relatives of pea allowed the identification of evolutionary chromosome translocations within the genus *Pisum* [212; **Fig. 1**].

Gene mapping and cloning

We have utilized the newly obtained genome sequences of barley and wheat and our chromosome-based experimental approaches to identify and clone agronomically important genes. Thus, in bread wheat, we have analyzed the influence of *Ppd-B1* gene copies on wheat heading date and assessed the role of epigenetic modifications on the vernalization phenomenon and characterized the Polycomb repressive complexes 1 and 2 [475]. We also made significant progress in cloning a gene confering resistance to Russian wheat aphid. Combining a chromosome-based approach with marker development, optical mapping, and long-read sequencing of BAC clones, we identified *EPOXIDE HYDROLASE 2* as the candidate for the *Dn2401* resistance gene [296]. We have also identified a candidate gene for powdery mildew resistance QPm.tut-4A, which was introduced to bread wheat from tetraploid wheat relative *Triticum militinae* [187; **Fig. 2**]. Further, we made an important step towards the cloning of the *Ph2* gene in bread wheat. We have developed and characterized a set of lines with deletions evenly covering the chromosome 3D, which harbors this gene involved in the control of correct chromosome pairing during meiosis [476].

Cloning genes in cereals requires a significant research capacity, limiting the number of genes that can

be cloned by one research team. Thus, to utilize the power of our chromosome-centric strategy and clone more genes, we have been collaborating with foreign research teams. These joint efforts have led to cloning important genes in wheat, such as the semi-dwarfism gene [29], the powdery mildew resistance gene *Pm21* [138b], and the gene SuSr-D1, which encodes Med15, a subunit of the Mediator complex, and which suppresses stem rust resistance [377]. We also contributed to the identification of *Aegilops umbellulata*-derived candidate genes *Lr76* and *Yr70* for leaf rust and stripe rust resistance [331]. Finally, as a starting point to cloning leaf rust resistance gene *Lr49*, we have fine-mapped the gene locus [444]. Our contribution was also crucial in identifying a *Yellow Early Senescence-1* (*YES-1*) locus in tetraploid wheat [178]. We also contributed to the cloning of the first leaf rust resistance gene, *Rph1*, from cultivated barley [165]. Another barley gene to whose cloning we have contributed was the *LYS3* gene, which encodes a prolamin-box-binding transcription factor that controls embryo growth [448].

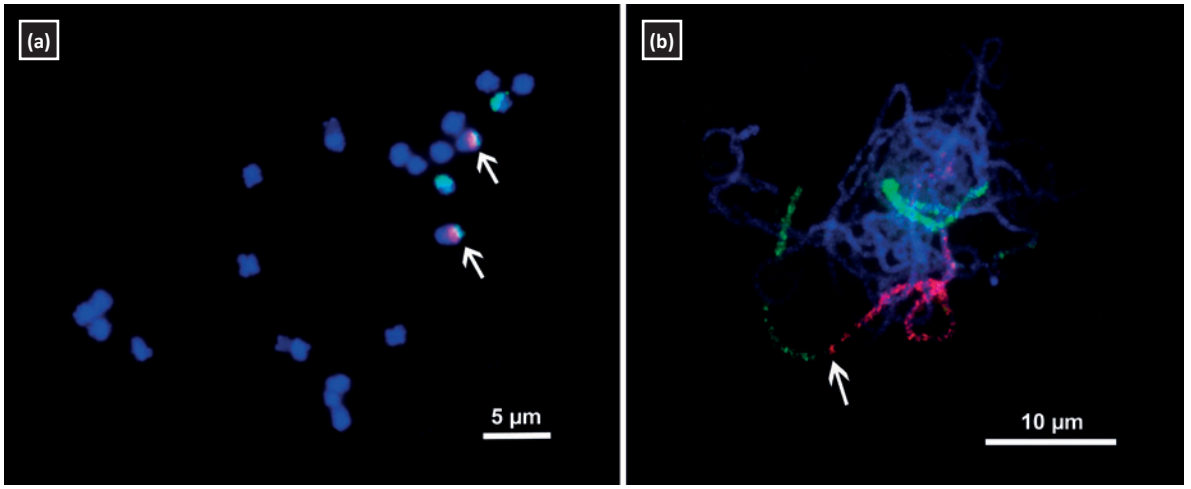


Figure 3. Fluorescence *in situ* hybridization using chromosome-specific oligonucleotide probes on mitotic metaphase chromosome **(a)**, and meiotic pachytene chromosome spread **(b)** of *Musa balbisiana* "Tani" (2n=2x=22). Chromosomes 1 and 3 are labelled in red and green, respectively, and counterstained by DAPI (blue). The arrows point to chromosome translocation breakpoints.

Banana (*Musa* spp.) genetic diversity and genome organization

Our long-term research of *Musa* aims to support the conservation of genetic diversity, characterize genome changes that accompanied the formation of seedless cultivated clones, and develop tools to facilitate the breeding of this staple food crop in many developing countries. In collaboration with Bioversity International (Montpellier, France), we have characterized genetic diversity by DNA flow cytometry and by the SSR genotyping of wild and cultivated bananas in the Autonomous Region of Bougainville, Papua New Guinea [120]. To characterize the genome structure of the Musa species, which contributed to the evolution of edible banana cultivars, we have developed and applied oligonucleotide painting FISH [288, 480; **Fig. 3**]. This advance allowed us to identify individual chromosome arms, anchor them to the *Musa* reference genome sequence, and perform comparative karyotype analysis, which identified putative progenitors of cultivated clones.

These insights are needed to select appropriate parents for cross-hybridization in banana breeding. We have collaborated with the International Institute of Tropical Agriculture in Uganda and Tanzania to support the breeding of the East Africa Highland Banana (EAHB). As part of these efforts, we have genotyped a representative collection of EAHB [88]. This analysis grouped the EAHB accessions into four clusters and suggests that EAHB cultivars originated from a single hybrid clone. The availability of genotyping by sequencing (GBS) allowed us to evaluate the predictive ability of six genomic prediction models for 15 traits in a multiploidy training population. High predictive values of fruit filling and fruit bunch traits showed the potential of genomic prediction to increase selection efficiency in banana breeding [92]. In a follow-up study, we revealed clustering of significant SNPs on chromosome 3, indicating that fruit filling was under the control of a few quantitative trait loci with major effects.

Genome evolution in interspecific hybrids

We have succeeded in making substantial advances in understanding the genome organization and stability in plant interspecific hybrids. The majority of our work focused on Festulolium (*Festuca × Lolium*) grass hybrids

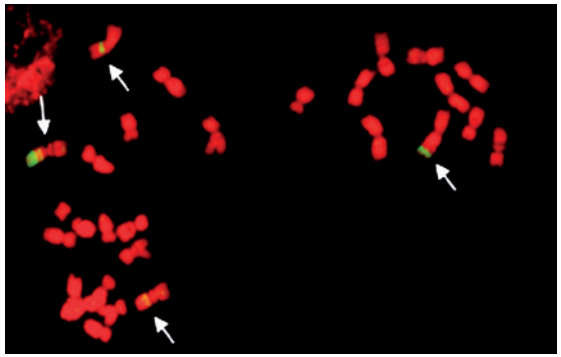


Figure 4. Cytogenetic analysis revealed that introgressed segments of *Festuca pratensis* (green, highlighted by arrows) in tetraploid *Lolium multiflorum* (red) tend to be eliminated within about 3–4 subsequent generations of ×Festulolium introgression-form cultivars.

of agricultural interest, which display homoeologous chromosome pairing and recombination [417]. This work revealed a dominance of the ryegrass (*Lolium*) genome over that of fescue (*Festuca*) in successive generations, which results in the replacement of *Festuca* chromosomes by those of *Lolium*. This leads to the elimination of Festuca chromatin within three to four generations in introgression cultivars [207; Fig. 4].

Apart from analyzing genome dynamics in *Festuca* × *Lolium* hybrids, we also investigated their drought tolerance and after-drought recovery rates [346]. Our results showed that *Festulolium krasanii* (*L. multiflorum* × *F. arundinacea*) is a good candidate to replace pure tall fescue (*F. arundinacea*) stands. Similarly, a large variability for drought tolerance and recovery rates in *Fl. braunii* (*L. multiflorum* × *F. pratensis*) and *Fl. loliaceum* (*L. perenne* × *F. pratensis*) permit the selection of genotypes that can outperform cultivars of pure species *L. multiflorum* and *L. perenne*. We participated in the discovery of triploid hybrids of *Festuca pratensis* × *F. apennina* in the Swiss alpine swards with outstanding competitiveness relative to their parental species in the sites of sympatric occurrence [60]. The values for the midparent heterosis for dry biomass production observed were the highest ever reported for forage crops and point to a hitherto unexploited potential of heterosis for biomass yield within the economically important *Festuca-Lolium* complex [340]. In a follow-up study, the triploid hybrids were found to be only marginally fertile, suggesting that vegetative propagation by rhizomes was the cause of their competitive success in grassland. Moreover, triploid progeny retained the chromosome constitution of their mother plants, indicating the possibility of apomixis.

Three-dimensional genome architecture

We made significant advances in unraveling the principles of the three-dimensional organization of plant genomes. To answer the question of how this organization is affected by genome size, we analyzed DNA replication timing of telomeres and centromeres, as well as of euchromatic and heterochromatic regions [441; **Fig. 5**]. A conserved order of DNA replication was observed as well as stable chromosome positioning while transitioning through different stages of interphase. These findings indicate a more complex interplay between genome size, the organization of repetitive DNA sequences along chromosomes, and higher-order chromatin structure and its maintenance in interphase. We have contributed to the development of the CRISPR/Cas9-based RNA-guided endonuclease *in situ* labeling method [245] to visualize DNA sequences in three-dimensional nuclear space. The method can be combined with immunostaining and labeling using thymidine analogue, ethynyl deoxyuridine to study three-dimensional organization of DNA repeats, histone marks, and DNA replication sites [245]. Our analysis, using 3D-FISH, of the nuclear disposition of alien rye and barley chromosomes and chromosome arm introgressions into wheat revealed a stable chromosome positioning in various tissues and during the cell cycle phases. The results also support

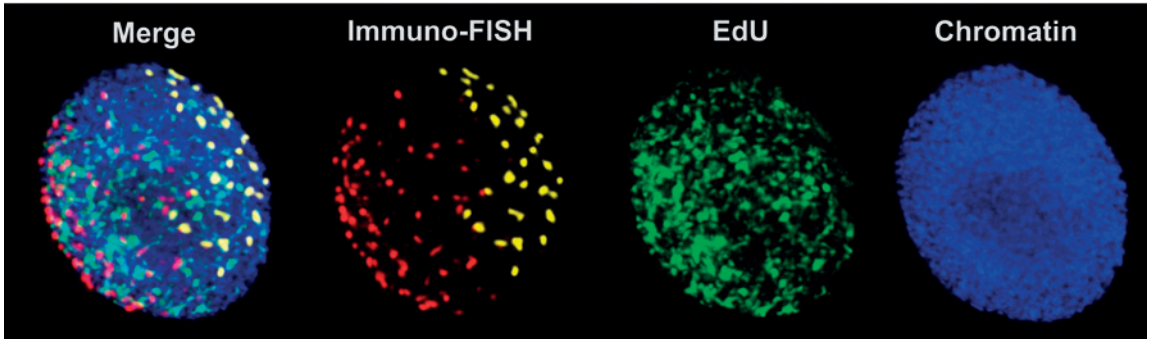


Figure 5. Cell nucleus of bread wheat at the middle stage of S phase. Replicating DNA was labelled by EdU (green), centromeres were visualized using immunolabeling with CenH3 antibody (yellow), and telomeres were visualized by FISH (red). Nuclear DNA was stained with DAPI (blue). According to [441].

the hypothesis that shorter chromosomes and chromosome arms are more centrally located in the 3D nucleus, while longer ones are peripherally positioned, close to the nuclear envelope [205].

Alien introgressions have been used to introduce beneficial alleles into existing crops. However, alien chromosomes show reduced meiotic pairing and may be eliminated over generations. Using 3D-FISH with somatic cell nuclei of a wheat-rye chromosome addition line, we found that while the introgressed rye chromosomes or chromosome arms occupied discrete positions in the Rabl orientation similar to chromosomes of the wheat host, their telomeres frequently occupied positions away from the nuclear periphery. We conclude that the improper positioning in the nuclei may impact the ability of introgressed chromosomes to migrate into the telomere bouquet at the onset of meiosis, preventing synapsis and chiasma establishment, and leading to their gradual elimination over generations [259]. In a complementary study we used 3D imaging confocal microscopy to analyze meiosis in a heterozygote for an inversion of a rye chromosome arm in wheat, in which a distal segment of the normal homologue is capable of chiasmata pairing with its counterpart in the inverted arm, located near the centromere [260]. This demonstrated that the out-of-position placement of the rye telomeres may be responsible for reduced pairing during the first meiotic division of rye chromosomes in hybrids with wheat and their disproportionate contribution to aneuploidy. However, it appears responsible for initiating the chiasmata pairing of distantly positioned segments of homology in an inversion heterozygote.

Maintenance of genome stability

An important line of our research focused on the crosstalk between chromatin and genome stability maintenance using the model plant species *Arabidopsis thaliana*. There is emerging evidence that cytidine analog-based epigenetic inhibitors cause genomic instability, but the nature of this damage and its repair remain unclear. We compared the effects of 5-azacytidine, 2-deoxy-5-azacytidine, and zebularine on transcriptional gene silencing and DNA damage repair and found that the damage is repaired by multiple pathways, with homologous recombination and the SMC5/6 complex playing a critical role [443]. Via suppressor genetic screen, we have found that at least part of the cytidine analog-induced DNA damage is represented by little-known but highly toxic types of lesions – DNA protein crosslinks (unpublished). This finding allowed us to establish a forward-directed genetic screen for the identification of the DNA-protein crosslink (DPC) repair factors in plants. The screen has already yielded several novel DNA repair candidates (unpublished) and has also pointed to the important role of the enigmatic SMC5/6 complex in DPC repair. Therefore, we functionally characterized as yet undescribed *Arabidopsis* kleisin subunits of the SMC5/6 complex [163]. This opens up the possibility of using cytidine analogs to understand the mechanisms of genome stability maintenance in plants, as well as in biotechnology.

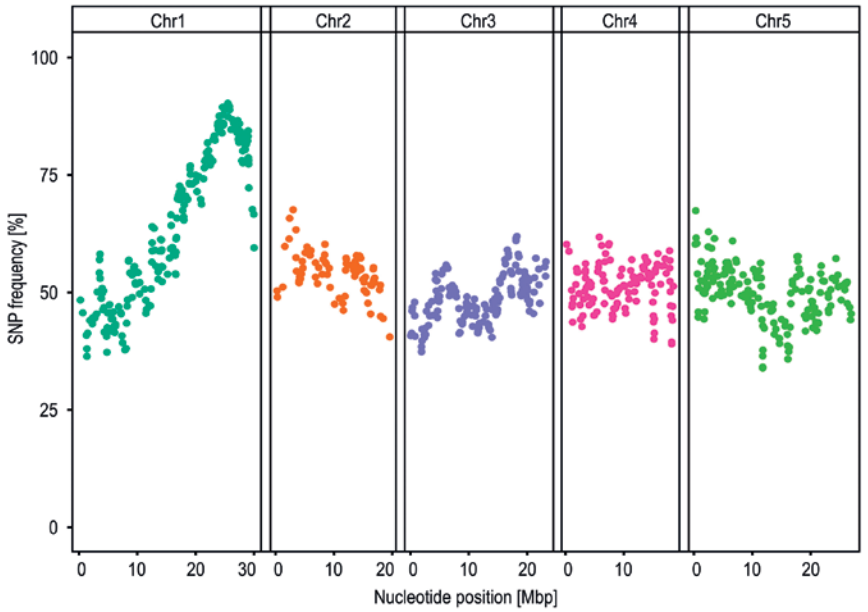


Figure 6. Example of mapping-by-sequencing used for a candidate gene identification in our forward-directed genetic screen. DNA damage hypersensitive mutant plants were selected from the F2 segregating population, bulked and deep sequenced. Individual dots indicate frequency of the ethyl methanesulfonate-induced single nucleotide polymorphisms (SNPs) in the sequencing reads. The region containing a candidate gene is indicated by the peak on chromosome 1. Markers on the other chromosomes segregate at random.

Research projects: 11–2, 6, 12, 19, 23, 28–29, 34, 36–37, 42, 48–50, 55, 58–60, 64, 72, 74, 77, 81, 96, 105–106, 108, 110, 113

Imaging Facility

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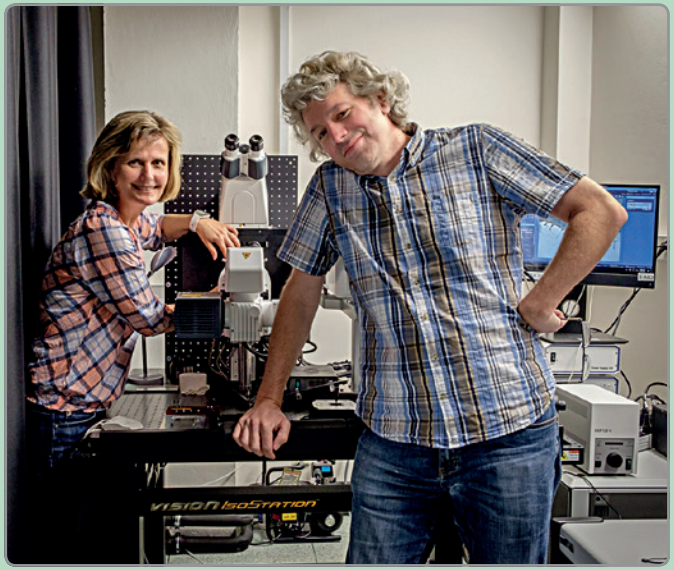
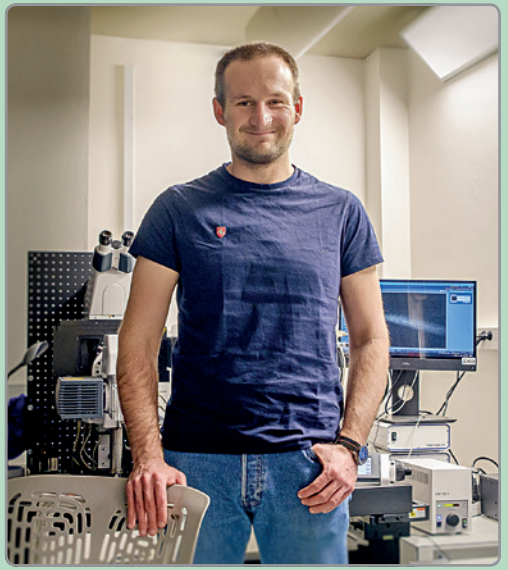
The Imaging Facility of the institute (IF IEB) provides high-end instrumentation and expertise for demanding tasks in the field of non-invasive in vivo advanced fluorescence microscopy in high spatio-temporal resolution. In 2018–2020, the facility served in a number of projects performed in the laboratories of the IEB CAS, including studies of membrane trafficking, cytoskeleton dynamics, hormonal regulations, the involvement of membrane lipids in signalling pathways, plant reproduction, the reaction of plants to pathogen attack, and the dynamics of cell wall biosynthesis. In addition, it also offered microscopy services for external users from the Czech Republic and abroad.





In the pictures (from left to right):
Ing. Kateřina Malínská, Ph.D. / researcher, RNDr. Jan Petrášek, Ph.D. / head of the facility, Mgr. Ivan Kashkan / Ph.D. student.

The Imaging Facility of IEB CAS (IF IEB; www.ueb.cas.cz/if) is a well-established facility that provides high-end instrumentation and expertise for demanding tasks in the field of fluorescence microscopy in plant research. Between 2018-2020, the instrumentation of the Imaging Facility was used every year by around 70 independent users (researchers, masters and Ph.D. students), from both IEB CAS laboratories and external locations, including foreign research institutions.

IF IEB is equipped with high-end confocal laser scanning microscopes serving for a spectrum of techniques for fast and sensitive detection of fluorescence signals. In 2018–2020, we introduced a unique, plant-optimized confocal microscope vertical stage and sample mounting (**Fig. 1a**). This setup of Zeiss LSM880 with Airyscan allows for the imaging of plant seedlings under natural gravity vector as well as controlled gravistimulation by rotation stage insert (**Fig. 1b**). In addition, the Airyscan detector improves the spatial resolution of CLSM imaging. This technology is not commercially available at the moment. This investment is a huge step forward in providing users with the set-ups that allow non-invasive observation conditions for plants, which require gravity-oriented culture conditions (**Fig. 1c**).

Another crucial factor in *in vivo* imaging, apart from sensitivity and resolution, is speed. Due to enormous progress in the development of scientific cameras, it was beneficial to upgrade our system for fast imaging. Methods of non-invasive *in vivo* fluorescence microscopy in high time and spatial resolution are performed on the inverted spinning disk confocal microscope Nikon Eclipse Ti-E with Yokogawa CSU-X1, newly equipped with Photometrics ultrasensitive sCMOS cameras Prime 95B and Prime BSI for fast imaging in high resolution. In 2020, our first confocal microscope, a Zeiss LSM5 Duo, purchased in 2006, was rebuilt into a fully motorized widefield fluorescence Zeiss Axiovert 200M microscope, which has outstanding optics and is still in use today. Finally, the portfolio of microscopes was extended by a fluorescence stereomicroscope Leica M205 FA, which serves for the imaging of larger objects and for screening for fluorescence-positive transformants on the level of calli, seeds, seedlings, or mosses. We are also continuously improving our post-processing portfolio of methods for the improvement of spatial resolution (e.g. SRRF) and image analysis.

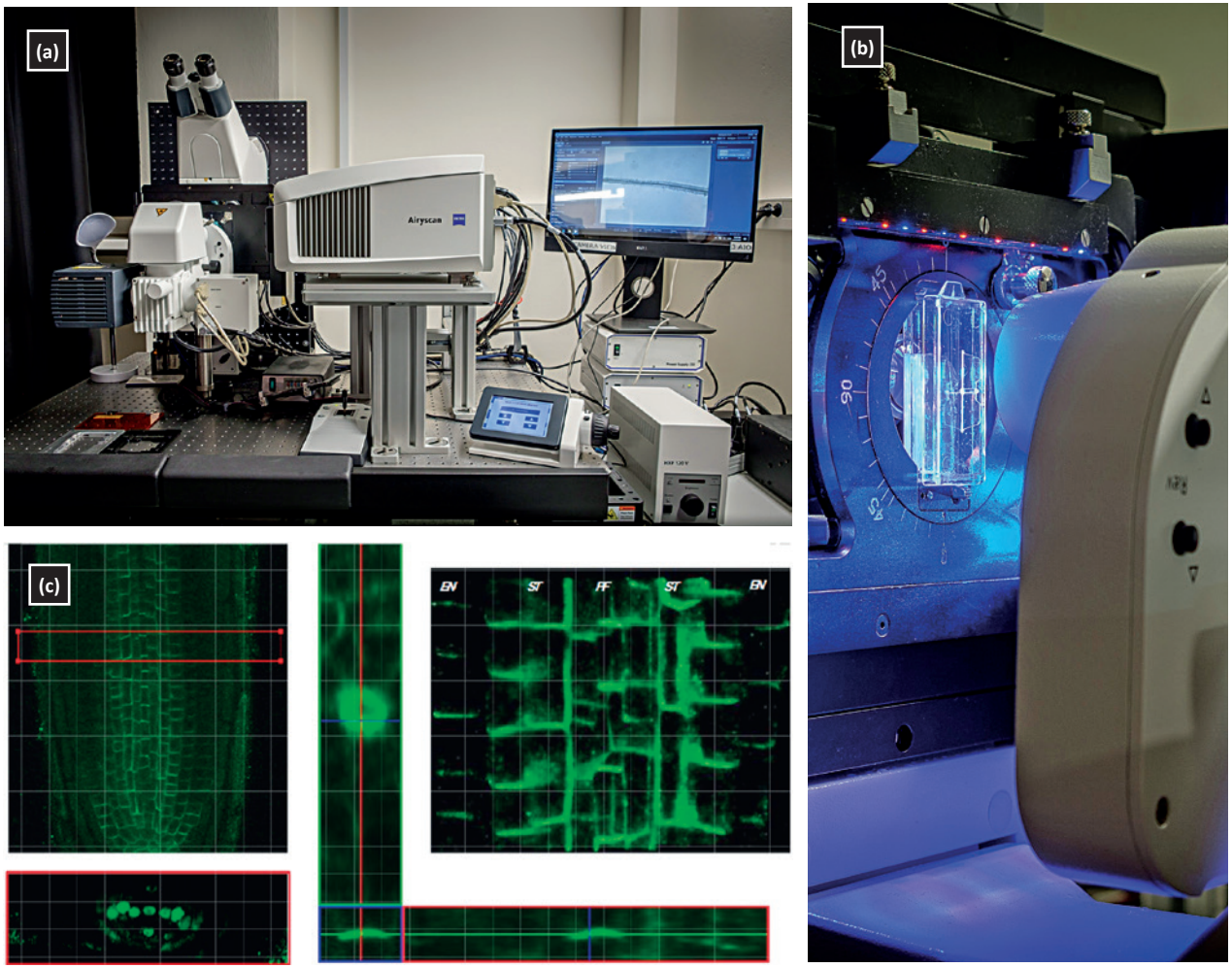


Figure 1. Microscopes for advanced fluorescence microscopy in the Imaging Facility of IEB CAS. **(a)** Plant-optimized microscope Zeiss LSM880 with Airyscan detector and vertical sample mounting. **(b)** Detailed view of microscopy chambered coverglass with growing seedling placed in rotation stage insert. **(c)** *In vivo* confocal fluorescence microscopy of *Arabidopsis* auxin efflux carrier AtPIN1 tagged with GFP. Localization of AtPIN1-GFP in the root tip (left) and a detailed 3D view of protophloem-specific AtPIN1 structures [419].

The Imaging Facility is a partner of the project in the framework of the "National Infrastructure for Biological and Medical Imaging" (Czech-BioImaging, CzBi; www.czech-bioimaging.cz), which has been approved for funding by the Ministry of Education, Youth and Sports for the periods 2016–2019 [project 79] and 2020-2022 [project 80]. In 2018–2020 the IF took part in two European Regional Development Fund projects focused on the modernization of the national infrastructure for biological and medical imaging Czech-BioImaging [projects 10, 13]. Through Czech-BioImaging, the IF IEB is integrated within Prague's node of the large European research infrastructure Euro-BioImaging (www.eurobioimaging.eu). IF IEB also takes part in investment calls of the Czech Academy of Sciences and is supported by IEB. Through the combination of all these financial sources, the facility is continually developing and is able to provide high-end instrumentation and service to all of its users.

Nearly 30 original contributions were published by local and external users in high impact journals between 2018–2020, including reports on cytoskeletal dynamics, plant reproduction, the role of integral and peripheral plasma membrane proteins, plasma membrane associated-tethering complexes, lipid dynamics, endomembrane dynamics, cell wall biogenesis, and reaction to pathogens [3, 63, 104, 190, 224, 238, 270, 280, 347, 362, 391, 407, 409, 419–420, 430, 455, 488, 528, 534; Schwarzerová *et al.* 2019, Sci Rep 9: 5725].

We would like to continue in our mission, i.e. to steadily improve the imaging options for the demanding tasks of modern plant cell biology research and to help in the integration of students and young researchers into up-to-date imaging protocols.

Research projects: 10, 13, 79, 80

Isotope Laboratory

Head of the laboratory:

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The research performed in the Isotope Laboratory can be divided into four basic fields:
(1) Development of urea derivatives as plant growth regulators for application in practice.
(2) Preparation of cytokinin derivatives and other required compounds, including radiolabeling.
(3) Development of heterocyclic derivatives of a synthetic origin (purine-based compounds), including radiolabeling whenever required.
(4) Investigation of pharmacologically important plant products, including their derivation resulting in developing semisynthetic compounds with improved physico-chemical and ADME characteristics, and primarily with enhanced pharmacological activity in comparison with their parent natural products.

The research is mainly oriented to biomolecules, their structure and analysis, activity, and molecular and cellular mechanism of action, as well as applications in different fields. Synthetic compounds are used as plant growth regulators or other agents with different modes of action in the environment.

Cytokinins and radiolabeling

Long-term research in the field of cytokinins (CKs) has resulted in a finding that the *cis*-zeatin (*c*Z)-type occur generally in the plant kingdom. A survey of employed bioassays illustrates the ability of high doses of *c*Z-type CKs to induce various physiological responses and CK signaling. These data argue against the image of *c*Z-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 [177, 305, 387, 405].

In the picture (from left to right):
Front row: Jana Maňáková / technician, Ing. Veronika Zemanová, Ph.D. / researcher, Ing. Zülal Özdemir / Ph.D. student, Martina Wimmerová / technician.
Second row: Mgr. Jaroslav Nisler, Ph.D. et Ph.D. / researcher, doc. Ing. Milan Pavlík, CSc. / researcher, doc. Ing. Libor Havlíček, CSc. / researcher, Ing. Lukáš Drašar, Ph.D. / researcher, Mgr. Sándor Forczek, Ph.D. / researcher, Mgr. Uladzimir Bildziukevich, Ph.D. / researcher, Dr. Josef Holík / researcher, prof. Ing. Zdeněk Wimmer, DrSc. / head of the laboratory, PharmDr. Lenka Zahajská, Ph.D. / researcher.

Not pictured:
RNDr. Martin Vlk, Ph.D. / researcher.

Urea derivatives as plant growth regulators

The research in this area includes the design, synthesis, and analysis of the biological activity of chemical compounds which are derived mainly from urea. The former group of these compounds has been used as inhibitors of the enzyme cytokinin oxidase/dehydrogenase, which degrades cytokinins in plants. These compounds have the potential to be used in agriculture for yield improvement, as well as in plant tissue culture techniques. The latter group of compounds is capable of increasing the resistance of plants to abiotic stress, thus mitigating yield loss under different stressful conditions (**Fig. 1**) [91].

Natural phytochemicals as potential nano-drug candidates

The current interest in this area has been focused on the investigation of novel derivatives of triterpenoids with potential cytotoxicity, antimicrobial activity, anti-HIV, anti-HSV, and other types of pharmaceutical activity. The synthetic protocol has been designed in a sustainable way and divided into several general methodologies applicable

to the compounds synthesized. Cytotoxicity was tested on several important cancer cell lines, and additional studies of apoptosis were performed wherever possible. ADME parameters, as well as selected physico-chemical parameters, were either measured or calculated to support experimentally obtained results. The physico-chemical characteristics of the prepared compounds were studied due to the investigation of the supramolecular characteristics of potential biological systems, and they contribute to the newly emerging area of supramolecular chemical biology and nano-drug application. A number of the prepared compounds, derived from natural triterpenoids, display improved bioavailability and enhanced pharmacological effects, despite the low bioavailability of the parent natural triterpenoids. Recently, we have described a relation between supramolecular characteristics and pharmacological activity [338], resulting in the discovery of novel application patterns in supramolecular systems that are capable of being used not only as drug carriers but also as nano-drugs by their nature (**Fig. 2**) [9, 94, 153–154, 292, 416, 449].

Other fields of research

Research in the area of different types of biomass and microorganisms, and their role in different interactions within the living environment [135–136, 191, 298, 386]. The role of environmental stress has been studied to focus on a recently emerging field in agricultural research [315, 451, 511–512].

The synthesis and complex biological investigation of pyrimidine derivatives has also been realized during the evaluated period [11, 194].

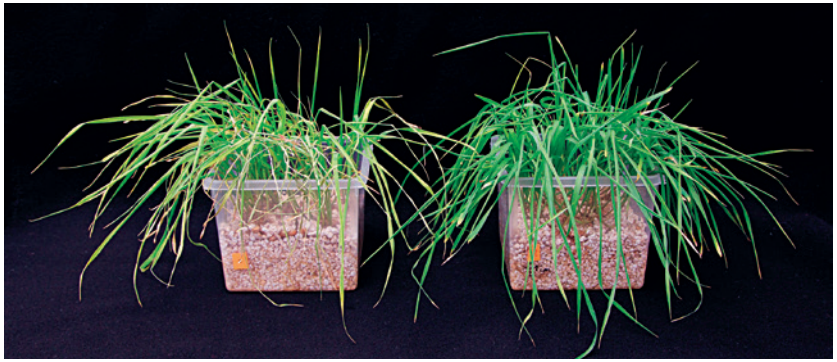

Figure 1. Untreated wheat (left) and wheat treated with an anti-stress compound (right) that has been exposed to drought.

Future perspectives of the Isotope Laboratory in 2021–2024:

It is expected that all three basic areas of research will be continuously developed. In the area of cytokinins, radiolabeling will continue upon requests from other research groups. Research in the area of cytokinin mimics will be focused on the further development of urea-based structures with a high potential in practical applications (collaboration with Palacký University in Olomouc). The investigation of different potential heterocycles-based drugs will be focused on practical applications as well (collaboration with Palacký University in Olomouc). Agriculture-based research will be focused on the role of toxic elements in plant stress, and on the investigation of biomass (collaboration with the Czech University of Life Sciences and the Institute of Microbiology of the Czech Academy of Sciences). Finally, plant products will be the subjects of structural modifications to achieve progress in designing self-assembly systems with potential in supramolecular chemical biology (collaboration with the University of Chemistry and Technology in Prague, the Institute of Organic Chemistry and Biochemistry of the Czech Academy of Sciences, and with several universities in Finland: Helsinki, Jyväskylä, and Tampere).

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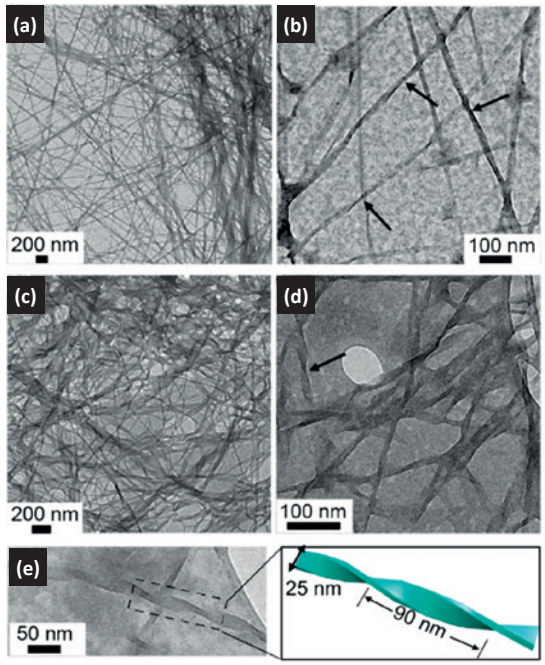

Figure 2. Transmission electron microscopy: **(a,b)** TEM micrographs of the 1.0% 1-propanol gel of an oleanolic acid–spermine conjugate; **(c,d)** TEM micrographs of the 1.0% 1-heptanol gel of an oleanolic acid–spermine conjugate; and **(e)** a single fiber with a helical twist is shown (left) together with its graphical representation (right).

Research projects: 14, 32, 111, 114

Laboratory of Biologically Active Compounds

Head of the laboratory:

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The majority of the findings published by the Laboratory of Biologically Active Compounds between 2018–2020 can be assigned to three fields: 1) studies of somatic embryogenesis (SE) 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.

In the picture (from left to right):
Mgr. Kateřina Eliášová, Ph.D. / researcher, RNDr. Lucie Fischerová, Ph.D. / researcher, RNDr. Martin Vágner, CSc. / head of the laboratory, Mgr. Lenka Gemperlová, Ph.D. / researcher, RNDr. Milena Cvikrová / researcher, Jana Kališová / technician, RNDr. Zuzana Vondráková, CSc. / researcher, Ing. Jana Pavlíčková / graduated technical assistant, Jaroslava Špačková / technician.

Somatic embryogenesis in Norway spruce

SE is characterized as a developmental process where somatic cells, under suitable induction conditions, undergo restructuring through the embryogenic pathway to generate embryogenic cells, a somatic embryo, and consequently the entire plant. The key substances controlling the whole process are exogenous plant growth regulators and endogenous phytohormones, which trigger particular ontogenetic events. Most of the mechanisms and hormonal functions in the SE of conifers have not yet been described.

In our paper [137] we provided a detailed analysis of the spectrum of endogenous phytohormones including auxins, cytokinins, the abscisic acid, jasmonates, and the salicylic acid over the course of SE in Norway spruce. The results revealed that the concentrations of particular phytohormone classes varied substantially between proliferation, maturation, desiccation, and germination. Auxins reached their concentration maxima in the early maturation stage, suggesting their role in embryo polarization; ABA showed a maximum in the late maturation stage. To our knowledge, we have presented for the first time in conifer SE both the evidence for the involvement of the non-indole auxin phenylacetic acid, cis-zeatin and dihydrozeatin-type

cytokinins, or patterns of jasmonates and salicylic acid. The presented results provide the most comprehensive overview thus far of plant hormone levels in embryos throughout the entire process of conifer SE.

Polyamines are primarily known as the key substances in plant response to stress factors. The higher polyamine levels of fully developed embryos had positive effects on their ability to tolerate UV-B irradiation compared with the responses of early embryos. Elevated levels of spermine and spermidine and an increase in total phenolics as a consequence of irradiation with UV-B indicated their involvement in the stress response. The extent of cell damage was dependent on the UV-B dose applied, as well as the embryo developmental stage, and might be related to differentiation of the outermost cell layers and the formation of the protoderm. Developmentally more advanced embryos were superior to early embryos in terms of a more efficient stress defense response to UV-B exposure. UV-B irradiation evoked striking polyphenolic accumulation in specialized idioblastic cells [23]. In the study, advanced and sophisticated techniques of microscopy were used: double fluorescent staining for confocal laser-scanning microscopy and, for the very first time, the modified technique of environmental scanning electron microscopy AQUASEM II (collaboration with colleagues from the Institute of Scientific Instruments, Czech Academy of Sciences).

Somatic embryogenesis in Douglas-fir

Long-term cooperation with INRA, France (lab. of Prof. Lelu-Walter) resulted in three papers on the SE of conifers; our model, Norway spruce, was replaced with Douglas-fir here [32, 69, 172]. These very complex studies used transcriptomic and proteomic approaches, biochemistry, histology, and anatomy. Our laboratory took part mainly in histology and anatomy, in the proteomic study, in analyses of plant hormones and tissue cultures. A major part of all three papers was elaborated in our labs during the study stay of Florian Gautier at IEB, Prague.

Douglas-fir is a conifer species of major economic importance worldwide. We described some characterization and significant refinement of SE in Douglas-fir, with a focus on maturation. The most typical structures observed in the embryonal masses were large polyembryogenic centres with a broad meristem. Embryo development was enhanced following embryonal mass dispersion on filter paper discs. Moreover, increasing gellan gum concentration in the maturation medium improved both the quantity and quality of cotyledonary somatic embryos, which were subsequently able to germinate and develop into plantlets at high frequency. Interestingly, secondary SE could be induced from cotyledonary somatic embryos. The protein pattern was similar in both somatic and zygotic embryos, with major storage proteins identified as 7S-vicilin- and legumin-like proteins [69].

We published the first report of cellular and molecular changes after repetitive SE in conifers. To explore the poorly understood differences between primary and subsequent somatic embryogenic lines of plants, we induced secondary and tertiary lines from the cotyledonary somatic embryos of two Douglas-fir genotypes. The secondary lines exhibited significantly higher embryogenic potential (measured by the yield of somatic embryos) than the primary lines. We then compared primary, secondary, and tertiary lines at histo-cytological and proteomic levels [32].

In a follow-up, we focused on the issue of comparison of different sources of plant material used for induction of embryogenic cultures. SE techniques have been developed for most coniferous species, but only using very juvenile material. Therefore, embryonal

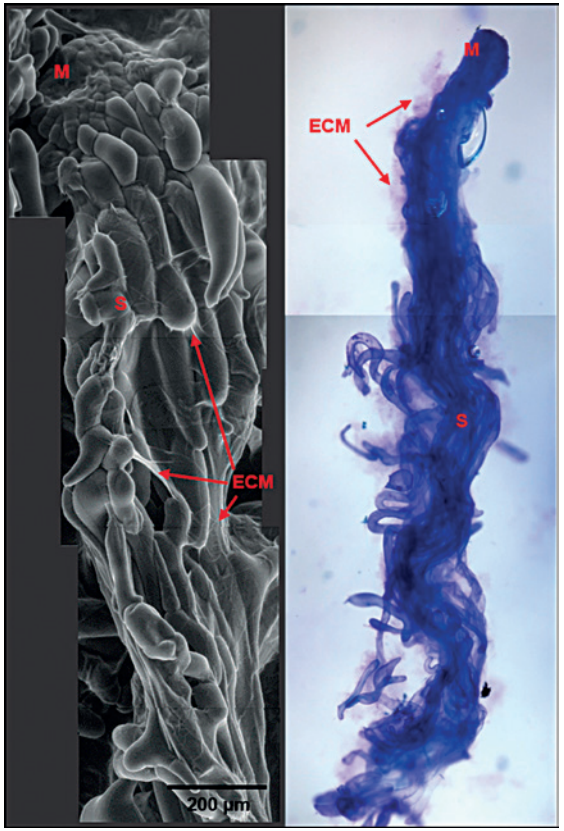

Figure 1. Early somatic embryo of Norway spruce. **Left:** Early somatic embryo imaged by environmental scanning electron microscope (ESEM) AQUASEM II at the Institute of Scientific Instruments, Czech Academy of Sciences. Extracellular matrix is visible as veils or wimples covering suspensor cells. **Right:** Early somatic embryo stained with Toluidine blue; metachromatic staining showed an extracellular matrix that surrounds and connects suspensor cells in a purple-pink colour, while cell walls are stained in blue. M – meristem, S – suspensor, ECM – extracellular matrix.

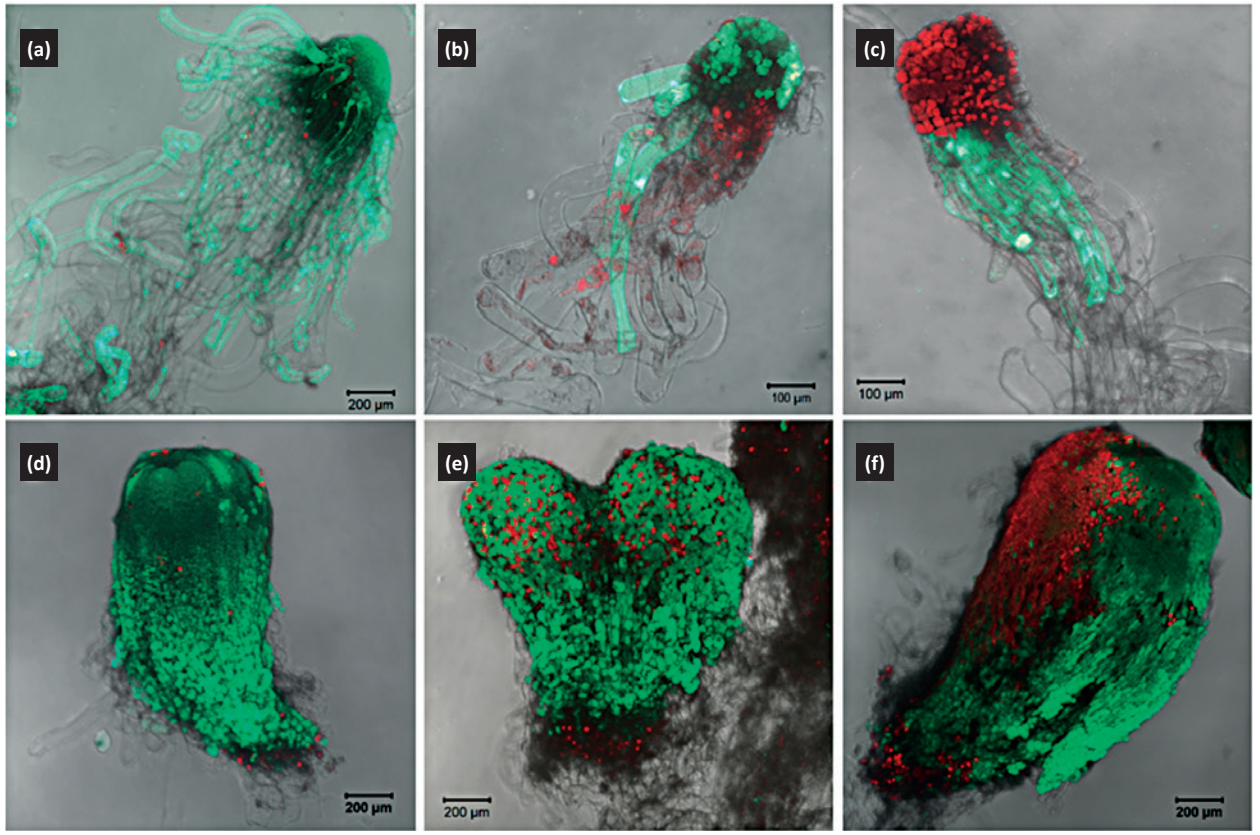

Figure 2. Assessment of cell viability in somatic embryos of Norway spruce after UV-B irradiation. Higher radiation intensity caused lethal injuries mainly to meristematic cells of early somatic embryos, while embryos after three weeks of maturation were less damaged. **(a–c)** Early somatic embryos; **(d–f)** somatic embryos after three weeks of maturation. **(a, d)** Untreated control; **(b, e)** 0.1 $Wm^{-2}h^{-1}$ UV-B; **(c, f)** 0.6 $Wm^{-2}h^{-1}$ UV-B. Double staining with fluorescein diacetate (live cells in green) and propidium iodide (dead cells in red). Images were acquired as a maximum intensity projection of optical slices from the confocal laser scanning microscope.

masses and non-embryogenic calli have been compared during proliferation at multiple levels. Embryonal masses and non-embryogenic calli originating from a single somatic embryo (isogenic lines) were used in the analyses, which included comparison of the lines' anatomy by transmission light microscopy, transcriptomes by RNAseq Illumina sequencing, proteomes by free-gel analysis, contents of endogenous phytohormones, and profiles of soluble sugar contents. The study shows the utility of a novel approach involving integrated multi-scale transcriptomic, proteomic, biochemical, histological and anatomical analyses to obtain insights into molecular events associated with embryogenesis and more specifically to the embryogenic state of cell in Douglas-fir [172].

Dormancy breaking in beechnuts

The experience with somatic embryos was utilized during the project QI102A256, in the study of the mechanisms of dormancy in beech zygotic embryos [504]. To improve our understanding of dormancy breaking in beechnuts, we investigated the effects of moisture content and temperature during storage, and analysed the contents of abscisic acid, abscisic acid metabolites, and indole-3-acetic acid in embryonic axes during storage and stratification, as well as histochemically-localized storage proteins [504].

Secondary metabolites in apples

A relatively new and prolific cooperation with the Station of Apple Breeding resulted in two publications [503, 505].

Phenolic compounds are produced by plants as secondary metabolites. Due to their antioxidant activity, they play crucial roles in plant defences against both biotic and abiotic stressors; moreover, they are an important component of the animal diet, and they are

highly beneficial for human health. Thus, the purpose of this study was to quantify free and glycosylated phenolic acids in apples in the course of fruit development, at harvest, and during five months of storage. The major free phenolic acid in both the peel and the flesh of the apples was chlorogenic acid, followed by (at much lower concentrations) three hydroxybenzoic acid derivatives (protocatechuic, vanillic, and gallic acids) and three hydroxycinnamic acid derivatives (*p*-coumaric, ferulic, and caffeic acids) [503].

In the second paper [505], we investigated how different storage conditions – boxes with controlled atmospheric conditions (1.2% O_2 and 2.2% CO_2) and temperature (1 °C), and boxes with a regulated temperature (1 °C) – affect antioxidant levels in three scab-resistant and powdery mildew-tolerant apple cultivars. The contents of carotenoids, along with free and glycosylated phenolic acids, were quantified. We demonstrated a continuous decrease in total carotenoid content during the storage period. Apples stored under controlled atmospheric conditions showed significantly higher carotenoid levels over three and five months of storage.

Cooperation with other teams

The scientists of our laboratory are often invited into cooperation thanks to their knowledge of anatomy and microscopy [289, 301]. We cooperated with colleagues from the Laboratory of Reproduction of Plants on the regulation of floral induction of *Chenopodium ficifolium* and *C. suecicum* [289]. The objective of the cooperation with the Czech Agricultural University was to induce and detect somaclonal variation in arracacha (*Arracacia xanthorrhiza*) plants regenerated via indirect morphogenesis, in order to evaluate the potential of this technique to produce new genotypes for breeding purposes of this crop [301].

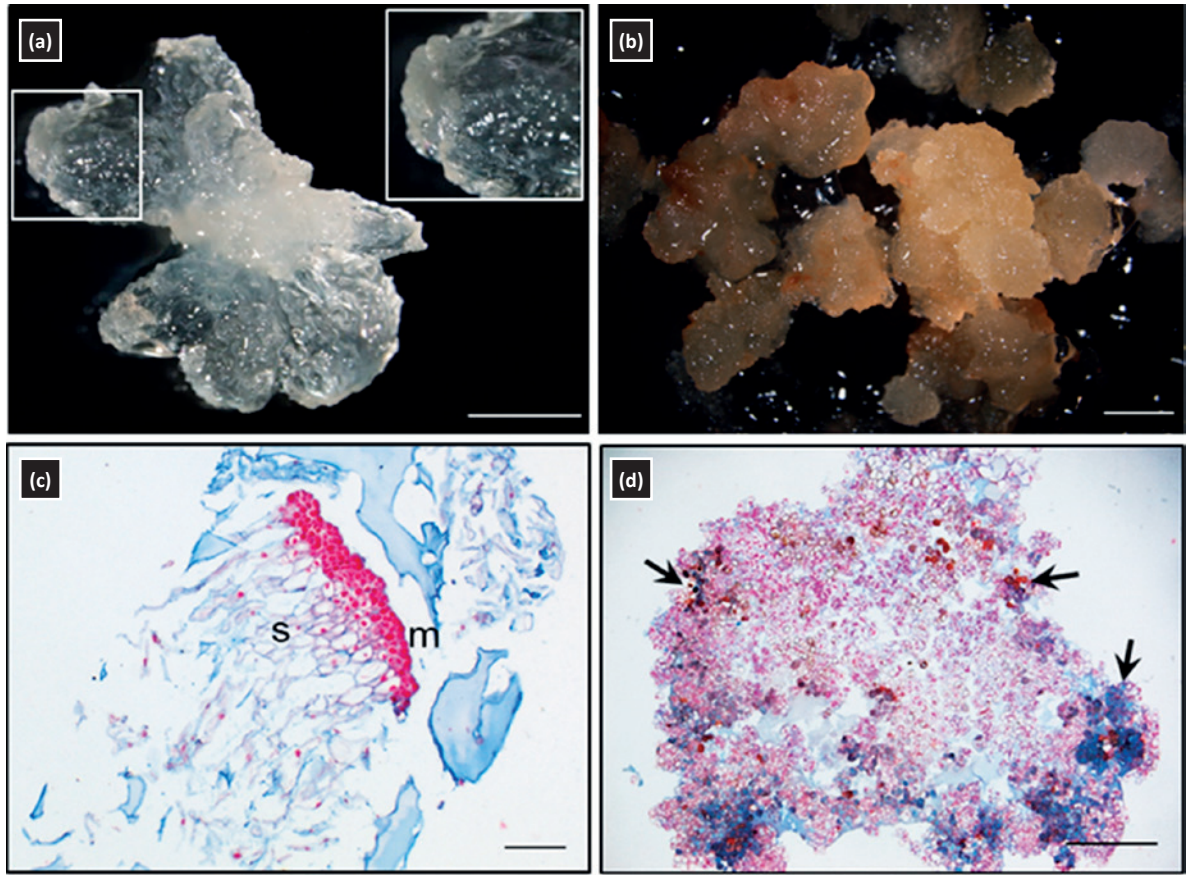

Figure 3. Comparison of embryogenic and non-embryogenic cell lines of Douglas-fir. Embryogenic line **(a)** consists of early embryos **(c)** composed of meristematic (m) and suspensor (s) cells. Non-embryogenic line **(b)** consists of undifferentiated cells composing callus. These cells often accumulate polyphenolic compounds, as shown in **(d)** by arrows. **(a, b)** Morphology of the lines – inset in **(a)** shows a detail of the embryo meristem; **(c, d)** histological sections stained with Nuclear Fast Red (red colour of cell nuclei) and Aniline Blue (blue colour of cell walls). Scale bars: **(a, b, d)** 2 mm; (c) 200 µm.

Research projects: 87, 89, 91

Laboratory of Cell Biology

Head of the laboratory:

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Since its inception, the Laboratory of Cell Biology has focused on the study of several molecular modules involved in the regulation of plant cell polarity and morphogenesis, with a particular focus on those operating at the intersection of the secretory pathway, plasma membrane lipids, and the actin cytoskeleton. We divide our attention between two main processes that give plant cells their shape-oriented cell division and differential cell growth, and we focus on intracellular molecular mechanisms driving cellular morphogenesis such as exocytosis. The laboratory research is centred around the detailed characterization and regulation of the plant vesicle tethering complex exocyst in various cell types across plant species and biological processes, including plant-pathogen interactions. The exocyst is a heterooctameric protein complex, crucial for the tethering of secretory vesicles to the plasma membrane during exocytosis, conserved throughout all eukaryotic lineages. Strikingly, compared to other eukaryotes, the exocyst subunit EXO70 is represented by many isoforms in land plants whose biological roles and modes of regulation remain mostly unknown. Detailed studies of different EXO70 exocyst isoforms are thus an essential part of our research.

In the picture (from left to right):
Upper row: Martin Potocký, Ph.D. / head of the laboratory, Viktor Žárský, Ph.D. / senior researcher, Tamara Pečenková, Ph.D. / researcher, Lucie Brejšková, Ph.D. / researcher, Michal Hála, Ph.D. / researcher, Edita Drdová Janková, Ph.D. / researcher, Přemysl Pejchar, Ph.D. / researcher.
Middle row: Lukáš Synek, Ph.D. / researcher, Roman Pleskot, Ph.D. / researcher, Natalia Serrano, Ph.D. / postdoc, Peter Sabol, Ph.D. / postdoc, Anksuh Saddhe, Ph.D. / postdoc, Antonietta Saccomanno, Ph.D. / postdoc, Vedrana Marković / Ph.D. student.
Lower row: Klára Batystová, M.Sc. / Ph.D. student, Samuel Haluška, M.Sc. / Ph.D. student, Matěj Drs, M.Sc. / Ph.D. student, Ondřej Novotný, M.Sc. / Ph.D. student, Andrea Potocká, Ph.D. / research assistant, Hana Soukupová, Ph.D. / research assistant, Jana Šťovíčková, B.Sc. / technician.

In parallel, another significant area of research undertaken in the lab is understanding the functions of negatively charged membrane lipids in establishing and maintaining plant cell polarity. Although they represent only a minor fraction of total cell membranes lipids (often less than 1%), they are critically important for many membrane-related processes, including membrane identity, charge, shape, generation of second messengers, and recruitment of peripheral proteins (including exocyst subunits). Notably, we are interested in the role of two anionic phospholipids in the plasma membrane, namely phosphatidic acid (PA) and phosphatidylinositol 4,5-bisphosphate (PIP_2).

Overall research summary

In 2018–2020, we made significant progress in all of the main research topics studied in the lab. We significantly expanded our understanding of the exocyst role

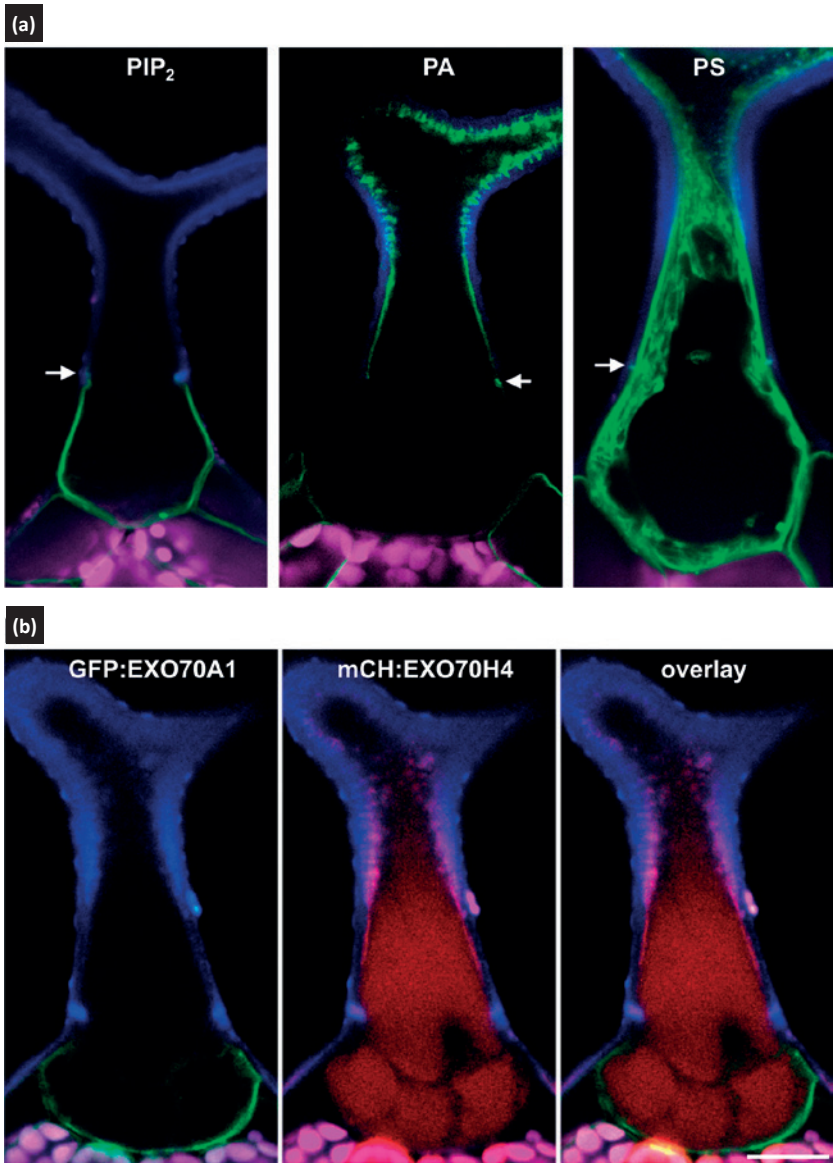

Figure 1. *Arabidopsis* trichome contains two plasma membrane domains with different lipid compositions which attract distinct EXO70 subunits. **(a)** Minor membrane lipids localize to distinct domain of trichome plasma membrane in *Arabidopsis*. **(b)** Trichome plasma membrane domains recruit different EXO70 proteins. Adapted from [215].

in the polar expansion of several plant cell types, and we linked the specific exocyst localization with a distinct distribution of anionic membrane lipids in the plasma membrane. We have described the link between phospholipid localization and the targeting of exocyst subunits [215], and we have participated in the pioneering study describing the phospholipid-based identity of plant membranes [104]. We performed a detailed characterization of the phospholipase D family producing PA during pollen tube tip growth [455]. We have described the role of the specific exocyst subunit EXO70H4 in the maturation of *Arabidopsis* trichomes, where it regulates the deposition of distinct cell wall components [63]. Our understanding of the distinct functions of EXO70 isoforms was significantly expanded by the analyses describing redundant and diversified roles among selected *Arabidopsis* EXO70 paralogs during biotic interactions [453] and the role of the EXO70A2 isoform in pollen maturation and germination [420]. Significantly, we described the protein-protein interaction among exocyst subunits and SNARE proteins and established a hierarchy of interactions leading to secretion in *Arabidopsis* [409]. We also discovered a novel and unexpected role of the exocyst complex in the development and organization of the root-shoot junction in *Arabidopsis* [190]. We have summarized the recent developments in the characterization of the plant EXO70 exocyst subunits and their function [98, 519].

Distinct anionic phospholipids define the identity of plasma membrane domains and control the localization of EXO70 exocyst subunits

A conserved feature of endomembrane organelles is their distinct phospholipid composition, which was proposed to specify membrane identity and function. We participated in a large study, which revealed that in plant cells, each endomembrane organelle has a distinct electrostatic signature created by a combination of various anionic phospholipids (our contribution was the generation of the genetically encoded sensor for phosphatidylserine and the detailed microscopic analysis of its dynamics in tip-growing cells). We proposed that this “electrostatic code” represents a fundamental patterning principle of the endomembrane system and acts as a critical determinant of protein subcellular targeting [104].

To test whether distinct EXO70 isoforms have specific interactions with plasma membrane-defining phospholipids, we used *Arabidopsis* trichomes, where two markedly different domains—the basal domain, with a thin cell wall, and the apical domain, with an extremely thick cell wall, are formed. We showed that the mature trichome contains, along with two cell wall domains, two distinct plasma membrane domains that differ in their phospholipid composition and their ability to recruit dif-

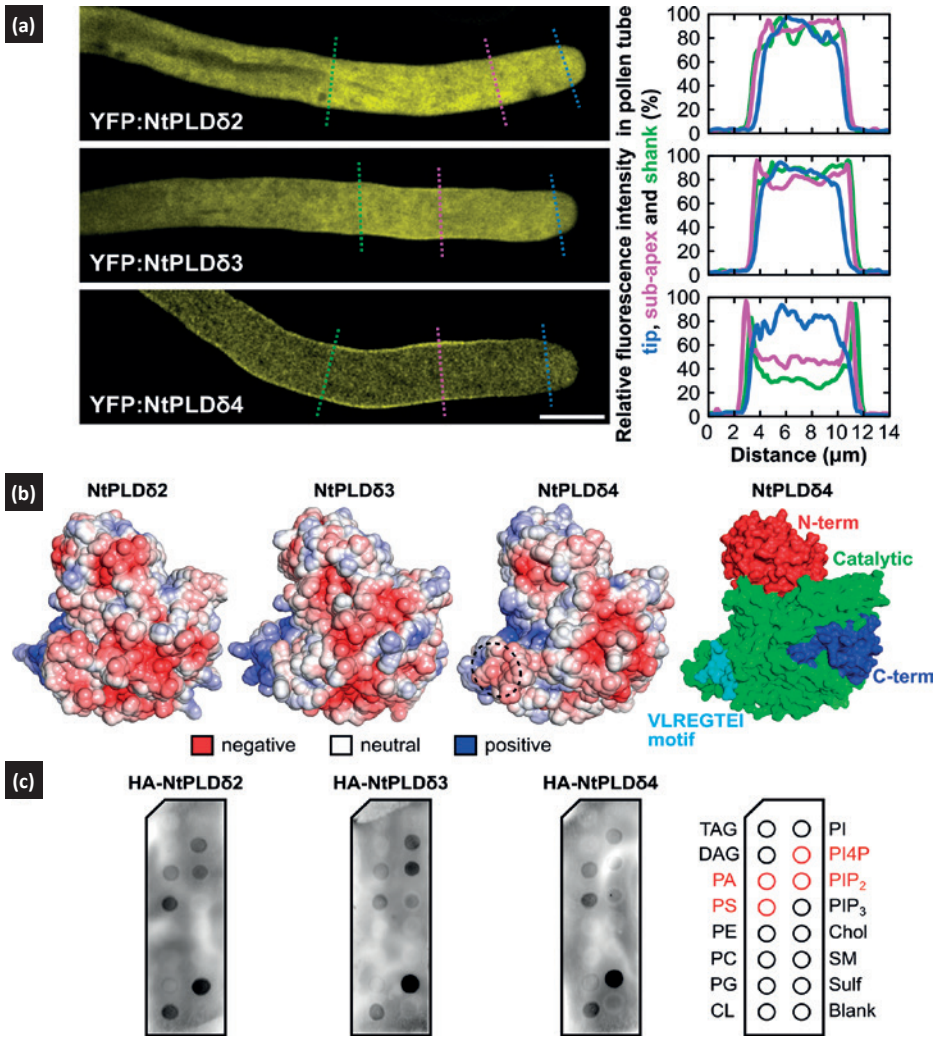

Figure 2. Distinct tobacco phospholipase Dδ isoforms show different localization **(a)**, structural features **(b)**, and lipid-binding properties **(c)**. Adapted from [455].

ferent EXO70 proteins (**Fig. 1**). While the apical domain, phosphatidylserine- and PA-rich, recruits EXO70H4, the basal domain recruits PIP_2-rich EXO70A1, which corresponds to the biochemically determined lipid-binding capacities of these two paralogs [215].

To characterize the PA production on the plant plasma membrane, we performed a comprehensive analysis of five phospholipase D (PLD) δ isoforms, using growing tobacco pollen tubes as a model. We demonstrated a distinct localization and membrane dynamics for individual PLDδs and identified sequence features important for the PM binding of selected PLDδ isoforms (**Fig. 2**). We observed that elevated levels of PA produced by overexpression of the main pollen isoform NtPLDδ3 induced specific morphological phenotypes, indicating a disturbed balance in vesicular trafficking and membrane recycling [455].

Novel functions uncovered for the EXO70 subunits in *Arabidopsis* gametophyte and sporophyte

In order to explore the extent of specificity and redundancy among *Arabidopsis* EXO70 paralogs, we analyzed their roles in reproduction, plant development, and biotic interactions. We found that among seven EXO70 isoforms expressed in the *Arabidopsis* male gametophyte, EXO70A2 is the main isoform, like its sibling, EXO70A1, in the sporophyte. However, EXO70A2 is essential not only for pollen germination and highly polarized pollen tube growth, but also for pollen grain maturation (**Fig. 3**). This indicates that the exocyst plays a role in functional continuity between pollen maturation and the processes that follow, pollen germination and pollen tube growth. Notably, despite the deep evolutionary split in eudicots, EXO70A2 still retains the ability to fully substitute for the EXO70A1 function in the sporophyte. Conversely, EXO70A1 lost the capacity to function in pollen development [420].

Independently, we tested the possible redundancy and specialization among EXO70 isoforms in *Arabidopsis* sporophyte. We focused on root hair growth and reaction to pathogenic bacteria as proxies for plant development and biotic interactions, respectively. Our results demonstrated that despite evolutionary relatedness, overlapping mRNA expression patterns, and similar lipid-binding affinities, each EXO70 isoform might have a unique function. Our analysis uncovered less functional redundancy among isoforms than we could suppose from whole sequence phylogeny. Even paralogs with overlapping expression patterns and similar membrane-binding capacities appear to have exclusive roles in plant development and biotic interactions [453].

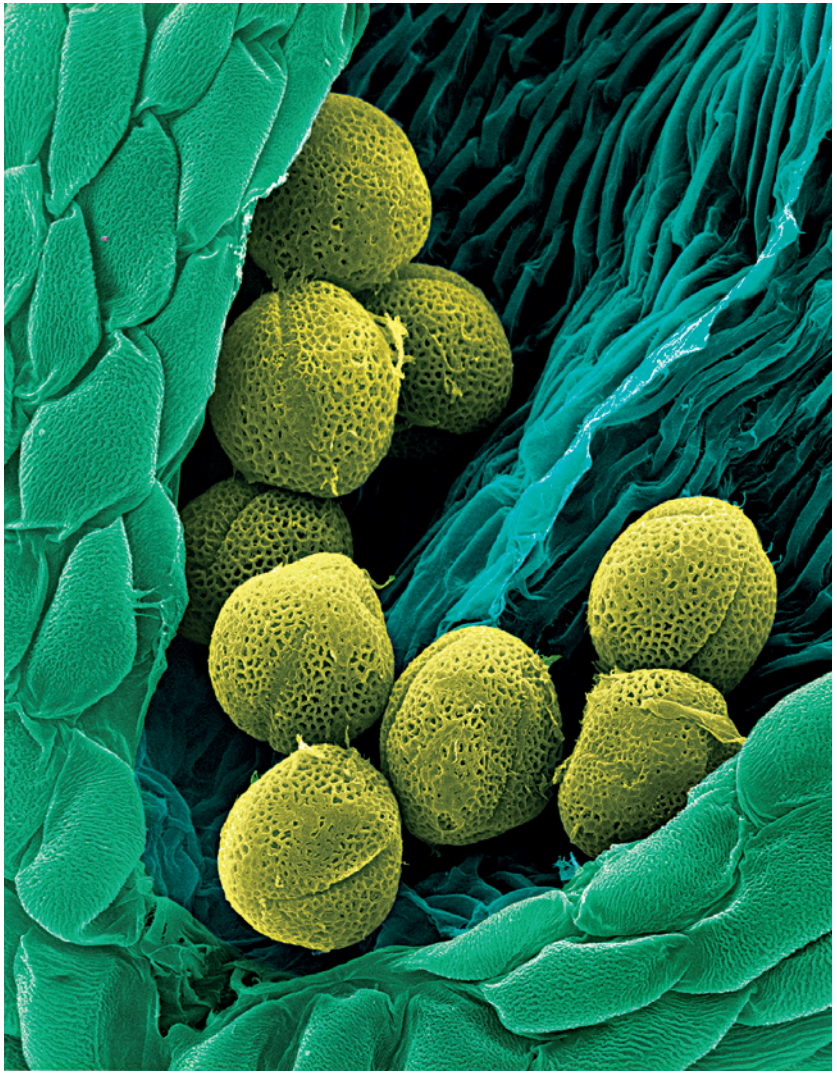

Figure 3. A pollen-specific component of the exocyst, a protein complex regulating cellular secretion, plays an important role in pollen development and function in *Arabidopsis*. The paper on this topic published in *Plant Physiology* [420] was accompanied by a journal cover photo depicting *Arabidopsis* pollen grains in an open anther (authors Vedrana Marković and Lukáš Synek, scanning electron microscopy, coloured).

Unexpected role of exocyst complex in the developmental plasticity of *Arabidopsis* root-shoot transition zone

The collet (root–hypocotyl junction) is a vital transition zone in angiosperms, and its correct organization is crucial for plant fitness. We uncovered a new role of the exocyst complex in the collet formation and hypocotyl ontogeny reprogramming [190]. We found that exocyst mutants can form ectopic collet hair-like structures located above the typical collet region. This defect, which, to our knowledge, has never been observed in any *Arabidopsis* WT or mutants, is accompanied by changes in auxin response, impaired PIN3 localization, and ectopic starch accumulation in the affected region. These observations suggest the essential role of the exocyst in environmentally regulated hypocotyl developmental plasticity related to polar auxin transport and signalling.

Functional hierarchy in exocytosis during plant vegetative growth

Models of exocytosis have generally divided the process into three stages: vesicle tethering, docking, and fusion, each thought to occur as part of a serial progression with distinct sets of proteins that regulate each step. Major protein assemblies contributing to this progression include exocyst and SNARE complexes, each of which relies on interactions between a discrete set of protein subunits and their correct cellular location for function. We described *in vitro* and *in vivo* interactions between members of the exocyst complex EXO70 subunit family that are important for vesicle tethering and recruitment to the plasma membrane and the SNAREs that drive the final stages of membrane fusion. Furthermore, the functional bias evident among these interactions leads to a clear hierarchy between exocyst–SNARE binding partners with differential consequences for SNARE protein localization, secretion, cellular expansion, and vegetative growth [409].

Research projects: 7, 8, 11, 15, 40, 61, 65, 69, 75

Laboratory of Growth Regulators

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The Laboratory of Growth Regulators (LGR) was created in 1996 as a joint facility of the Institute of Experimental Botany, the Czech Academy of Sciences, and the Faculty of Science, Palacký University. The purpose of this laboratory is to pursue research in the field of the molecular and physiological mechanisms of the action of growth regulators in living organisms and to develop the necessary technology. LGR focuses on scientific research and teaching in the field of Experimental Biology, especially in the preparation of new growth regulators with potent biological activities, in the development of relevant analytical methods, and in the study of the functions and effects on the growth and developmental process in cells, tissues, and whole organisms, including the development of drugs derived from plant hormones. Research on genes, mechanisms that regulate their expression, and the development of mutant organisms with controlled gene expression are included in the LGR scientific profile. Researchers at the LGR work mainly with cytokinins but have recently also worked with other groups of plant growth regulators. One globally renowned contribution of the LGR in this field is the expansion of a number of cytokinins, especially the aromatic cytokinins **topolins** and their **olomoucine**-derived deriva-

In the picture (from left to right):
Standing group: Ing. Jaromír Mikulík, Ph.D. / assistant, Mgr. Ota Blahoušek / research assistant, doc. Mgr. Ondřej Novák, Ph.D. / associate professor, prof. RNDr. Martin Fellner, Ph.D. / associate professor, Batcho Anicet / Ph.D. student, Mgr. Pavel Jaworek, Ph.D. / researcher, Miroslava Špičáková / technician, RNDr. Miroslav Kvasnica, Ph.D. / researcher, Mgr. Jana Oklešťková, Ph.D. / researcher, Magdaléna Vlčková / technician, Ing. Věra Doleželová / research assistant, Mgr. Terezie Urbanová, Ph.D. / researcher, RNDr. Jiří Pospíšil, Ph.D. / researcher, Mgr. Lucie Rárová, Ph.D. / researcher, Mgr. Danuše Tarkowská, Ph.D. / researcher, Mgr. Veronika Turečková, Ph.D. / researcher, Mgr. Lenka Plačková, Ph.D. / researcher, doc. Mgr. Lucie Plíhalová, Ph.D. / associate professor, Mgr. Marie Kvasnicová Ph.D. / researcher, prof. Ing. Miroslav Strnad, CSc., DSc. / head of the laboratory.
Sitting group: Mgr. Daniel Chrenko / Ph.D. student, Tereza Miksteinová / technician, Mgr. Jakub Hajný, Ph.D / researcher, Bc. Tereza Trávníčková / technician, Mgr. Lucie Maděrková / technician, Mgr. Aleš Pěnčík, Ph.D. / researcher, Mgr. Veronika Večeřová / technician, Mgr. Jakub Hrdlička, Ph.D. / researcher, Mgr. Ivan Petřík / Ph.D. student.

Not pictured:
doc. RNDr. Jitka Frébortová, Ph.D., doc. RNDr. Jan Krekule, DrSc., doc. RNDr. Vladimír Kryštof, Ph.D. / associate professors, Mgr. Dr. Karel Doležal, DSc., Mgr. Radek Jorda, Ph.D., Ing. Ludmila Ohnoutková, Ph.D., Mgr. Tomáš Vlčko, Ph.D., Mgr. Jiří Voller, Ph.D. / researchers, Mgr. Magdaléna Bryksová, Mgr. Daniela Konrádová / Ph.D. students, Ing. Jana Kočířová, Pavel Sedláček / technicians, Jitka Hansgutová, DiS / secretary.

tives. Olomoucine was the first in a line of anti-tumour agents derived from cytokinins. The development of other, more effective inhibitors of cyclin-dependent kinases – key enzymes of the cell division cycle – such as **bohemine, roscovitine, olomoucine II,** and others, followed. Roscovitine was licensed by Cyclacel Pharmaceuticals, Inc. and under its commercial name, **Seliciclib®**, has undergone phase II clinical trials for cancer treatment in Europe and the USA. LGR is also successful in agricultural research. For example, we discovered how to increase the amount of endogenous cytokinins using an inhibitor of cytokinin oxidase/dehydrogenase called **INCIDE**, which supports plant growth and development. Owing to this discovery, we were able to increase the yield of a number of agricultural crops and improve plant stress resistance. Recently, we developed a cytokinin product which retards ageing in humans and restores youthfulness to the skin. The product under the trade name **Pyratine®** is derived from cytokinins. This not only treats skin roughness, wrinkles, and pigmentation, but it is also effective for treating various forms of acne. LGR publishes in prestigious international journals and submits a number of applications for international patents annually.

New phytohormones, biostimulants and biomolecules

New phytohormones, their derivatives and probes, biostimulants, and labelled derivatives for basic research, biotechnological and agricultural applications

Our laboratories have long-standing experience in organic synthesis, the labelling of phytohormones, and the production of phytohormones and probes labelled with heavy or radioactive isotopes [10–11, 59, 62, 152, 177, 317]. There are also several reviews on this topic from our laboratory [124, 130, 138, 309, 341–342, 423, 507]. Additionally, we studied their biological activities *in vitro* and *in vivo* [91, 133, 406; Brunoni *et al.* 2020, New Phytol 226: 1753-1765].

We also discovered several new natural phytohormones. We developed and examined the effect of *meta*-topolin and several novel aromatic cytokinin (CK) derivatives on *in vitro* adventitious shoot production, rooting, and photosynthetic pigment content of different regenerated plants *in vitro*. Its carry-over effect on *ex vitro* growth, photosynthetic performance, and the antioxidant enzyme system of different plants was also investigated. The treatments with some of the aromatic CK (ARCK) gave the highest number of adventitious shoots when compared to thidiazuron (TDZ) application and the control. In many cases, we also evaluated the distribution pattern of cytokinins (CKs), other phytohormones, and phenolic compounds in different organs of *in vitro* propagated plants to better understand their physiology, which can provide an essential basis for coherently achieving a conservation/micropropagation-driven strategy for valuable plant species [64, 78, 183, 241, 281]. We also investigated the effect of many different biostimulants of (un)defined chemical characteristics (eckol, phloroglucinol, phenolic compounds, algae leachate, seaweed extracts, silicon, Kelpak®, smoke-derived karrikinolide, volatiles, allelochemicals, silver nanoparticles, etc.) on the growth and phytochemical and phytohormone content of many different plant species [20, 81, 84, 97, 168, 175, 217, 229, 284; Tan *et al.* 2020, Current Biol 30: 381-395].

New phytohormone molecular targets and compounds modulating phytohormone perception, biosynthesis and degradation

Cytokinins, a class of phytohormones, are adenine derivatives common to many different organisms. In plants, these play a crucial role as regulators of plant development and the reaction to abiotic and biotic stress. Key enzymes in cytokinin synthesis and degradation in today's land plants are the **isopentyl transferases (IPT)** and the **cytokinin dehydrogenases (CKX)**, respectively. For example, we proposed an important role for endogenous cytokinin biosynthesis and AHK4-mediated cytokinin signalling in the control of de novo-induced organ identity [101]. We have also shown that the cytokinin signal is not only mediated by receptors located within cells, but that functional cytokinin receptors are also found on their surface [325, 405]. We identified the REPRESSOR OF CYTOKININ DEFICIENCY 1 (ROCK1) as an ER-localized transporter of UDP-GlcNAc and UDP-GalNAc in plants. Furthermore, utilizing the overproduction of single-chain Fv antibodies selected for their ability to bind trans-zeatin riboside and targeted to the endoplasmic reticulum, we post-synthetically modulated cytokinin ribosides, the proposed transport forms of cytokinins [33]. In another study, we showed that CKX1 is a type II single-pass membrane protein that localizes predominantly to the endoplasmic reticulum (ER) in *Arabidopsis*. This indicates that this CKX isoform is a bona fide ER protein directly controlling the cytokinin, which triggers the signalling from the ER. By using various approaches, we demonstrated that CKX1 forms homodimers and homooligomers *in vivo* [89].

We also showed that class I *KNOX* gene activity is necessary and sufficient for axis extension from an intercalary region of determinate moss shoots. Class I *KNOX* activity can promote cytokinin biosynthesis by the *PpIPT3* gene. *PpIPT3* promotes axis extension, and *PpIPT3* and exogenously applied cytokinin can partially compensate for loss of class I *KNOX* function. By outgroup comparison, the results suggest that a pre-existing *KNOX*-cytokinin regulatory module was recruited

into vascular plant shoot meristems during evolution to promote indeterminacy, thereby enabling the radiation of vascular plant shoot forms [158]. Our recent findings demonstrate the usefulness of ectopic *CKX* gene expression for achieving root enhancement in oilseed rape, and this underpins the functional relevance of a larger root system. Furthermore, the lack of major developmental consequences on shoot growth in cytokinin-deficient oilseed rape indicates species-specific differences of *CKX* gene and/or cytokinin action [244]. We showed that cytokinin signalling functions as a lateral root-specific, anti-gravitropic component, promoting the radial distribution of the root system. We performed a genome-wide association study and revealed that signal peptide processing of CKX2 affects its enzymatic activity and, thereby, determines the degradation of cytokinins in natural *A. thaliana* accessions [307]. We also described synthetic auxins, RubNeddins (RNs), which act as selective auxin agonists. The RN with the greatest potential for dissecting auxin perception was RN4, which we used to reveal a role for the chromatin remodelling ATPase BRAHMA in apical hook development [297].

Bioanalytic chemistry of phytohormones and its application

The analysis of plant hormones is challenging, as these compounds are present in trace amounts and 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. Since 2008, this methodology has been gradually developed in LGR for plant hormone analyses (cytokinins, auxins, tryptophan-related neuroactive substances, JAs, ABAs, gibberellins, brassinosteroids, ecdysteroids, phenolics, isoflavonoids, tocopherols, ingenol, phytocannabinoids, karrikins, and other phenylpropanoids) [8, 14, 99, 102, 149, 182, 363, 489]. Tissue- and cell-specific approaches in plant hormone analysis have also been recently introduced. We also developed a method for the simultaneous targeted profiling of 101 phytohormone-related analytes from minute amounts of fresh plant material (less than 20 mg). Rapid and nonselective extraction, fast one-step sample purification, and extremely sensitive UHPLC-MS/MS enable concurrent quantification of the main phytohormone classes: cytokinins, auxins, brassinosteroids, gibberellins, jasmonates, salicylates, and abscisates [127].

The application of new technologies led to several good papers and also to important discoveries [5, 12, 22, 25, 28, 34, 47, 74, 80, 93, 103, 105, 108, 112, 125, 128, 173, 181, 239, 272, 277, 279, 283, 291, 308, 352, 364–365, 493; Castander-Olarieta *et al.* 2020, Trees 35: 1075-1080]. To elucidate the link between proteasome function, NO resistance, and pathogenesis of *Mycobacterium tuberculosis,* we reported that an obligate human pathogen secretes several cytokinins. Finally, we determined that the Rv1205-dependent accumulation of cytokinin breakdown products is likely responsible for the sensitization of *Mycobacterium tuberculosis* proteasome-associated mutants to NO [119]. AtNHX5 and AtNHX6 are endosomal Na^+,K^+/H^+ antiporters that are critical for growth and development in *Arabidopsis.* We found that *nhx5 nhx6* exhibited growth variations of auxin-related defects because it was affected in auxin homeostasis. Genetic analysis showed that AtNHX5 and AtNHX6 were required for the function of the endoplasmic reticulum (ER)-localized auxin transporter PIN5 [24]. We investigated the role of PIN phosphorylation during gravitropic response. Loss- and gain-of-function mutants in PINOID and related kinases – but not in D6PK kinase – or mutations mimicking the constitutive dephosphorylated or phosphorylated status of two clusters of predicted phosphorylation sites partially disrupted PIN3 phosphorylation and caused defects in gravitropic bending in roots and hypocotyls (Grones *et al.* 2018, Sci Rep 8: 10279). Furthermore, we showed that the auxin response increases in ovules after fertilization, due to upregulated auxin biosynthesis in the integuments, and this maternally produced auxin is required for proper embryo development [116]. We also showed that anthranilic acid (AA) rescues root gravitropic growth in the AA-deficient mutant at concentrations that do not rescue IAA levels. Treatments with, or deficiency in, AA result in defects in PIN polarity and gravistimulus-induced PIN re-localization in root cells [164]. Using loss-of-function mutants, we showed that three Aux/IAA genes, *IAA6, IAA9*, and *IAA17*, act additively in the control of adventitious root (AR) initiation. We demonstrated that *TIR1* and *AFB2* are positive regulators of AR formation, and that TIR1 plays a dual role in the control of jasmonic acid (JA) biosynthesis and conjugation, as several JA biosynthesis genes are upregulated in the *tir1-1* mutant [220–221]. Using the *Arabidopsis* model, we showed that the chromatin-modifying enzyme HISTONE DEACETYLASE 9 (HDA9) is essential for promoting an open plant architecture that allows for efficient mitigation of the impact of warm temperatures. HDA9 does not affect hypocotyl elongation in response to different light conditions, setting it apart from the shade-avoidance response that phenotypically resembles acclimation to warmth. We demonstrated that HDA9 is required for transcriptional activation of YUCCA8 [299]. In another study, we analysed the auxin distribution and expression of PIN auxin efflux carriers from early phases of germination, and showed that the bending of the root in response to gravity is the crucial

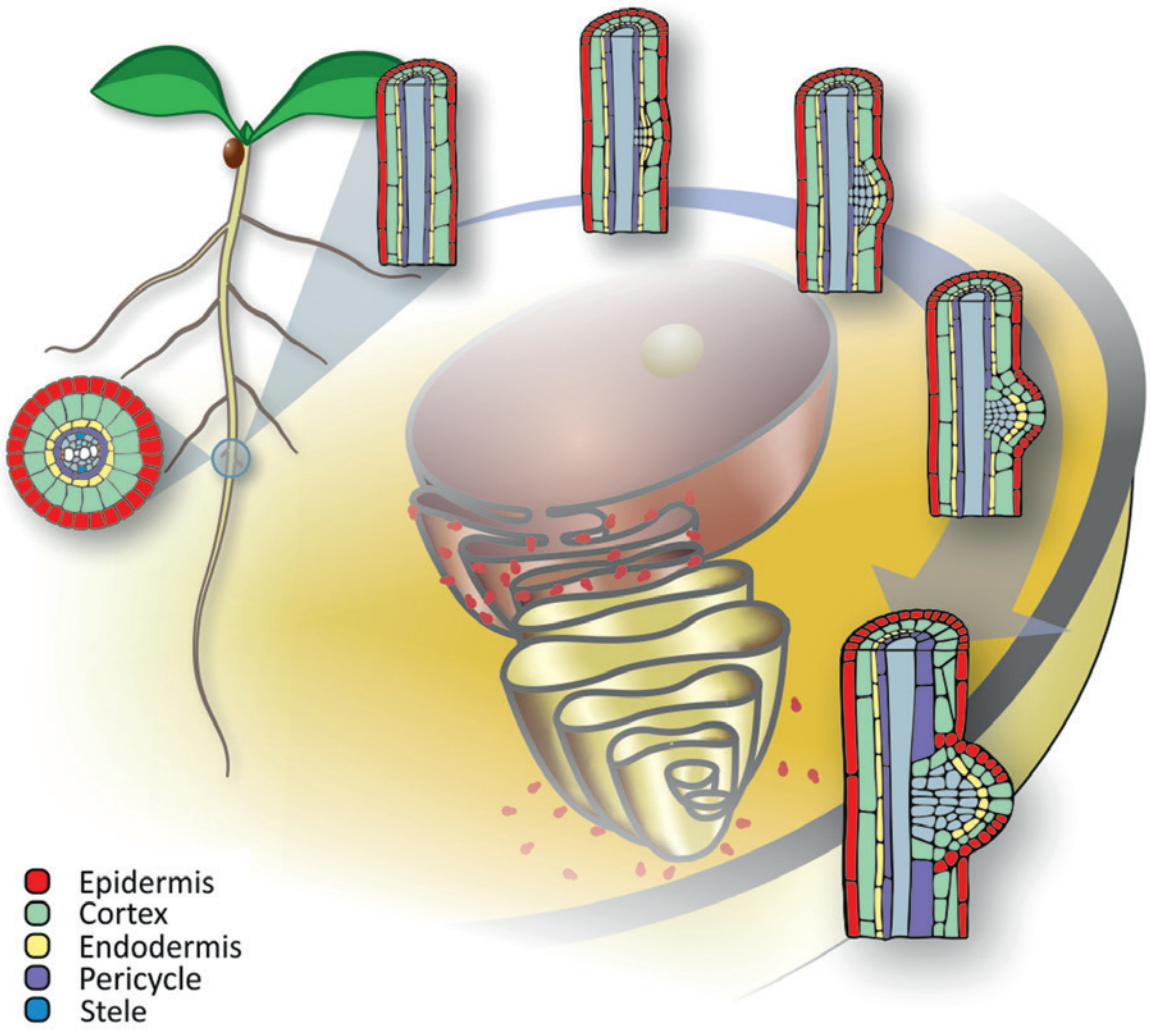

Figure 1. Different stages of lateral root development in *Arabidopsis thaliana* seedlings. Lateral root primordia are initiated not very far from the tip of the primary root, from the pericycle cell layer. The developing lateral roots must penetrate through three different cell layers in order to emerge – the endodermis, cortex, and epidermis.

initial cue that governs the hypocotyl bending required for apical hook formation. Importantly, polar auxin transport machinery is established gradually after germination starts as a result of tight root-hypocotyl interaction and the proper balance between abscisic acid and gibberellins [316].

Medicinal chemistry

Chemical modulators of kinases

During 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 [1, 388–389, 398]. The potential of CDK inhibitors in different therapeutic areas was also reviewed several times [51, 216]. New generations were prepared following well-established methods, including our previously described syntheses of purines, pyrazollo[4,3-d] pyrimidines, 8-azapurines, fluoroaryl benzimidazoles, and arylazopyrazoles (for patents, see www.espacenet.com). We reported on the synthesis, activity testing, docking, and quantum mechanical scoring of novel imidazo[1,2-c]pyrimidin-5(6H)-one scaffold for cyclin-dependent kinase 2 inhibition [1]. A novel series of 4,6-disubstituted pyrazolo[3,4-d]pyrimidines have been designed and synthesized by molecular hybridization. All the synthesized compounds were evaluated for *in vitro* CDK2/cyclin E and Abl kinase inhibitory activity as well as anti-proliferative activity [42]. FLT3 tyrosine kinase is a potential drug target in acute myeloid leukemia in patients with FLT3-ITD mutations. Recently, we presented novel 2,6,9-trisubstituted purine derivatives with potent FLT3 inhibitory activity [35]. We also investigated the selectivity of commercially available CDK inhibitors and identified compounds that will be suitable for further studies to identify the CDKs responsible for S81-AR phosphorylation [50].

3,5,7-substituted pyrazolo[4,3-d]pyrimidine inhibitors of CDK and their evaluation in lymphoma models was recently reported [194]. The activity of 2,6,9-trisubstituted purines as potent PDGFRα kinase inhibitors with anti-leukemic activity was also described [271].

Natural phytochemicals as potential drug candidates

We also identified new triterpenoid compounds with anti-cancer activity [201, 233, 258, 499], new natural bioactive cytokinins and their derivatives [39–40, 53, 197, 304, 311], new anti-inflammatory and anti-cancer substances [66, 68, 73, 79, 142, 210, 268, 425; Shulha *et al.* 2019, Phytochem 170: 112196], new steroid growth regulators – steroids, brassinosteroids, and ecdysteroids [26, 46, 114, 169, 189, 193, 195–196, 219, 250, 382], new chemopreventive phytochemicals, redox-reactive antioxidants, phenolics [7, 65, 83, 100, 150, 157, 225, 234–235, 312, 497], and finally natural and synthetic alkaloids [86, 227].

Plant molecular physiology

Phytohormones and light

The group, for example, indicated the existence of a link between osmotic stress and blue light signalling and the involvement of the 7B-1 mutation in this cross-talk [6, 145]. We also used two species of the genus *Geranium* to study the involvement of auxin, brassinosteroids, and gibberellins (GAs) in supplemental far-red--induced elongation growth [522]. Blue light suppression accelerates the senescence rate of wheat leaves. In order to study whether this effect is accompanied by the alteration of different cytokinin (CK) metabolites, by CK-degradation, and by the expression of CK-perception,-inactivation,-reactivation and/or-turnover genes, leaf segments of 30-day-old plants were placed in boxes containing bi-distilled water and covered with blue (B) or green (G) light filters, which supplied

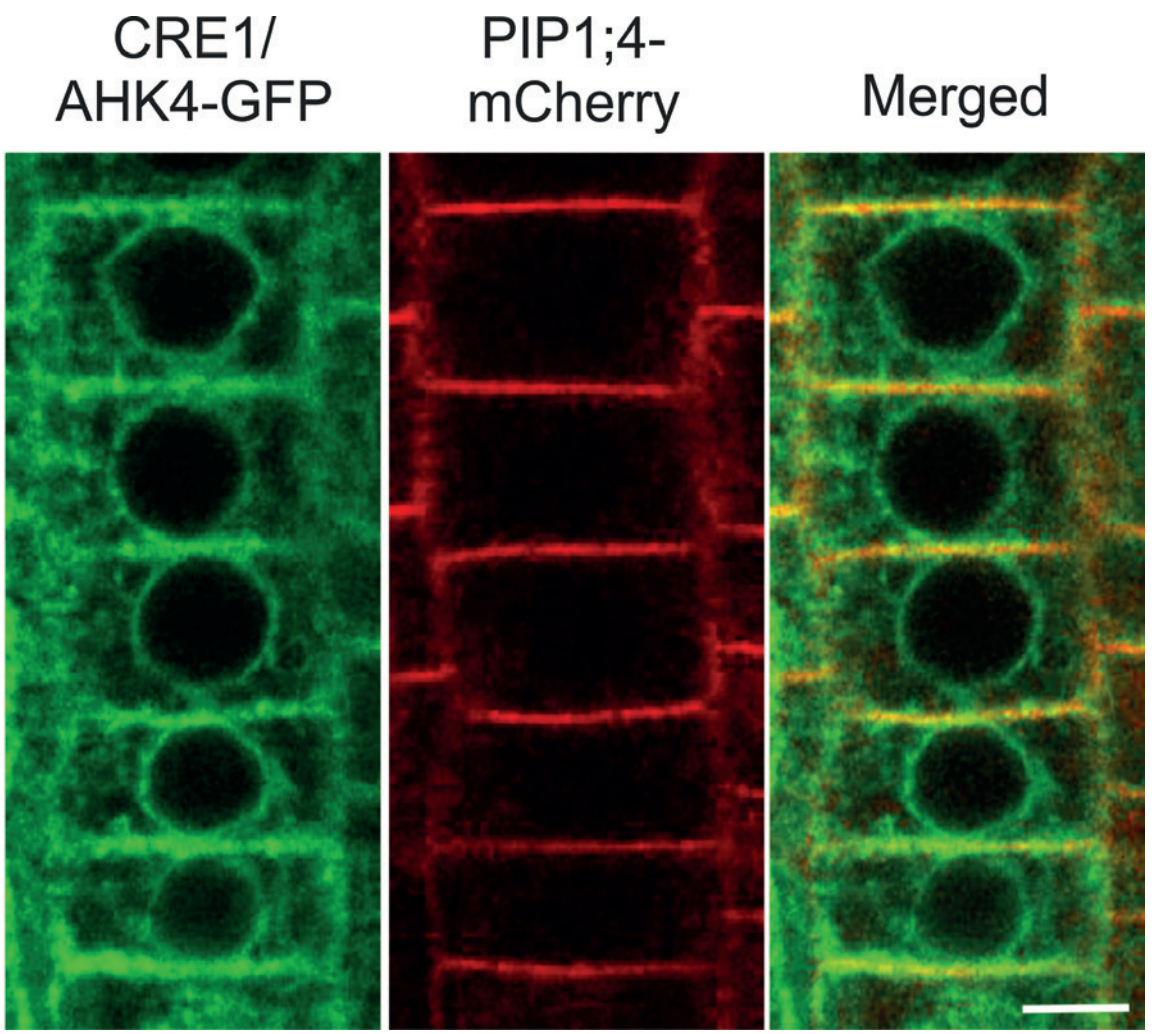

Figure 2. Localization of the cytokinin receptor CRE1/AHK4 in cells of *Arabidopsis* root. The cytokinin receptor was labelled with the green fluorescent protein (left). Plasma membranes on the cell surface were marked with the red fluorescent compound PIP1;4-mCherry (middle). The merged image on the right shows that the cytokinin receptor is located both inside the cell (green) and on the plasma membrane (yellow). Scale bar = 5 μm.

a similar irradiance but differed in the percentage of BL transmitted (G << B) [77]. We identified leaves as a site for the perception of seasonal shifts and revealed that components of floral transition such as FLOWERING LOCUS T (FT) and plant hormone GA have been recruited to function as long-range signals to communicate seasonal changes perceived in leaves to the shoot apical meristem to control its activity to synchronize bud set with the change of seasons in perennials [236].

Phytohormones and stress responses

Here we found that short-term salt stress in *Brassica rapa* seedlings causes alterations in auxin metabolism [95, 257], while drought stress causes other responses on physiological, biochemical, and hormonal levels [96]. A genome-wide transcriptional analysis was also performed on leaves and roots of three-day salt treated and untreated plants of two rice varieties, which differ in salt sensitivity. Genes correlated with hormonal pathways were identified and analysed [30]. This study examined how two different stresses – salt and oxidative stress – affect changes in both cytokinin levels and whole plant transcriptome response in *Solanum lycopersicum* seedlings (Keshishian *et al.* 2018, Plant Direct 2: e00071). The content of endogenous brassinosteroids together with various aspects of plant morphology, water management, photosynthesis, and protection against cell damage were also assessed in two maize genotypes that differed in drought sensitivity [132]. Singlet oxygen produced from triplet excited chlorophylls in photosynthesis is a signal molecule that can induce programmed cell death through the action of the OXIDATIVE STRESS INDUCIBLE 1 (OXI1) kinase. Here, we identified two negative regulators of light-induced programmed cell death that modulate OXI1 expression: DAD1 and DAD2, homologs of the human anti-apoptotic protein DEFENDER AGAINST CELL DEATH [147].

Phytohormones in plant-pathogen/insect interaction

Phytohormone levels and the expression of genes encoding key enzymes participating in hormone biosynthetic pathways involved in plant-pathogen/insect interactions were investigated in many different plant species. We discovered that infection by *Rhodococcus fascians* maintains cotyledons as a sink tissue for the pathogen [186]. Furthermore, the inhibited root growth, the greening of the roots, and the expression of the pea response regulators in the infected roots were indicative of a response to cytokinin, but a role for the 'classical' cytokinins as virulence determinants was not established [15]. We also reported that two mutations in the truncated *Rep* gene RBR domain delayed the Wheat dwarf virus infection in transgenic barley plants (Cejnar *et al.* 2018, J Integr Agr 17: 2492-2500). Another study examined the temporal changes in the leaf content of defence-involved phytohormones in pepper plants responding to a green peach aphid (*Myzus persicae* Sulzer) infestation, at both the local and systemic levels [28]. Recombinant expression of limen, a small, cysteine-rich peptide isolated from lima beans with activity against micromycetes in both a prokaryotic and plant system, was performed to demonstrate the wide range of its activities with a potential for further use (Řehořová *et al.* 2018, J Pharm Pharmacol 6: 945-955). We evaluated and reconsidered IAA metabolism in *Bradyrhizobium japonicum* E109, one of the most widely used strains for soybean inoculation around the world [131]. Mal de Río Cuarto virus infection was shown to cause hormone imbalance and sugar accumulation in wheat leaves [159]. We also described how a pectin-modifying enzyme, PECTIN ACETYLESTERASE 9, affects the *Arabidopsis* transcriptome, secondary metabolome, and aphid performance [203]. The effect of plant heat-shock pre-treatment on *Pseudoidium neolycopersici* development in the susceptible and moderately resistant *Solanum* spp. genotypes was studied together with biochemical responses – endogenous concentrations of salicylic, jasmonic, and abscisic acids, and peroxidase activity [247]. In addition, we explored changes in the levels of phytohormones in maize and mango plant tissues infected with *Fusarium* [306].

Seed dormancy and germination

We used phylogenetic and comparative analyses of fruit and seed anatomy, biomechanics, physiology, and environmental responses to study fruit and seed heteromorphism, a typical morphological basis of the bet-hedging strategy of plants, in the annual growth of the Brassicaceae species *Aethionema arabicum* [70, 144, 231, 310]. We also found that polishing and washing of the sugar beet fruits had a positive effect on both germination performance and seedling phenotype, and when combined, this positive effect was stronger. Polishing as well as washing removed germination inhibitors from the pericarp, specifically, ABA, ABA metabolites, and ions [184]. This study provides a comparative analysis of the dormancy and germination mechanisms of the indehiscent fruits of hoary cress (*Lepidium draba* L.) and hairy whitetop (*L. appelianum* Al-Shehbaz), two invasive weeds of the Brassicaceae [237].

Research projects: 11–12, 17, 35, 44, 47, 51, 67–68, 71, 76, 81, 111, 114

Laboratory of Hormonal Regulations in Plants

Head of the laboratory:

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The laboratory has been focused on elucidation of the mode of action and the developmental roles of auxins and cytokinins, including their crosstalk with other plant hormones and the environment. In 2018–2020, the main research topics were auxin transport and homeostasis, metabolism and physiological functions of cytokinins, and the interaction of plant hormones with the environment. Our mission is to understand the role of plant hormones in their complexity. For this, we have utilised a range of methods, including molecular genetics, high-throughput profiling of transcriptomes and proteomes, biochemistry, plant phenotyping, analytics of phytohormones and their metabolites, advanced fluorescence confocal microscopy, and a mathematical modelling approach.

In the picture (from left to right):
Mgr. Daniel Nedvěd / Ph.D. student, RNDr. Adriana Jelínková, Ph.D. / researcher, Nayyer Abdollahi Sisi, Ph.D. / researcher, Ing. Klára Hoyerová, Ph.D. / researcher, Ksenia Timofeyenko, M.Sc. / Ph.D. student, Mgr. Sylva Přerostová, Ph.D. / researcher, Bc. Marie Korecká / technician, Elena Zemlyanskaya, M.Sc. / Ph.D. student, Eva Kobzová / technician, RNDr. Radomíra Vaňková, CSc., DSc. / researcher, Ing. Karel Müller, Ph.D. / researcher, Ing. Jana Jarošová, Ph.D. / researcher, RNDr. Alena Gaudinová / research specialist, Ing. Roberta Filepová / research specialist, Bc. Vojtěch Schmidt / master student, Mgr. Zuzana Vondráková / research specialist, Ing. Jozef Lacek / Ph.D. student, Mgr. Tomáš Hluska, Ph.D. / researcher, Ing. Kateřina Malínská, Ph.D. / researcher, Ing. Václav Motyka, CSc. / researcher, RNDr. Jan Petrášek, Ph.D. / head of the laboratory, Ing. Milada Čovanová, Ph.D. / researcher, Ing. Petre Dobrev, CSc. / researcher, Mgr. Kamil Růžička, Dr. rer. nat. / researcher, Mgr. Petr Klíma, Ph.D. / researcher, Bc. Vojtěch Knirsch / technician, RNDr. Martina Laňková, Ph.D. / research assistant.

Not pictured:
RNDr. Nikoleta Dupľáková, Ph.D. / researcher, Ing. Miroslav Kamínek, CSc. / researcher, Ing. Petr Skůpa, Ph.D. / researcher, prof. RNDr. Eva Zažímalová, CSc. / researcher, Ing. Petr Hošek, Ph.D. / postdoctoral fellow, Ing. Eva Pokorná, Ph.D. / postdoctoral fellow, Dr. rer. nat. Katarzyna Retzer, Ph.D. / postdoctoral fellow, Ivan Kashkan, M.Sc. / Ph.D. student, Mgr. Barbara Kramná / Ph.D. student, Mgr. Roman Skokan / Ph.D. student, Bc. Lenka Helusová / master student, Lenka Novotná / bachelor student, Bc. Jiří Danko / technician, Mgr. Nikola Drážná / technician, Bc. Karolína Holečková / technician, Tereza Košťálová / technician.

Auxin

Research on auxin produced significant outputs in the fields of regulation of auxin transport and homeostasis, cellular biology of auxin transporters, and the evolution of auxin transport mechanisms.

Utilising the model of tobacco cell lines, well-established in the laboratory [528–529], we revealed a new way of regulation of the number of auxin carriers on cell membranes based on auxin-driven gene expression and co-operation between auxin influx and efflux transporters [238]. Auxin transport characteristics predicted by the mathematical model for the most potent auxin efflux carrier, NtPIN11, were confirmed by

qRT-PCR and cultivation in auxin-free conditions, justifying the modelling approach developed in our laboratory. In the frame of this work, we have also successfully initiated extensive RNAseq profiling of tobacco cell lines BY-2 and VBI-0 and made them accessible for the community through the Genevestigator database. Using tobacco cells, we also provided novel evidence regarding the mechanism of action of silver ions in plants cells [56], showing that silver ions primarily act through the modification of the activity of calcium channels with downstream effects on the permeability of the plasma membrane for small compounds, including auxins and cytokinins. In collaboration with IST Austria, we have contributed with microscopy analysis and auxin transport assays in tobacco cells to the identification of lipid-dependent phosphorylation cascade regulating morphogenetic auxin fluxes [488] and to the identification of the phosphorylation-based inhibitory effects of salicylic acid [486] and its derivatives [487] on auxin efflux carriers.

In collaboration with BOKU, Vienna, Austria, we significantly contributed to the identification of novel crosstalk between auxin transport and brassinosteroids, based on their inhibitory effect on the endocytosis of auxin efflux carrier PIN2 [270]. Using the roots of *Arabidopsis thaliana*, the brassinosteroid-induced stabilisation of PIN2 at the plasma membrane was shown to be instructive for the tuning of differential cell elongation during the bending response of the roots to gravity. Modulation of PIN2 trafficking caused by hydrogen peroxide and associated with a change in the actin dynamics was found to contribute to root stress acclimation [318]. In collaboration with the Faculty of Science, Charles University, we showed that actin-nucleating complex ARP2/3 is required for auxin-driven cell expansion through the regulation of the amount of auxin carriers at the plasma membrane [366]. A new high-resolution confocal microscopy platform in the Imaging Facility of IEB allowed us to perform *in vivo* observations of *Arabidopsis* seedling root in a natural gravitational vector and to provide *in vivo* evidence for the presence of the unique organisation of PIN1 auxin efflux carrier in dividing provasculature cells [419]. We complemented the work of colleagues from the University of Lausanne, who provided evidence from fixed preparations.

In collaboration with IST Austria, we brought the first experimental evidence on the evolutionary origins of PIN-mediated carrier-driven auxin efflux [280]. By testing auxin transport activities in several heterologous models, including tobacco cells (**Fig. 1**), we show that PIN homolog from *Klebsormidium flaccidum* is capable of auxin transport at the plasma membrane, which is typical for the PIN proteins of land plants. Unlike these canonical PINs, KfPIN is not localised in polar domains, suggesting its evolutionary-basal role in the non-directional auxin export. Several scenarios on the ancestral role of auxin have been suggested in our review, bringing up-to-date phylogenetic evidence for the presence of auxin transporter-related sequences in algae [506].

We have summarised, in a critical form, the up-to-date evidence on the function of ER-localised PIN carriers [474] and the mechanism of action of auxin influx carrier AUX1 [122], and have described in detail a unique set of reporters (**Fig. 2**) for the visualisation of gene splicing acting in hormonal synthesis signalling and transport [391].

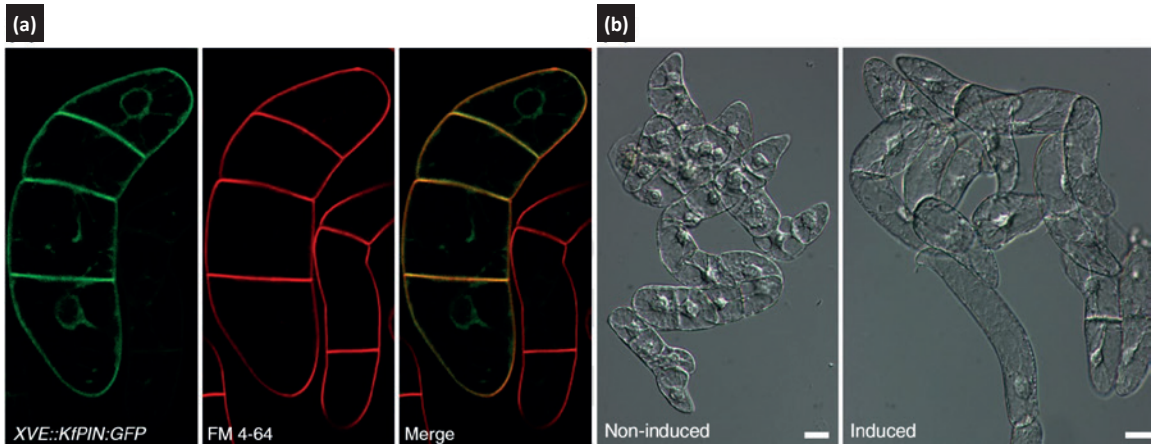

Figure 1. Inducible overexpression of the homolog of PIN auxin efflux carriers from the green alga *Klebsormidium flaccidum*. **(a)** Tobacco cells BY-2 expressing the algae homolog of PIN (XVE::KfPIN:GFP cells). The signal of GFP is predominantly at the plasma membrane (left, green), which is co-stained with FM 4-64 dye (middle, red). (b) Nomarski differential interference contrast of 2-day-old XVE::KfPIN tobacco BY-2 cells, non-induced (left) and induced (right); scale bar, 25 µm. Note that upon the expression of the PIN homolog (right), cells are expanded and have a typical auxin starvation phenotype. Modified from [280].

Cytokinins

Research on cytokinins has been focused on their biosynthesis and metabolism in a range of developmental and environmental contexts. We also addressed the evolution of their biosynthesis, including the relation to other phytohormones.

We have continued in our efforts to uncover the role of *cis*-zeatin-type, often overlooked, cytokinins. We demonstrated the involvement of cis-zeatins in somatic embryogenesis in conifers [137], during phosphate starvation in *Arabidopsis* roots [110], and in the maize pathogen *Colletotrichum graminicola* [357], as well as in fern arsenic accumulators [315]. These outputs implied that the *cis*-zeatin-type cytokinins have a much higher impact for cytokinin biology, being more relevant and prevalent in plants than previously supposed.

In contradiction to a generally accepted hypothesis that *N*-glucosylation inactivates cytokinins irreversibly, we have shown cytokinin *N*-glucosides to be subject to metabolic conversions that differ between *N*-glucosides of N^6-(Δ^2-isopentenyl)adenine and *trans*-zeatin in *Arabidopsis* [379]. This work represents the first large-scale study of cytokinin metabolism in planta that reveals directionality and kinetics of yet uncharacterised cytokinin metabolic pathways. We constructed a mathematical model (**Fig. 3**) that provides estimates of the metabolic conversion rates, which support the qualitative observations. Our findings fill in fundamental gaps in the current understanding of cytokinin metabolism in *Arabidopsis*; in particular, the hydrolysis of cytokinin *N*-glucosides was shown for the first time. The topic was summarised in our review on new insights into the metabolism and role of cytokinin *N*-glucosides in plants [381]. We also continued in our efforts to understand the role of *N*-glucosyltransferase pathways in plants, showing that cytokinin N-glucosides represent major cytokinin forms in *in vitro* cultured potato plants [460], where they show demonstrable diurnal rhythmicity [500]. On the other hand, cytokinin N-glucosides are totally absent in ferns [315]. Our expertise in the determination of the enzymatic activity of cytokinin oxidase/dehydrogenase was con-

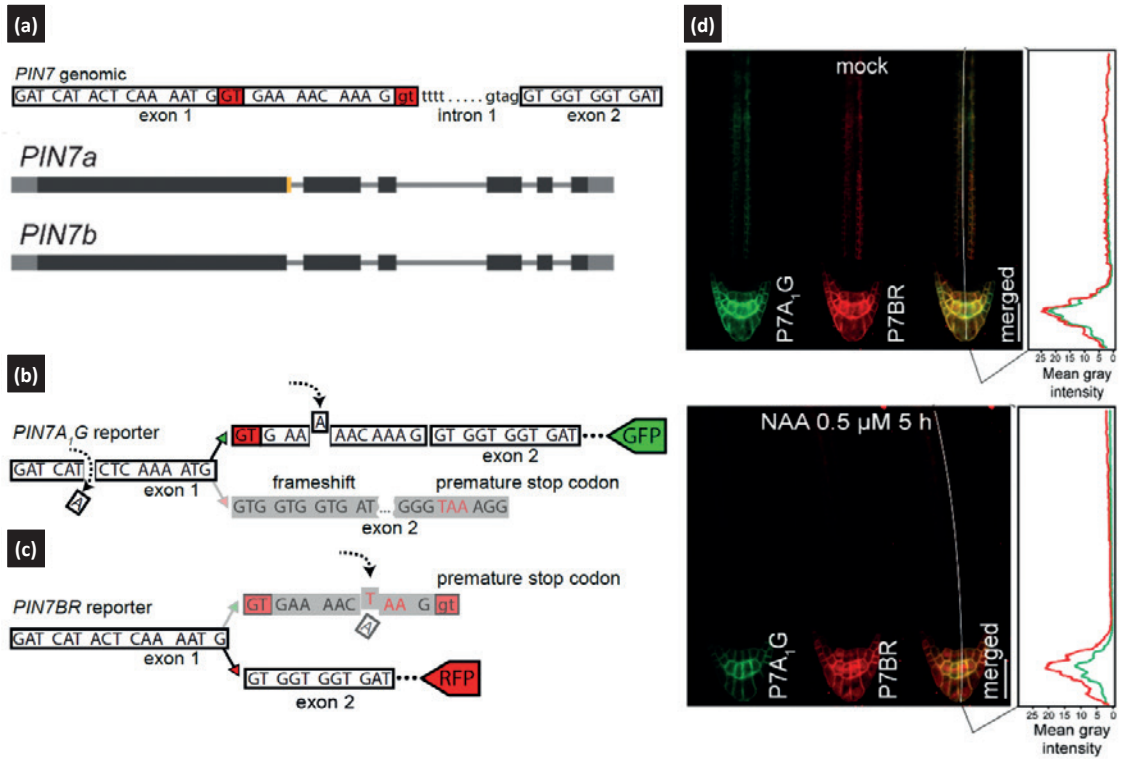

Figure 2. Reporters for the visualization of alternative splicing of PIN7 auxin efflux carriers in the root tip of *Arabidopsis thaliana*. **(a)** Diagram of the coding regions of the PIN7 gene. The canonical PIN7b isoform differs from PIN7a by the presence of the 12-nucleotide region (yellow). Black – coding regions, grey – UTRs, thin grey line – introns, yellow – regions modified by alternative splicing. **(b)** Scheme of the P7A1G reporter for visualizing the PIN7a isoform. Removing the nucleotide prior to the alternative splice site leads to a frameshift in the PIN7b transcript. The frame is restored by insertion of the nucleotide into the region exclusively encoded in the P7A1G sequence following the alternative splice site. **(c)** The P7BR reporter, with introduced termination codon into the protruding region encoded entirely by PIN7a. P7AG and P7BR are encoded by two constructs that are separately transformed and then crossed. **(d)** Following treatment with the synthetic auxin NAA, a differential decrease of expression is observed in the root columella cells. Modified from [391].

tributional to the collaborative work with CEITEC, Brno, describing the immunomodulation of cytokinins as a tool for studying cytokinin homeostasis [33].

We further focused on the role of cytokinin metabolism in the regulation of developmental switch points and reaction to the environment. The long-term focus of the laboratory on cytokinins has been extended with an emphasis on the parallel analysis of whole plant hormonome, which allows us to address numerous phytohormonal crosstalks. This approach allowed us to provide the most comprehensive overview of endogenous phytohormone levels during the somatic embryo development and germination in conifers [137, 172] and during plant organogenesis [13]. In collaboration with Université Catholique de Louvain, Belgium, we have contributed to the understanding of phytohormone function in plant fruit development [533] and during lignification in hemp plants [148]. Other collaborations based on phytohormonal profiling also allowed for differentiation between vernalisation- and heat stress-induced flowering in chicory [421], to characterize the onset of berry shrivel ripening [371], and to validate the mutagenesis approach in the developing xylem of poplar [461].

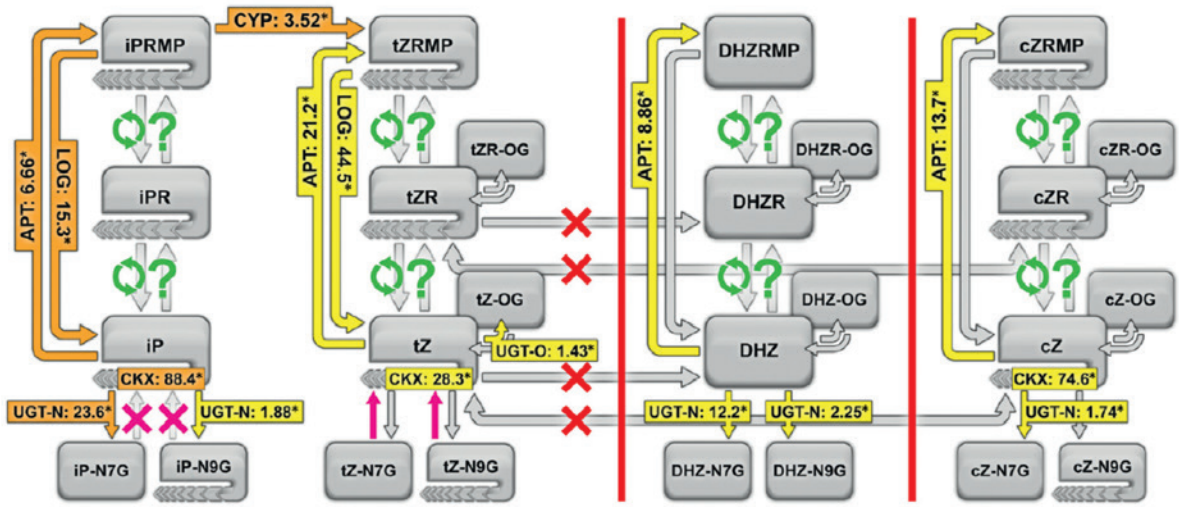

Figure 3. The cytokinin metabolic network in *Arabidopsis* derived by estimating enzyme kinetics for selected metabolic conversions, as published in [379]. Principal observations are depicted using the following colour coding: red, the DHZ and *c*Z CK pathways are isolated, no zeatin reductase or *cis-trans* isomerase activity was observed; magenta, while *t*Z-N7G and *t*Z-N9G are converted to *t*Z, iP N-glucosides are not metabolized; orange and yellow, conversion kinetics estimated by the mathematical model of CK base application (yellow) and of iP and iPRMP application (orange, * = pmol μM^{-1} min^{-1} mg^{-1} protein); green, mutual interconversions between ribotides and ribosides and between ribosides and bases cannot be unambiguously estimated from the data. Metabolite interconversions are organized vertically for each CK-type from left: iP, isopentenyladenine; *t*Z, *trans*-zeatin; DHZ, dihydrozeatin; *c*Z, *cis*-zeatin. Abbreviations: R, riboside; OR, O-glucoside; N7(9)G, N-7(9) glucoside; MP, monophosphate.

Phytohormones in stress signalling

The advanced analytics of hormonomes during heat, cold, and drought stress, as well as in reaction to nutrient deficiency, during plant defence against biotic stress and heavy metals was utilised in our research on the role of phytohormones in the reaction of plants to stress conditions. Analytical profiling of phytohormones has been systematically correlated with other analyses, including quantitative determination of gene transcription and photosynthetic parameters.

Within the field of heat stress signalling and the role of phytohormones, the main attention was paid to the role of cytokinins. Cytokinins play an important role in the early response to heat stress by stimulating stomata opening and transpiration, which helps to decrease leaf temperature until the defence is activated (approximately 30 min). To pinpoint changes associated with enhanced heat stress tolerance, the complex phytohormones were compared in *Arabidopsis thaliana* after direct heat shock and in heat-stress pre-acclimated plants. Because exogenous administration of cytokinins stimulates degradation/deactivation mechanisms, cytokinin levels were increased by the cytokinin oxidase/dehydrogenase inactivating enzyme inhibitor (INCYDE). It was found that increasing cytokinins before acclimation has a positive effect on plant resistance. An increase in cytokinins immediately before heat stress had a negative effect. Longer-stimulated transpiration has led to water loss and a decrease in water potential. The results showed the importance of the timing of changes in the levels of these hormones depending on the response phase [458]. Hormonal regulations

of cold stress responses continued in cooperation with the Agricultural Research Institute, Martonvásár, Hungary [126].

As both cytokinin decrease and upregulation was shown to diminish drought impact, in cooperation with the Julich Research Centre, Julich, Germany, we have performed an extensive comparative study to decipher their role (**Fig. 4**). Our results show that cytokinin downregulation had a positive impact on the retention of water potential, while their increase promoted plant recovery after re-watering [108]. This complex phenotyping study evaluated the effect of the timing of cytokinin modulation (permanent, before stress, during the stress progression). Our findings may be utilised in the elevation of plant fitness in stress conditions by exogenous cytokinin treatment or by their downregulation, respectively. In addition, the increase of cytokinins in reaction to drought in gymnosperms was shown in collaboration with the Timiryazev Institute of Plant Physiology, Moscow, Russia [256, 516]. It seems that endogenous phytohormones are stimulated in response to salt stress, rather than by a passive absorption of exogenous compounds, as shown by our analysis of vermicompost leachate reducing the impact of salinity in tomato [334].

We have also addressed the impact of nutrient deficiency by analysing organ-specific response to phosphate deficiency in *Arabidopsis thaliana* [110]. The nutrient deficiency was associated with the downregulation of active cytokinins, especially of the *trans*-zeatin type, and gibberellins, predominantly in apices and leaves. In roots, upregulation of *cis*-zeatin was observed. The decisive role of strigolactones was indicated by the downregulation of strigolactone repressors and after exogenous strigolactone application. We published the original review on strigolactones, emphasising the importance of relevant experimental

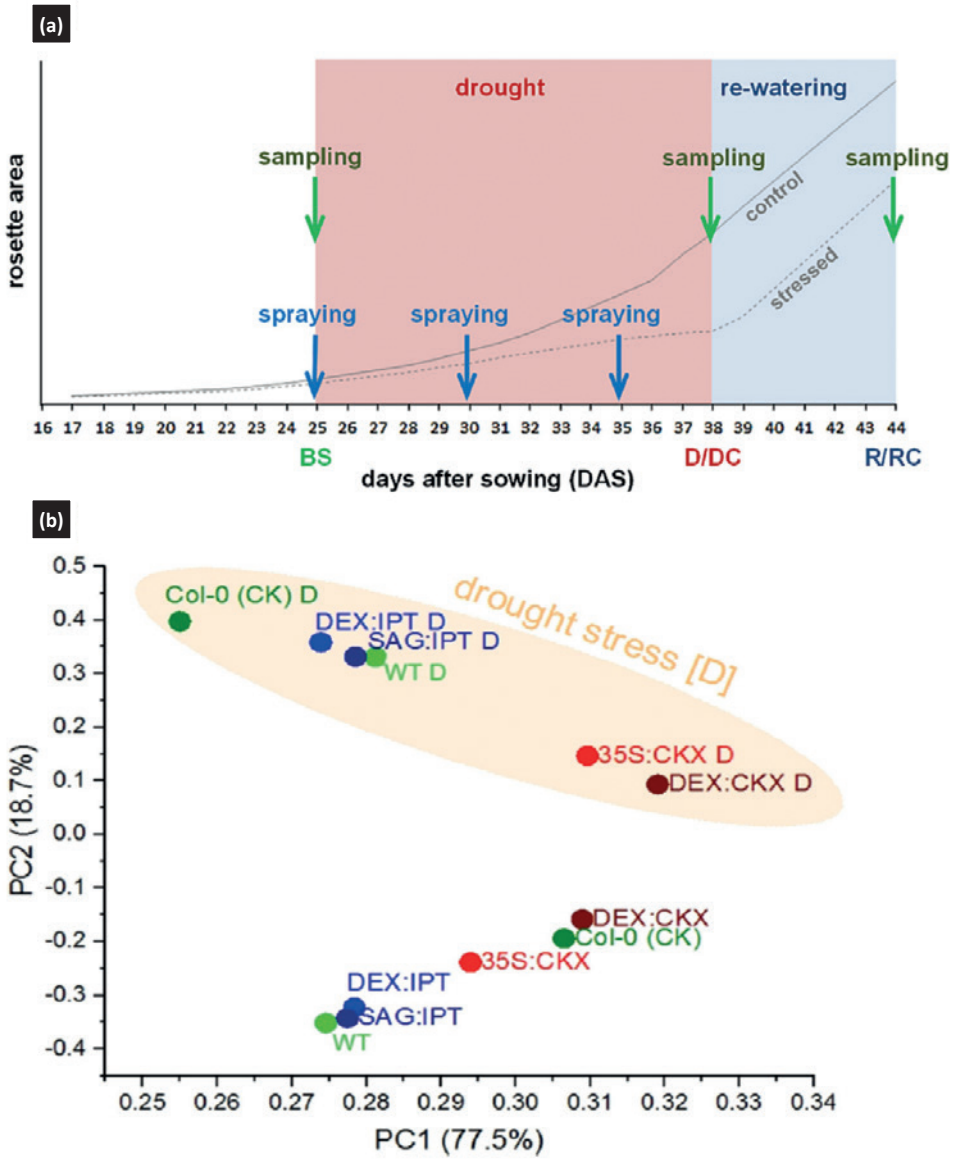

Figure 4. The effects of cytokinin pool size on the *Arabidopsis* response to drought stress and rewatering. **(a)** Scheme of the typical experiment. Drought starts 25 days after sowing, resumption of watering is at day 38. Leaf treatment by spraying with exogenous cytokinin is performed at days 25, 30 and 35. Samplings are made before stress (BS), after stress (D/DC), and 6 days after re-watering (R/RC). Lines illustrate growth curves of watered control plants and drought-stressed plants. **(b)** Effects of drought and cytokinin pool size on growth rates of *Arabidopsis* plants. The growth rates of individual *Arabidopsis* lines recorded during the drought stress and recovery period and of their respective controls are analysed by principal component analysis (PCA). The PCA clearly separates the drought-stressed plants from the control groups along the PC2, and PC1 illustrates a similarity in the growth rate dynamics between lines with the constitutive and inducible CKX expression. Modified from [108].

conditions. Many observed effects of strigolactones on plant physiology were found to be concentration-dependent [211].

Several of our studies addressed the role of phytohormones in the reaction of plants to biotic stressors. We have contributed to the elucidation of phytohormone responses that accompany the efficient defence of *Brassica napus* plants against *Plasmodiophora brassicae* infection. The comparison of two cultivars differing in their resistance to *P. brassicae* revealed that upregulation of salicylic acid is associated with enhanced resistance, while stimulation of jasmonic acid pathway is associated with increased plant sensitivity to the pathogen [109]. Moreover, these changes were accompanied by faster downregulation of auxins and cytokinins. In cooperation with BOKU, Tulln, Austria, significant induction of jasmonic acid signal transduction was observed during insect probing by grape phylloxera *Daktulosphaira vitifoliae*, and a reduction being found during early gall formation [167]. Modulation of plant cytokinin levels by the leaf-mining moth *Phyllonorycter mespilella,* which causes "green islands" in leaves, was characterised in cooperation with CNRS/Universite Francois-Rabelais de Tours, Tours, France [140]. The application of ozonated water as a soil drench or foliar spray was tested in cooperation with CNR, Bari, Italy, for the potential control of the root-knot nematode *Meloidogyne incognita* and the airborne pathogen Tomato spotted wilt virus infection in tomato [264]. Ozonated water diminished infection at the place of application, but no systemic effects were observed. In collaboration with Charles University, Faculty of Science, we also characterised phytohormonal response in reaction to soil oomycete *Pythium oligandrum* [333].

In collaboration with other laboratories, we have also determined a spectrum of phytohormones in response to oxidative stress [450] and heavy metals including copper [269], arsenic [451], aluminum [513], and cadmium [479]. Transcriptome analysis revealed distinct stress effects of the anti-inflammatory drug naproxen and anthelmintic praziquantel [67]. The analysis of polyamines showed their involvement in plant resistance against pathogens [224], but also during the development of wheat dwarf mutants [254].

Collaboration with other institutions

Research on auxin transport and homeostasis has been coordinated with Prof. Jiří Friml (IST Austria, Klosterneuburg, Austria), sharing experimental material and publishing joint papers [280, 486–488]. Other collaborators with whom we exchanged material and published papers on this topic included Prof. Richard M. Napier (School of Life Sciences, University of Warwick, Coventry; project CAS MSM200381701; [122]) and Prof. Christian Hardtke (University Lausanne, Switzerland; [419]). On auxin crosstalk and posttranslational modifications of auxin carriers, we collaborated with Prof. Christian Luschnig (BOKU, Vienna, Austria), sharing material and publishing joint papers [270], and on auxin-cytoskeleton interaction and evolution we collaborated with Dr. Kateřina Schwarzerová and Dr. Stanislav Vosolsobě (Department of Plant Experimental Biology, Faculty of Science, Charles University; [366, 506]).

Research on the developmental roles of cytokinins has been performed within the frame of a well-established collaboration with Prof. Stanley Lutts (Earth and Life Institute, Université Catholique de Louvain, Louvain-la-Neuve, Belgium) and Dr. Marc Behr (Luxembourg Institute of Science and Technology, Esch-sur-Alzette, Luxembourg). We shared material and published common papers [148, 533]. Other collaborators with whom we exchanged material and published papers on this topic included Dr. Kalina Danova (Institute of Organic Chemistry with Centre of Phytochemistry, Sofia, Bulgaria, project BAS 17-17; [13]), Dr. Dragan Vinterhalter and Dr. Martin Raspor (Institute for Biological Research "Siniša Stanković", Belgrade, Serbia; [460, 500]), Prof. Autar Mattoo (USDA-ARS-SASL, Beltsville, MD, USA; project USDA 58-8042-7-089F), and Assoc. Prof. Jan Hejátko (CEITEC Brno; [33]).

Research on the role of phytohormones in the reaction of plants to stress was performed through collaborations including the exchange of materials, joint projects, and publications, namely with Dr. Fabio Fiorani and Prof. Ulrich Schurr (Julich Research Center, Julich, Germany; [108]). Hormonal regulations of cold stress responses were studied in cooperation with Dr. Gabriela Szalai, Departments of Genetics and Plant Physiology, Agricultural Research Institute, Martonvásár, Hungary; [479]), reaction to drought in collaboration with Prof. Vladimir V. Kusnetsov (Timiryazev Institute of Plant Physiology, Moscow, Russia; [256, 516]), reaction to biotic stimuli with Prof. Astrid Forneck (Institute of Viticulture and Pomology, BOKU, Tulln, Austria; [167]) and with Prof. David Giron (Institut de Recherche sur la Biologie de l'Insecte, CNRS/Universite Francois-Rabelais de Tours, Tours, France; [140]). The application of ozonated water as a soil drench or foliar spray was tested in cooperation with Dr. Pasqua Veronico (Institute for Sustainable Plant Protection, CNR, Bari, Italy; [264]).

Research projects: 10–11, 13, 21–22, 24, 26, 30, 56–57, 62, 66, 70, 78–80, 83, 99, 101

Laboratory of Mass Spectrometry
Service Department

Head of the laboratory: **Ing. Jiří Malbeck, CSc.**
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The main task of the service laboratory is to provide chemical analyses both to other research groups at the home institution and to other research institutes and universities, with whom we collaborate as well. Currently, we provide analytical services to other entities in the Czech Republic and abroad.

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

We are focused on the quantitative analysis of biologically active compounds in plant matrixes using chromatographic methods with mass spectrometric detection. Our analytical results are included in the publications of colleagues from our institute, as well as those of external scientific institutions, whether it be an analysis of cytokinins [172, 361, 460], polyamines [23], auxins [172, 504], abscisic acid and its metabolites [172, 504] or phenolic acids [23, 503, 505].

In the picture (from left to right):
Ing. Alena Trávníčková / technician, Ing. Jiří Malbeck, CSc. / head of the laboratory.

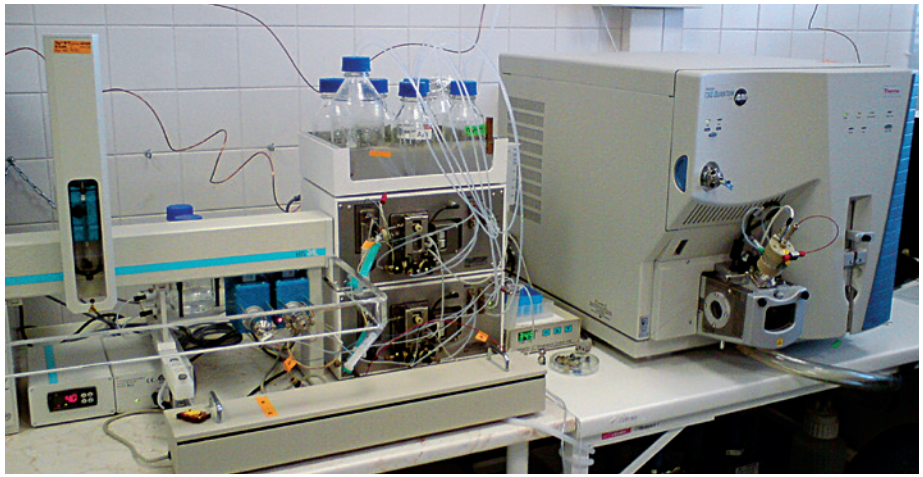

Figure 1. LC-MS system TSQ Quantum Ultra AM with Rheos 2200 chromatograph and CTC HTS autosampler.

Laboratory instrumentation

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

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


WiseTherm
Heating Mantle

Laboratory of Pathological Plant Physiology

Head of the laboratory:

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Our laboratory focuses on important aspects of plant-microbe interactions underlying host resistance to bacterial and fungal pathogens. The main interest of the laboratory is hormonal and phospholipid signalling implicated in plant defence responses. In addition to plant pathogens, the studied pathosystems have been extended to herbivores and molecular mechanisms involved in tri-trophic interactions. Our recent research has been devoted to: (1) the salicylic acid signalling pathway and its connection with other plant signalling systems, (2) the interconnection between salicylic acid signalling and the actin cytoskeleton, (3) the fungal phytopathogen *Leptosphaeria maculans* – auxin metabolism and the mapping of avirulence genes, (4) induced resistance to plant pathogens, and (5) three-way interactions between plant, pathogen, and insect.

In the picture (from left to right):
Jan Kapr / BSc. student, Jitka Svatoňová / BSc. student, Ing. Daniel Stehlík / Ph.D. student, mag.ing.agr. Nikoleta Rubil / Ph.D. student, Ing. Lukáš Maryška / Ph.D. student, Mgr. Romana Pospíchalová / technician, Ing. Barbora Jindřichová, Ph.D. / researcher, doc. Ing. Lenka Burketová, CSc. / head of the laboratory, Magdalenka / future plant biologist, Mgr. Hana Leontovyčová, Ph.D. / postdoctoral fellow, MSc. Anastasia Starodubtseva / Ph.D. student, MSc. Tetiana Kalachova, Ph.D. / researcher, MSc. Marzieh Mohri / Ph.D. student.

Not pictured:
Ing. Martin Janda, Ph.D. / research fellow, Mgr. Lucie Trdá, Ph.D. / research fellow (maternity leave), MSc. Oksana Iakovenko, Ph.D. / visiting researcher, MSc. Natalia Kornienko / visiting student, Ing. Vladimír Šašek, Ph.D. / researcher (currently farmer), Ing. Lucie Lamparová / technician (maternity leave), Bc. Kamila Pluhařová, Bc. Pavla Nováková, Bc. Věra Stoudková, Bc. Denisa Macková / master students, David Řejha / BSc. student.

Salicylic acid signalling pathway and its connection with other plant signalling systems

Salicylic acid (SA) is a phytohormone known to regulate many physiological processes, such as seed germination, cell expansion, respiration, stomata closing, senescence, and fruit yield. It also participates in the response to abiotic stress factors and is one of the most important molecules regulating a plant's reaction to infection. There are two known SA biosynthetic pathways in plants. Most of the SA produced upon infection is synthesized via the isochorismate pathway, where the isochorismatesynthase (ICS) is a main enzyme. A key protein in the SA signalling pathway is NPR1 (nonexpressor of pathogenesis related 1).

We study the cross-link between the SA biosynthesis/signalling and other plant signalling systems and general metabolism (**Fig. 1**), as well as the role of elevated temperature on PAMPs-induced defence [188].

The connection of SA signalling with phospholipid signalling

Our previous research showed that some of the key players in lipid signalling and endomembrane trafficking, phosphatidyl inositol-4-kinases β1 and β2 (PI4Kβ1/β2) enzymes, are negative regulators of SA biosynthesis. This effect depends on functional SA signalling and involves general hormone reprofiling [390]. We are now aiming to discover the molecular background of this link (**Fig. 2**).

The connection between the SA signalling and the actin cytoskeleton

We have previously found that SA signalling is activated rapidly after actin cytoskeleton dynamics are disrupted, and that SA itself can affect the actin cytoskeleton dynamics. Such a disruption is sufficient to prime plant resistance to further infection [224]. Going into the details, we discovered that such perception requires functional phospholipid turnover [198; Kalachova *et al.* 2019, Mol Plant-Microbe Interact 32: 128]. Nevertheless, the question as to how plants perceive actin cytoskeleton disruption and the matter of why the SA pathway is affected remains open [413].

The connection of endogenous SA level and plant growth

It has often been mentioned that plants with constitutively high levels of SA are retarded in their growth and might experience early senescence. On the other hand, if the SA signalling remains intact, SA-overaccumulators are also more resistant to biotrophic pathogens. Up until now, the reasons for this have remained unclear. We have established a collection of SA-overaccumulating mutants (**Fig. 3**), to dissect the mechanisms of how the SA level is sensed and how exactly it causes metabolic changes [263].

Characterization of novel components of auxin metabolism in the fungus *Leptosphaeria maculans*

The production of phytohormones by the filamentous hemibiotrophic ascomycete *L. maculans* represents another interesting topic. In our previous research we demonstrated that *L. maculans* produces a wide range of phytohormones both *in vitro* and *in planta*, including cytokinins (CK) and auxins, and we proposed a model of CK metabolism pathways in this pathogen. The following study focused on the identification of genes encoding putative enzymes of different IAA biosynthetic pathways, orthologous to those previously characterized in plants, fungi and bacteria. We found conserved genes for the indole-3-pyruvate (IPyA), indole-3-acetonitrile (IAN), and indole-3-acetamide (IAM) pathway. Our findings suggest that *L. maculans* biosynthesizes IAA mainly via the IPyA pathway. We show that among the analysed biosynthetic orthologs, those predominantly induced were *LmTAM1*, encoding putative tryptophan aminotransferase, and *LmIPDC2* and *LmIPDC1* genes, encoding putative indole-3-pyruvate decarboxylases [414].

Mapping avirulence genes in *L. maculans* isolates populations in the cultivation areas of oilseed crop in the Czech Republic

Leptosphaeria maculans and *Leptosphaeria biglobosa* is a complex species responsible for a serious disease in oilseed rape worldwide called “black leg”. The main

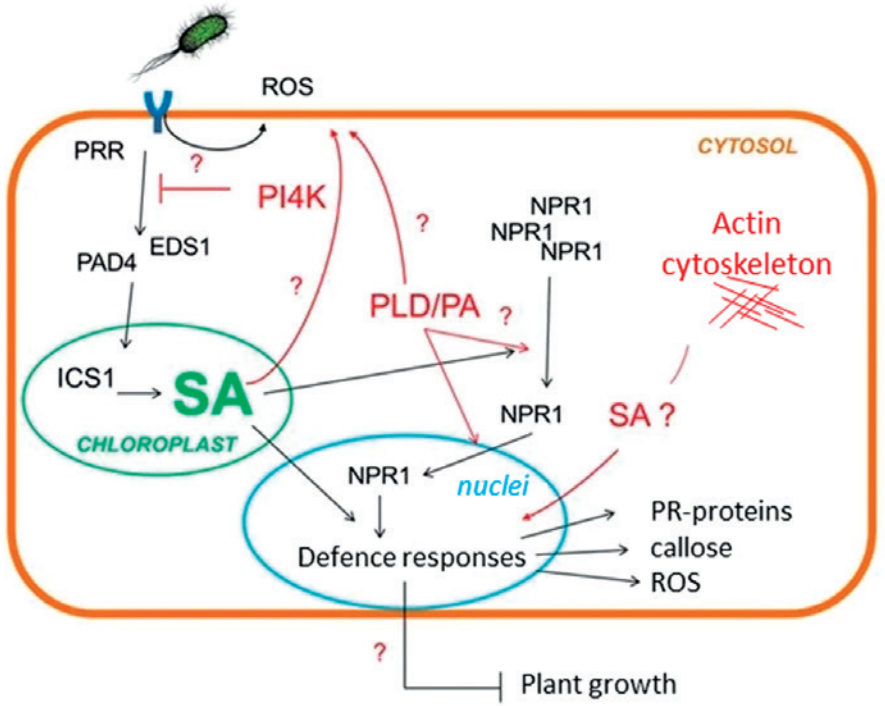

Figure 1. Studied areas cross-linking with salicylic acid signalling (marked in red). PLD – phospholipase D, PA – phosphatidic acid, SA – salicylic acid, NPR1 – nonexpressor of pathogenesis related 1, PAD4 – phytoalexin deficient 4, EDS1 – enhanced disease susceptibility 1, ROS – reactive oxygen species, PI4K – phosphatidyl inositol-4-kinases β1 and β2, PRR – pattern recognition receptors.

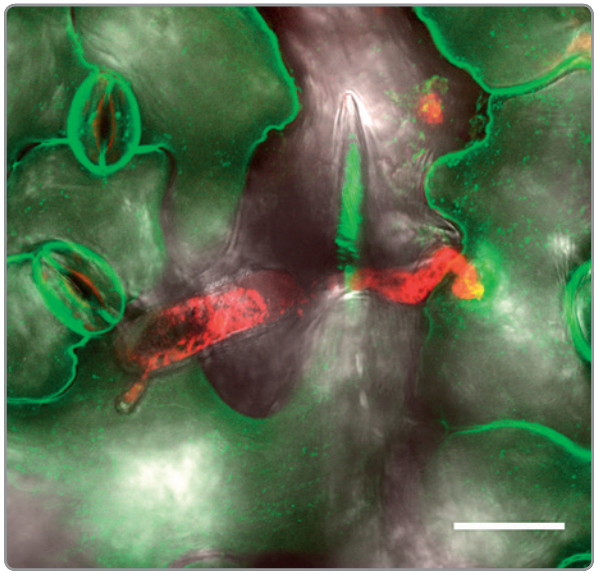

Figure 2. Penetration attempt of *Blumeria graminis* f. sp. *hordei* into *Arabidopsis thaliana* leaf tissues. PEN1-GFP protein accumulation 24 h post inoculation. Scale bar = 5 µm.

threat to oilseed rape (*Brassica napus*) protection is the strong evolutional potential of this pathogen, which enables quickly overcome resistance genes in new cultivars. The knowledge on the incidence of these *Leptosphaeria* spp. and individual avirulence genes in *L. maculans* populations will provide our five-year study granted by the Ministry of Agriculture, undertaken in collaboration with institutions of applied research (**Fig. 4**). The outcome of this study will provide important information for breeders and farmers, according to which they should choose appropriate oilseed cultivars to prevent the selection of more virulent *L. maculans* isolates in their fields. Additionally, within the frame of this project, we formed a wide collection of isolates, which is of high interest to others involved in *Leptosphaeria* spp. research. This collection will serve to reveal new races and avirulence genes or their mutations.

Induced resistance to plant pathogens

Searching for resistance inducers and elicitors represents another important branch of our research. Apart from the investigation of basal mechanisms underlying induced resistance, the research also turns to the practical side of this topic, which we consider prospective with respect to societal demand for non-toxic substitute of pesticides. We found efficient compounds among plant-derived saponins [294] and compost extracts [48] and described their mode of action. Research in this field led to utility models (33912 and 33723) granted by the Industrial Property Office of the Czech Republic in 2020. The subjects of these utility models are bio-based, resistance-inducing compounds/molecules useable as active substances in potential crop-protecting preparations.

Three-way interactions among plant, pathogen and insect

Research on the interconnection between plant defence systems activated during a concurrent attack by pathogens and herbivores was introduced in the laboratory relatively recently. Signalling pathways and defence mechanisms such as callose deposition are investigated using the model plant *A. thaliana* and the economically important crop oilseed rape, infected by bacteria *Pseudomonas syringae* and fungus *L. maculans*, respectively, and infested with the chewing herbivore *Plutella xylostella* and the sucking non-specialist *Myzus persicae* or specialist *Brevicoryne brassicae* (**Fig. 5**).

Collaboration with other institutions and applied research

The laboratory collaborates with several institutions within the Czech Republic. Phospholipid signalling in biotic stress is investigated within a well-established collaboration with Prof. Valentová's laboratory at

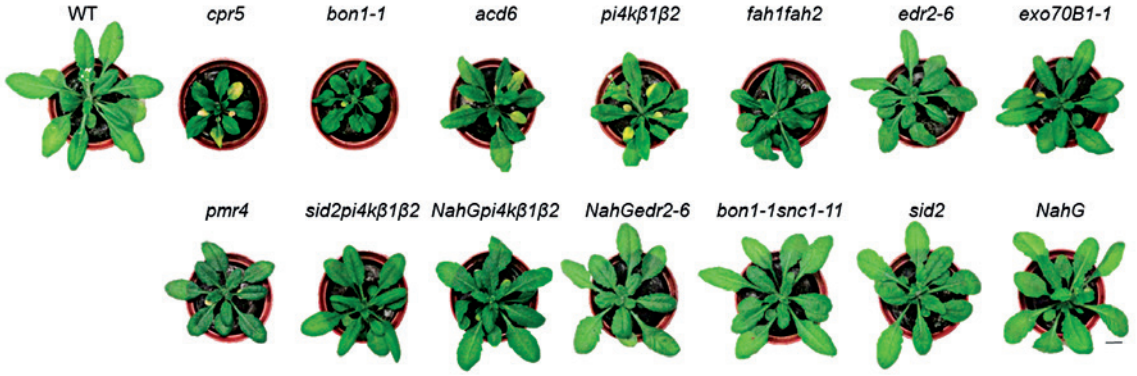

Figure 3. Collection of salicylic acid-overaccumulating *Arabidopsis thaliana* mutants. Representative images of rosettes of 4-week-old plants cultivated at 22 °C, 16 h light / 8 h dark.

Figure 4. Collection of *Leptosphaeria* spp. isolates in the field.

the University of Chemistry and Technology, Prague. Students of this university, as well as of the Faculty of Science of Charles University, work in our laboratory on their Bachelor's, Master's, and Ph.D. theses. New collaboration has been initiated with the University of South Bohemia in České Budějovice due to the movement of the former lab member Martin Janda to this university, where he will begin his own research. Collaboration with institutions involved in applied research concerns the project funded by the Ministry of Agriculture aimed at monitoring avirulence genes in *L. maculans* populations in Czech oilseed rape cultivation areas. *L. maculans* isolates are collected and identified in the Institute of Oilseed Crops (OSEVA Pro. Ltd.), OSEVA Development and Research Ltd., and the University of Life Sciences, Prague. Resistance inducers based on proteins were developed in collaboration with Tomáš Baťa University in Zlín, and the results of our laboratory tests are validated in field experiments provided mostly by OSEVA Pro. Ltd.

International collaboration

International collaboration is of great importance for the laboratory. Research on phospholipid signalling has been proceeding in close collaboration with Prof. Eric Ruelland from the Université de Technologie de Compiègne (France). The work involving *L. maculans* was carried out in collaboration with the laboratory of Prof. Thierry Rouxel, INRA, Centre de recherche

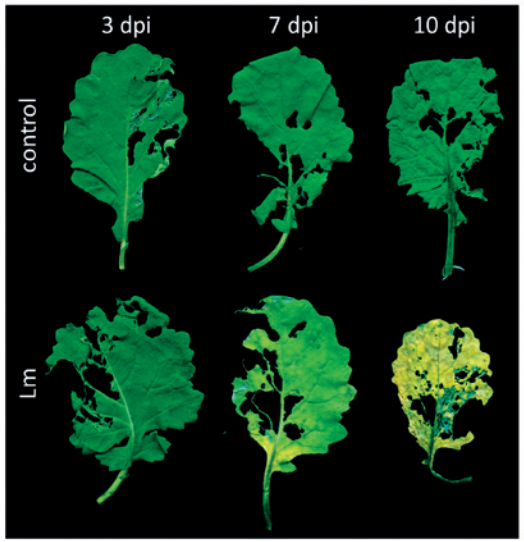

Figure 5. Role of *Brassica* napus plant preinoculation by *Leptosphaeria maculans* on the damage to leaves caused by caterpillars of *Plutella xylostella*.

Figure 6. A caterpillar of *Plutella xylostella*.

de Versailles-Grignon, France, as shown by a joint publication [414]. Resistance inducers were studied in collaboration with Prof. Enzo Montoneri from Biowaste Processing, Verona, Italy. Collaboration has recently begun with Prof. Thure Hauser, University of Copenhagen, on herbivores, which facilitated the study on three-way interactions. In addition, the laboratory also has a long-standing collaboration with Eötvös Loránd University in Budapest, Hungary (Dr. Károly Bóka) on electron microscopy, on fungal effectors with Dr. Peter Solomon from The Australian National University, Canberra, Australia, and on *L. maculans* produced phytohormones with Dr. Alexander Idnurm, The University of Melbourne, Australia.

Research projects: 4, 9, 11, 33, 86, 109, 1115

Laboratory of Plant Biotechnologies

Head of the laboratory:

RNDr. Mgr. Tomáš Vaněk, CSc.

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From 2018–2020, our laboratory followed a research programme focused predominantly on plant-xenobiotic interactions, the identification of secondary metabolites in plants, and the synthesis of their analogues. In total, we published 35 papers in international journals with impact factors and presented two lectures at international scientific meetings, as well as achieved some results for practice, including two patents. The research was funded by 15 grant projects from different grant agencies and included the following:

1) A detailed study of plant metabolism and plant stress responses, enabled by our success in obtaining OPPK grants for the purchase of the most sophisticated equipment – two-dimensional gas chromatography (GCxGC) with TOF MS detector (Pegasus 2D, Leco Co.), LC/MS/MS (Q-Trap, AB Sciex), and high-resolution LC-MS/MS system UHPLC Ultimate XRS a Orbitrap Q Exactive.
Since 2018, within the frame of the European Regional Development Fund-Project "Centre for Experimental Plant Biology", [project 11] we have been studying the effects of stress on plant lipids and volatile signalling.
2) The study of the fate of engineered nanoparticles in plants and their effect on plant metabolism.
3) The synthesis of analogues of biologically active plant metabolites, especially strigolactones and anti-inflammatory compounds.
4) Volatile research.
Plants emit volatile organic compounds (VOCs) as a means of warning other plants of impending danger. Nearby plants exposed to the induced VOCs stimulate their own defence in response. Accumulated data support this assertion, yet much of the evidence has been obtained in laboratories under artificial conditions where, for example, a single VOC might be applied at a concentration that plants do not actually experience in nature. Experiments conducted outdoors suggest that communication occurs only within a limited distance from the damaged plants.

In the picture (from left to right):
Front row: Mgr. Marcela Dvořáková, Ph.D. / researcher, Ing. Kateřina Moťková / technician, Zdena Hornychová / technician, Ing. Lenka Langhansová, Ph.D. / researcher, Mgr. Radka Podlipná, Ph.D. / researcher, RNDr. Mgr. Tomáš Vaněk, Ph.D. / head of the laboratory, Ing. Šárka Petrová, Ph.D. / researcher, Ing. Jan Rezek, Ph.D. / researcher.
Second row: RNDr. Mgr. Petr Soudek, Ph.D. / researcher, Ing. Přemysl Landa, Ph.D. / researcher, Mgr. Petr Maršík, Ph.D. / researcher, Mgr. Daniel Haisel, Ph.D. / researcher, Ing. Miroslav Šíša, Ph.D. / researcher.

Not pictured:
Žaneta Antonínová, Tereza Cyrusová, Markéta Hanulíková, Anna Hirnerová, Martin Lyška, Dagmar Mudrová, Anežka Nováková, Radka Opltová, Antonio Pavičic, Karolína Pumprová, Hedvika Roztočilová, Samanta Rysová, Filip Schenk, Eliška Syslová, Anna Zemanová, Tereza Zunová / students.

5) A new, emerging area of our research concerns lipidomics. It has been demonstrated that lipids not only provide structural bases for cell membranes and energy stocks for metabolism in plant cells, but they are also involved in defence reactions. The modification of membrane lipid composition can help to avoid stress-induced damages (e.g. during cold stress). Lipid changes during temperature stress responses will be followed and correlated with the stress tolerance to individual genotypes.
6) The application of our extensive knowledge of the use of plants in environmental protection (phytoremediation), achieved on a laboratory scale to semi-real and real conditions. This is part of our contribution resolving environmental contamination generally.

Plants and environment, selected results

Our main concern was focused on the evaluation of the environmental risk caused by new "emerging contaminants", which include pharmaceuticals, veterinary drugs, and engineered nanoparticles. Detailed information about the fate of these contaminants in plants is necessary for the complex evaluation of their ecotoxicological impacts, as they may become a part of the human food chain.

Pharmaceuticals

An integral part of this ongoing research is the evaluation of the fate of xenobiotics in plants at the enzymatic level. The risks and consequences of pharmaceuticals' escape into the environment and the potential role of phytoremediation technologies were considered and future perspectives were outlined.

Relevant study in this area is focused on the study of the influence of fenbendazole (FBZ) on the proteome and transcriptome of *Arabidopsis thaliana*. Our results clearly demonstrated that FBZ is taken up by plants and metabolized in 12 different metabolites. The presence of FBZ and its metabolites in *A. thaliana* influenced both gene expression and protein abundance [287].

Another study showed the uptake of Ivermectin (IVM) and its translocation to the leaves, but not in the pods and the beans. Four IVM metabolites were detected in the roots and one in the leaves. IVM exposure slightly decreased the number and weight of the beans and induced changes in the activities of antioxidant enzymes. In addition, the presence of IVM affected the proportion of individual isoflavones and reduced the content of isoflavone aglycones, which might decrease the therapeutic value of soybeans [439].

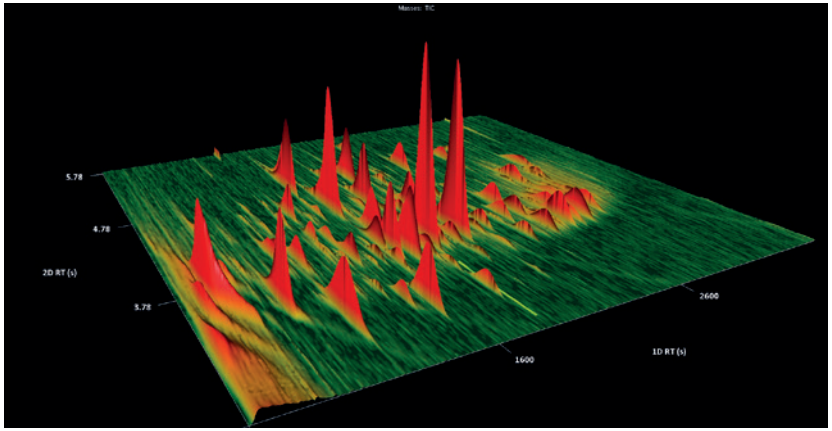

Figure 1. Volatile organic compound response of *Oryza sativa* to heat stress.

Plant stress

Part of our research was focused on the transcriptomic response of *Arabidopsis* plants to two pharmaceutically important drugs: naproxen and praziquantel. We demonstrated the specific effects of diverse classes of pharmaceuticals (naproxen is a non-steroidal anti-inflammatory drug, while praziquantel is an anthelmintic medicament). Both compounds represent rather common environmental contaminants. Potential risks and possible candidates in drug metabolism were suggested [67].

The threat of thorium contamination in the environment is becoming a current topic because of its possible use in nuclear power plants. Therefore, thorium effects are currently being intensively investigated. Our research could provide important insights into the understanding of the mechanism of thorium uptake into plants. This is crucial in relation to the increased risk of thorium exposure to the human population, which could be a substantial problem for human health [282].

Volatile plant signalling

We evaluated stress signalling among plants via volatile organic compounds (VOC). The VOCs play an important role in the interactions between plants and pests (insect pathogens). VOCs emitted by damaged plants can serve as attractants of plant pest predators or pest parasitoids. In cooperation with a plant hormone group, we characterize the impact of different stresses on the VOC profile of selected plant species, mainly *Oryza sativa*.

Nanoparticles

An important part of our research is the study of the impact of nanoparticles on plant behaviour (e.g. photosynthesis) and metabolism. Isotopic labelling of nanoparticles was done in order to gain the ability to follow their uptake and translocation in plants. Silver, iron, copper, and zinc oxide nanoparticles were characterized, including their impact on plant growth, transcriptome, and phytohormone pools.

In this study we demonstrated that isotopically labelled nanoparticles (NPs) in combination with single particle ICP-MS provide a useful tool for the study of

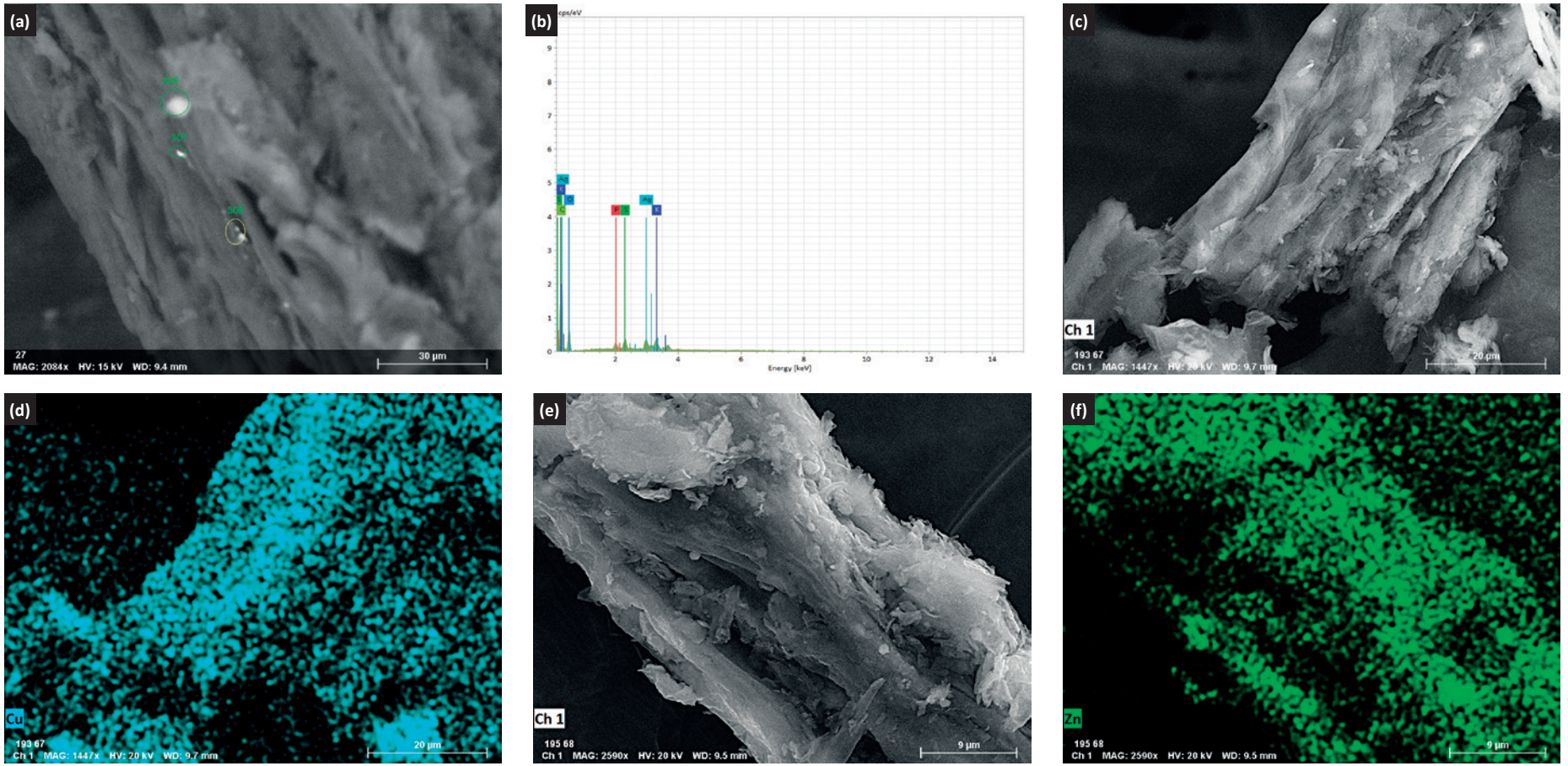

Figure 2. Scanning electron micrographs and respective energy dispersive X-ray spectroscopy (EDS) hypermaps of *Arabidopsis thaliana* roots exposed to ^{107}Ag **(a, b)**, ^{65}Cu **(c, d)**, and ^{70}ZnO **(e, f)** nanoparticles.

NP uptake by plants. We described the differences in the solubility of silver NPs, ZnO NPs, and CuO NPs in a cultivation medium, as well as their accumulation and translocation in the model plant *Arabidopsis thaliana* [87].

In another work, we studied the alleviation effect of zinc on cadmium-induced toxicity in a wetland plant species (*Carex vulpina*). In our short manuscript we bring the interesting results that zinc oxide nanoparticles have a different effect in comparison to their bulk counter particles and soluble metal salt. ZnO nanoparticles have significantly increased the negative effect of cadmium, which has been reflected mainly by changes in the content of photosynthetically active pigments. Since the question of the actual danger of NPs has still not been definitively answered, it is important (mainly in the case of practical applications) to prevent the spread of free NPs into the environment [176].

The bioaccumulation of nanoparticles in plants used for food and feed could be a major exposure pathway to nanoparticles, resulting in ecological and health risks. Isotopic labelling of nanoparticles enables their sensitive tracing in the presence of background elements in complex plant matrices. We investigate nine individual cases of plant–NP interactions and show the role of plants in the uptake and translocation of nanoparticles or their dissolution into metals [243].

Plant metabolites and analogues

Within this field, we continue in the search for new biologically active molecules, especially those exhibiting anti-inflammatory, anti-cancer, or anthelmintic activity. We also focus on the testing of the potential inhibitors of pro-inflammatory cytokines, such as interleukins and tumour necrosis factor alpha. We have evaluated the structure-activity relationships of selected secondary metabolites, and based on molecular modelling methods, we continue in the synthesis of analogues and derivatives of natural products with potential therapeutic effects.

Parasitic plants genus *Striga* or *Orobanche* represent a serious threat to agriculture, especially in developing countries. The seeds of these plants germinate in the presence of strigolactones, a recently recognized group of phytohormones, released by the roots of crop plants. The efficient treatment is the stimulation of their "suicide germination" before the sowing of crop seeds into the field. As natural strigolactones are extremely labile, more stable synthetic analogues are used. Active strigolactone mimics, based on triazolide, were successfully prepared.

A simple two-step synthesis of a new type of strigolactone mimics, based on resorcinyl scaffold, was performed. These mimics were highly stable, even at alkaline pH, and were able to induce seed germination of parasitic plants *Striga hermonthica* and *Phelipanche ramosa* at low concentrations, EC_{50} ~ 2×10^{-7} M (*Striga*) and EC_{50} ~ 2×10^{-9} M (*Phelipanche*). These results, namely simple synthesis and high stability, make these compounds an exciting target for their utilization as suicidal germinators [21].

Figure 3. Strigolactone analogues' effect on root elongation of *Arabidopsis thaliana*.

The synthesis of a new series of strigolactone mimics based on triazolide scaffold was done. These mimics were stable in an acidic as well as a basic environment and effectively induced seed germination of the parasitic plant *Phelipanche ramosa* with EC_{50} as low as 5.2×10^{-10} M. Such mimics may therefore potentially be used to control the occurrence of broomrape parasitic weed in fields [166].

Since a number of plant secondary metabolites and their derivatives can be used in human medicine, we focused on the search for cyclooxygenase-1/2 and 5-lipoxygenase (enzymes catalysing biosynthesis of inflammatory mediators) inhibitors.

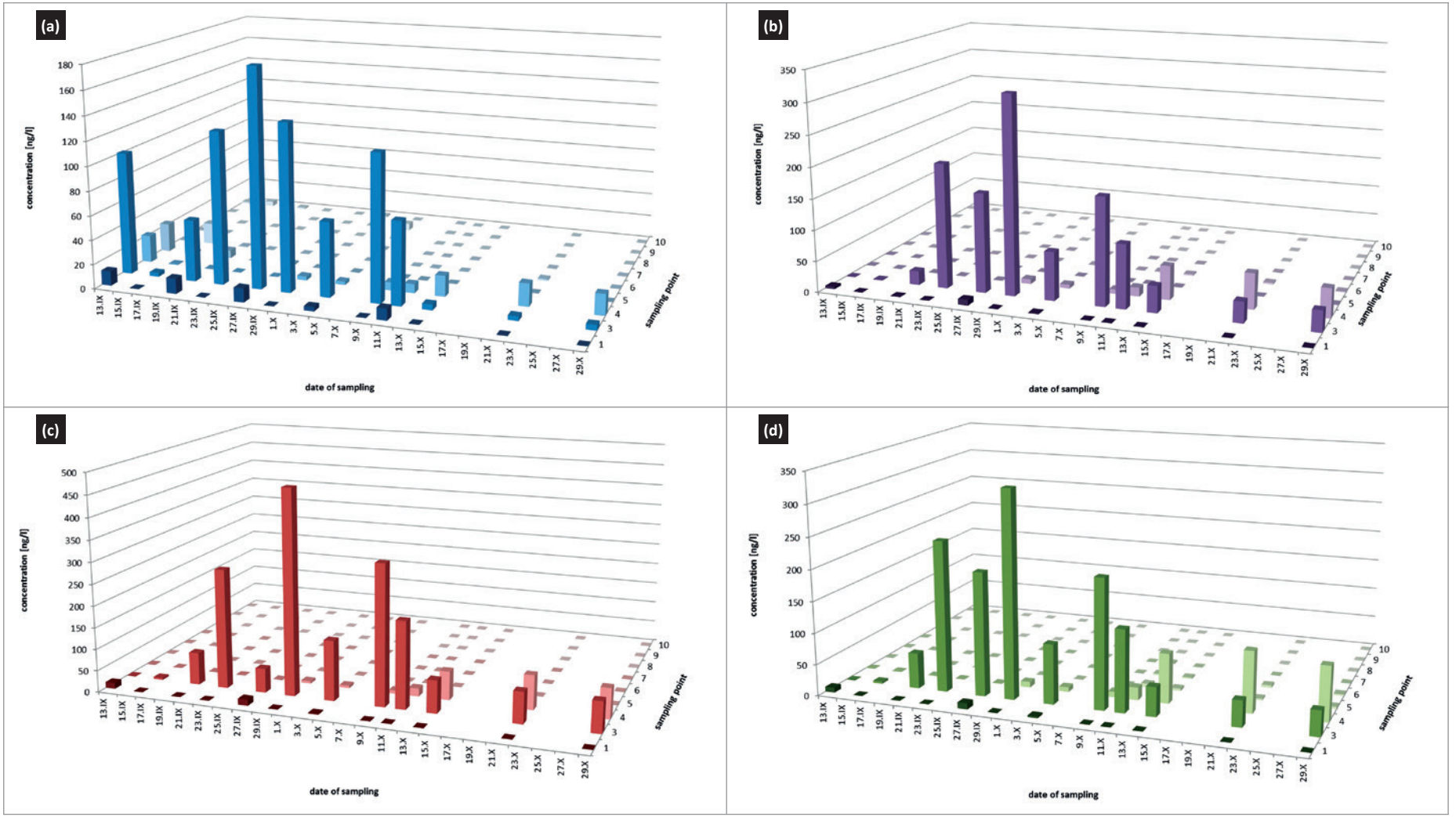

Figure 4. Degradation/accumulation of ibuprofen **(a)**, diclofenac **(b)**, ketoprofen **(c)**, and naproxen **(d)** in constructed wetland. Scale Z represents different sampling points.

Figure 5. Model system for purification and utilization of rainwater.

We investigated various natural phenolic compounds such as stilbenes, quinones, and their synthetic derivatives. Organic synthesis helped to improve the activity of parent compounds or decrease their toxicity [481].

Research for practice

Our comprehensive results in the area of plant utilization in environmental protection (phytoremediation) enabled us to extend our efforts to semi-real (rainwater purification and utilization) and real (constructed wetland for agrochemical cleaning) conditions. The aim was to contribute to solving environmental problems in general, not only in the Czech Republic.

Our laboratory also initiated, submitted, and ultimately was funded by the Czech Technology Agency for the large project "Support for the process of commercializing the results of research and development at the Institute of Experimental Botany AS CR, v.v.i.".

The general problem of water shortage led us to utilize a phytotechnology method to cope with it. Our project "Utilization of R&D results of the Institute of Experimental Botany AS CR, v.v.i." was supported by EU Structural Funds and the Prague municipality.

Selected practical results

Patent No. ZA 2017/08339, South Africa, 2018: Primin derivatives, method of preparation thereof and use thereof [patent 5].

Patent No. CZ308139, Czech Republic, 2019: Strigolactone derivatives for controlling parasitic plants seed germination. [patent 12].

International Collaborations

During the period 2018–2020, we continued to extend our international cooperation, mainly with Israel, the USA, China, South Africa, and other countries. We took part in five COST Actions, which gave us wide opportunities to cooperate with scientists from other European and COST countries. These collaborations led, among others, to the shared Czech-Israeli project "Uptake of engineered nanoparticles (ENPS) by plants and its implications for potential remediation of contaminated water and soil", acronym Nano-Phyto [project 5], and the preparation of a new project proposal for the new COST Action "CA18111- Genome Editing In Plants", as well as the preparation of proposals for Czech-USA cooperation and Czech-China cooperation.

Members of our laboratory are involved in research organizations, e.g. the International Society for Phytotechnologies and the European Plant Science Organisation (EPSO), and additionally, they are members of the editorial boards of the following journals: *Biologia Plantarum*, *Plant Science Today*, and *International Journal* of *Phytoremediation*.

Some outputs concerning GMO policy were published, e.g.:

Eriksson D, *et al.* (2018) Why the European Union needs a national GMO opt-in mechanism. NATURE BIOTECHNOL 36: 18-19.

Eriksson D, *et al.* (2019) Implementing an EU opt-in mechanism for GM crop cultivation. EMBO REP 20: e48036.

Research projects: 5, 11, 18, 31, 45–46, 88, 90, 92, 94, 100, 107, 111, 114–115

Laboratory of Plant Reproduction

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The laboratory was established in 2007. It follows two research avenues: the investigation of floral induction and the genomics and transcriptomics of plant mitochondria. We are focusing on two model plants. The main species of interest is *Silene vulgaris* (bladder campion or maiden's tear). Its mitochondrial genome is extremely diverse, containing numerous repeats, which are responsible for a high frequency of intramolecular recombination. Frequent recombinations may generate chimeric genes, consisting of various portions of other mitochondrial genes. They often show a detrimental impact on mitochondrial functions, which leads to pollen abortion or cytoplasmic male sterility (CMS). The phenomenon of CMS is widely used in agriculture for the production of high-yield hybrid seeds, and it is therefore studied preferentially in crops; much less is known about CMS in the wild. *S. vulgaris* is a very useful model for the research of CMS in wild populations that did not pass the genetic bottleneck associated with the domestication process and exhibit a vast array of CMS-related effects. For example, we described an interesting flip-flop recombination, capable of controlling the expression of the CMS gene in *S. vulgaris* [129].

In the picture (from left to right):
David Gutiérrez-Larruscain, Ph.D. / postdoc, Claudia Belz, Ph.D. / postdoc, Manuela Krüger, Ph.D. / postdoc, Helena Štorchová, Ph.D. / head of the laboratory, Ing. Oushadee A. J. Abeywardana, Ph.D. / research assistant, Roman Gogela, Ph.D. / postdoc.

Global warming is accelerating rapidly, which poses a serious threat for agricultural production. It leads to a high demand for the crops capable of growing in dry, salty, and warm regions. The traditional crop of the Andes in South America – *Chenopodium quinoa* – attracts attention owing to its high salt and drought tolerance. To expand the cultivation area of *C. quinoa*, appropriate timing of flowering and fruit production is necessary. Plants growing near the equator flower during short days, because they did not experience long

days during their evolutionary history. To expand their range to the north, it is necessary to breed cultivars induced to flowering during long days. Understanding the control of flowering in *C. quinoa* is the prerequisite for its successful introduction into new areas.

The traditional model for flowering-related studies in our lab is *Chenopodium (Oxybasis) rubrum*, which can be induced to flowering by a single period of 12-hour darkness. However, it is not a close relative of *C. quinoa*. We have therefore established a new model, Chenopodium ficifolium. This diploid species is a close relative of the ancestor of the subgenome B of tetraploid *C. quinoa* [76]. We revealed long-day and short-day ecotypes of *C. ficifolium* and analysed the adaptation of the two ecotypes to different photoperiods [289]. Our studies help to decipher the regulation of flowering in *C. quinoa*.

Mitochondrial genomes and transcriptomes of *Silene vulgaris* in the context of cytoplasmic male sterility (CMS)

Unlike the small, compact, and gene-dense mitochondrial genomes of animals, mitochondrial genomes of flowering plants are large and often multipartite, with large and highly rearranged intergenic regions. The genus *Silene* contains the species with the largest known plant mitogenomes (*Silene noctiflora* and *Silene conica*, 7 and 11 Mb, respectively), as well as a species with extremely rearranged mitogenome (*Silene vulgaris*). Frequent intramolecular recombinations are associated with DNA repair of double strand breaks in plant mitochondrial genomes. Recombinations sometimes give rise to chimeric genes composed of the portions of other genes, which may cause CMS. Nuclear fertility restorer (*Rf*) genes inhibit CMS gene expression and restore pollen production in male fertile (hermaphroditic) individuals.

Our lab identified the first CMS candidate in *S. vulgaris*. This gene, called Bobt, was located in the mitochondrial genome of an *S. vulgaris* collected in Krasnoyarsk, Russia (haplotype KRA) [129]. We confirmed *Bobt* as the only region more highly expressed in the females than in hermaphrodites, consistent with its role as the CMS determinant. The Bobt gene was co-transcribed with *Cytochrome b* (*cob*), which may constrain the inhibition of Bobt transcription and fertility restoration. Homologous recombination moved the cob gene out of the control of the *Bobt* promoter, which facilitated the suppression of *Bobt* and the restoration of male fertility (**Fig. 2**). We may compare the *Bobt* gene to a terrorist who is taking a hostage – the essential gene *cob*. The hostage is then liberated by homologous recombination. Our findings document the impact of mitochondrial genomic recombination on the expression of essential mitochondrial genes, which has not yet been evaluated.

CMS is not always associated with mitochondrial chimeric genes. We compared the mitochondrial transcriptomes in females and hermaphrodites of *S. vulgaris* KOV lacking any chimeric open reading frame (ORF). We found a region containing no ORF but encoding non-coding RNA. It was associated with CMS, although we do not know whether it is the cause or rather the consequence of CMS (Stone *et al.* 2017, J Exp Bot 68: 1599-1612).

Mitochondrial transcriptomes are frequently studied in flowering plants with CMS. Much less is known

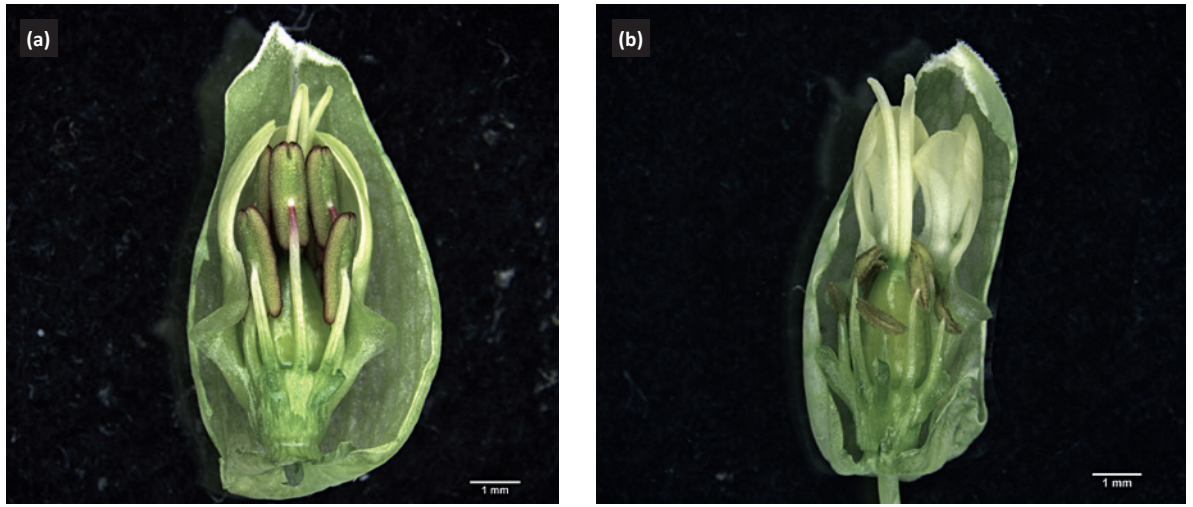


Figure 1. The sections of hermaphrodite **(a)** and female **(b)** flower buds of *S. vulgaris*. Well-developed anthers are visible in hermaphrodite flower buds, whereas anther abortion is observed in females. Orig. K. Eliášová.

about plastid transcriptomes. We constructed plastid transcriptomes of *S. vulgaris* and found no significant differences between the females and the hermaphrodites [214]. This observation is surprising because our recent analysis of the cytoplasmic transcriptomes found numerous genes highly differentially expressed between the genders, many of them encoding proteins targeted to plastids [404].

The genetic background of flowering in the *Chenopodium* species

The transition from the vegetative to the generative phase is the most essential commitment in plant life. It affects reproduction success as well as crop yield. Plants sense environmental and endogenous conditions, e.g. day length, temperature, and age. The signals are integrated by essential regulatory genes, which are capable of inducing flowering. The most significant floral regulator is *FLOWERING LOCUS T* (FT).

We studied the role of *FTs* in two contrasting ecotypes of *C. ficifolium*, the close diploid relative of *C. quinoa*. We found three *FT like* (*FTL*) genes in the *C. ficifolium* genome, and a complex set of 12 *FTLs* in *C. quinoa* [540]. The *FTL* expression was higher during short days in both ecotypes of *C. ficifolium*. However, short days accelerated flowering only in the short--day ecotype. The long-day ecotype flowered earlier without coincident activation of *FTLs*, which is unusual in angiosperms [289]. Our findings will shed light on the adaptation of *C. quinoa* to the long days that are typical at northern latitudes.

We applied the FTL markers in the comprehensive phylogenetic analysis of Euro-Asian representatives of the *C. album* aggregate, a taxonomically intricate group of species [76]. This study was performed in collaboration with Bohumil Mandák; our lab designed the primers and supervised the complex manual editing of intron alignments. We are now continuing the collaboration with Bohumil Mandák, aiming to reconstruct the evolutionary history of the American representatives of the *C. album* aggregate.

The *Chenopodium* species are both very interesting and useful models for the investigation of flowering. However, there is one obstacle hindering gene function analyses in *Chenopodium* – recalcitrance to transformation. We are therefore analyzing the *Chenopodium FTL* genes by complementing *Arabidopsis thaliana ft* mutants. We found that the *FTL1* gene of *C. ficifolium* promoted flowering in *A. thaliana*. We are also working hard to develop Virus Induced Gene Silencing (VIGS) in *C. ficifolium* and *C. quinoa* in collaboration with the Laboratory of Virology. The adoption of VIGS will open new avenues in the research of the *Chenopodium* species.

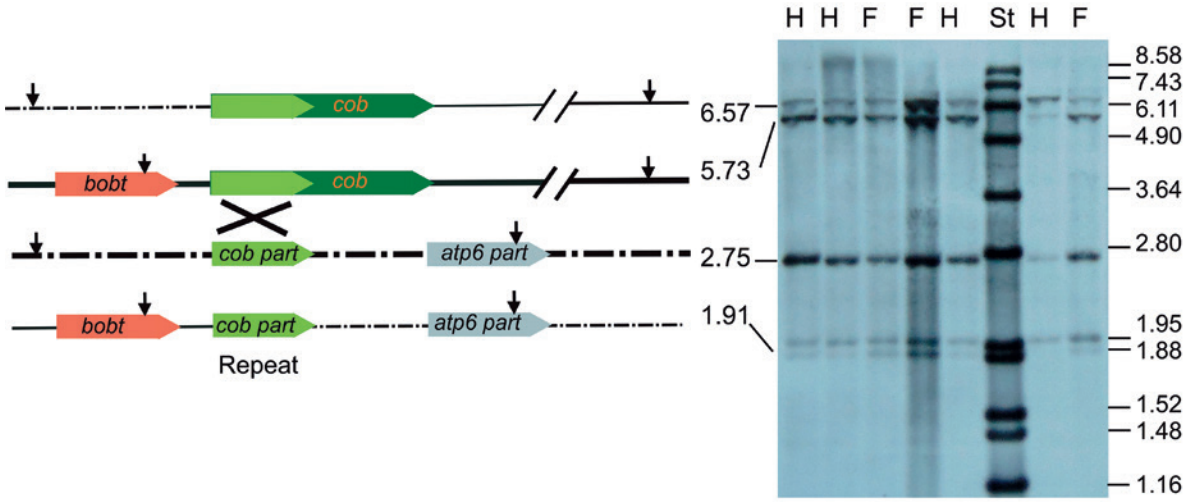
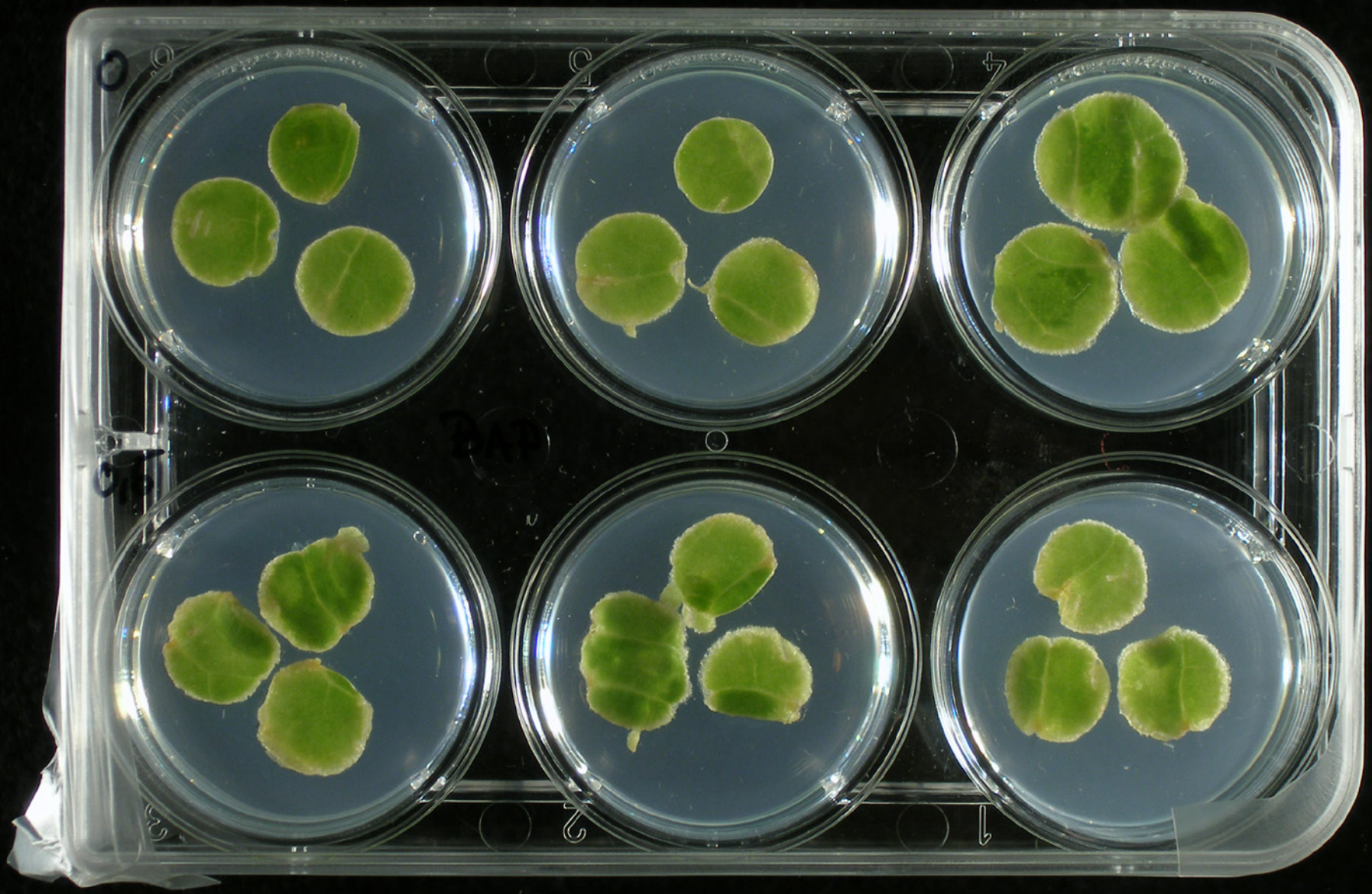


Figure 2. The liberation of a hostage – recombination across *cob* repeat. The cinnabar *Bobt* gene ("terrorist") controls the transcription of the green essential *cob* gene ("hostage"). This configuration is shown as the 5.73 kb band on the right Southern blot. This band is strong, and the configuration is therefore abundant in both females (F) and hermaphrodites (H), but not in all plants – note one H with a weak band. When the plant tries to suppress *Bobt*, it also inhibits *cob*. The homologous recombination across partial *cob* sequence (light green) places *cob* under the control of its genuine promoter, which corresponds to the 6.57 kb band on the right. The "hostage" is now free, and *Bobt* may be safely inhibited without influencing *cob* expression. Orig. [129].

Research projects: 11, 20, 52, 84



Laboratory of Pollen Biology

Head of the laboratory:

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The laboratory 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 *Physcomitrium, Marchantia, Amborella,* hops, and tomato. Moreover, we are continuously extending our activities, and our research is focused mainly on several aspects of pollen development, pollen communication with female tissues, and genome stability.

In the picture (from left to right):
Top row: Bc. Peter Darivčak / student, Christos Michailidis, Ph.D. / postdoctoral fellow, Mgr. Karel Raabe / Ph.D. student, RNDr. Jan Fíla, Ph.D. / postdoctoral fellow, prof. RNDr. David Honys, Ph.D. / head of the lab, RNDr. Karel J. Angelis, CSc. / researcher, Petra Rožnovská / research assistant, Mgr. Pavel Bokvaj / Ph.D. student, Mgr. Marcela Holá, Ph.D. / postdoctoral fellow, RNDr. David Reňák, Ph.D. / postdoctoral fellow.
Front row: Mgr. Alena Náprstková / Ph.D. student, Mgr. Božena Klodová / Ph.D. student, Ljudmilla Timofejeva, Ph.D. / researcher, Pelin Zobaroglu / visiting student, RNDr. Lenka Záveská Drábková, Ph.D. / researcher, Zahra Aghcheh Kahrízí, M.Sc. / Ph.D. student, Bc. Micheala Hromadová / student, RNDr. Lenka Steinbachová, Ph.D. / researcher, Said Hafidh, Ph.D. / researcher, Vinod Kumar, MSc. / Ph.D. student, Anna J. Wiese, Ph.D. / postdoctoral fellow, Ing. Radka Vágnerová / Ph.D. student.

Not pictured:
Daniela Impe, Ph.D., Mariana Limones Mendez, Ph.D. / postdoctoral fellows, Ing. Jana Feciková, RNDr. Zuzana Gadiou, Ph.D., Ing. Jana Kůrková, Ing. Klára Čermáková, Ing. Iveta Jelínková / research assistants, Mgr. Katarína Kulichová, Janto Pieters, MSc., Elnura Torutaeva, MSc. / Ph.D. students, Marek Földi, Veronika Jirásková, Bc. Helena Kočová, Bc. Oliver Pitoňak, Bc. Anna Popelářová, Bc. Petr Šesták / students.

Regulation of *Arabidopsis* pollen development

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 are interested in the identification and functional characterization of *Arabidopsis* pollen-expressed transcription factors (TF) involved in the regulation of pollen development, with a specific focus on MYB and dimeric basic leucine zipper (bZIP) TF families.

In collaboration with Prof. S.-K. Park, Kyungpook National University, Daegu, Korea, we demonstrated the key role of GAMYB TF, MYB81, in the developmental progression of microspores, enabling the formation of the two male cell lineages that are essential for sexual reproduction in *Arabidopsis* [445].

bZIP TFs regulate many critical processes. Developing *Arabidopsis* pollen expresses a versatile module of

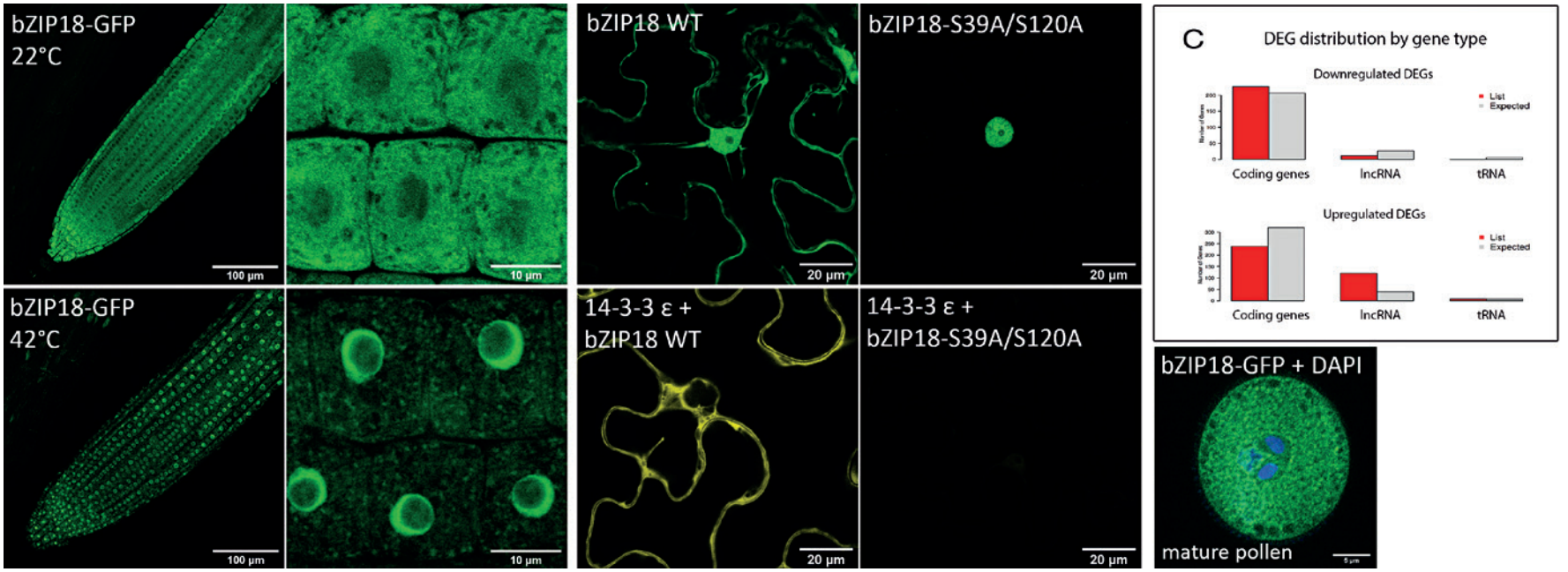

Figure 1. bZIP18 localization dynamics. The four panels to the left show bZIP18-GFP localization in root cells at 22 °C (top two panels) and following a 1 h treatment at 42 °C (bottom two panels). As can be seen, the nuclei become more compacted following heat stress, compared to the diffused nuclei under standard conditions. The middle panels show which amino acid residues are important for 14–3–3 binding, as revealed by mutational analyses. The top panel to the right shows differential gene expression in seedling transcriptomes, as it relates to DEG distribution by gene type, coding genes, lncRNAs, and tRNAs, with observed and expected values compared separately for DEGs downregulated and upregulated in heat stressed mutant seedlings. Finally, the bottom panel to the right shows bZIP18-GFP localization in mature pollen, where localization is observed in the cytoplasm and nuclei of the vegetative cell, but not the sperm cells.

bZIP TFs from Groups E (bZIP34, bZIP61) and I (bZIP18, bZIP52, bZIP 59 and bZIP69). We have revealed the dimerization preferences among individual bZIP TFs, with some (bZIP18) dimerizing more broadly than others. Moreover, detailed characterizations of bZIP18, bZIP34, and bZIP52 revealed their involvement in pollen development (Gibalová *et al.* 2009, Plant Mol Biol 70: 581-601; Gibalová *et al.* 2017, Plant Reprod 30: 1-17). We have revealed the involvement of bZIP18 and bZIP52 in the heat stress response in seedlings (Wiese *et al.* 2021, Int J Mol Sci 22: 530). Under standard conditions, the localization of both bZIP18-GFP and bZIP52-GFP is partitioned between the cytoplasm and the nucleus. Following heat stress, they accumulate in nuclei due to phosphorylation/dephosphorylation and 14-3-3 binding. Following heat stress, specific serine residues become dephosphorylated, allowing the bZIP TFs to dissociate from 14-3-3 proteins and re-localize to nuclei. A similar mechanism in pollen is currently being investigated.

Pollen as a model for post-transcriptional regulatory levels

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 and proteomic analyses of the tobacco male gametophyte representing the first plant species shedding bicellular pollen [36]. These datasets presented a benchmark for future functional studies using developing pollen as a model. We further showed the complexity of the tobacco male gameto-

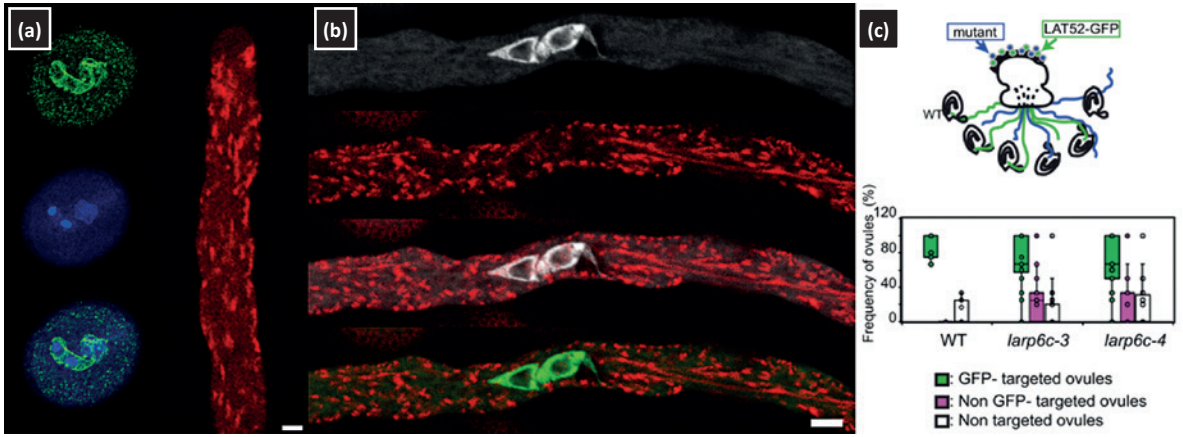

Figure 2. (a) Live cell imaging of fluorescently tagged RNA binding protein, YFP-LARP6C by confocal microscopy at pollen maturity and LARP6C-tRFP in pollen tube showing punctate RNPs in cytosol and anchoring on endo-PM of the vegetative cell. DAPI nuclear stain is shown in blue. Scale bars correspond to 5 um. **(b)** Confocal analysis of paralogous proteins LARP6A-GFP and LARP6C-tRFP localization during *in vitro* pollen tubes germination. The two proteins show no colocalization and are functionally unrelated, with LARP6A being predominantly in sperm cells, whereas LARP6C associate with cytoskeleton in vegetative cell cytosol. Scale bars correspond to 10 um. **(c)** Semi *in vivo* pollen tube guidance competition assays. Top, a cartoon representation of pollen tube guidance assay. Unfertilized wild-type ovules are arranged around a male sterile *ms1* pistil pollinated with both mutant *larp6c* and LAT52-GFP pollen. A limited pollination is performed with pollen from wild-type plants homozygous for LAT52-GFP reporter (hmLAT52-GFP) (labeled "WT"), with hmLAT52-GFP and *larp6c-3* pollen (labeled "*larp6c-3*") or with hmLAT52-GFP and larp6c-4 pollen (labeled "*larp6c-4*"). Ovules are then scored as: GFP positive (targeted by LAT52-GFP pollen tube), non-GFP ovules (targeted by mutant pollen tube), or non-targeted. The results are presented as whisker boxplots.

phyte transcriptome over the period of pollen development. 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 (Honys and Twell 2004, Genome Biol 5: R85). We observed a similar phenomenon in less advanced bicellular tobacco pollen (Bokvaj *et al.* 2015, Genomics Data 3: 106-111). Much broader evolutionary study within a multilateral collaboration resulted in the generation of gene expression atlases for various organs and gametes of 10 plant species comprising bryophytes, vascular plants, gymnosperms, and flowering plants. Comparative analysis of the atlases identified hundreds of organ- and gamete-specific gene families and revealed that most of the specific transcriptomes are significantly conserved (Julca *et al.* 2021, Nature Plants 7: 1143-1159).

Recently, we initiated a completely new direction in 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 non-translating monosomes 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 [36; Hafidh and Honys 2021, Ann Rev Plant Biol 72: 581-614]. Such an organization, involving eukaryotic translation initiation factors like eIF3 [265], is extremely useful in fast tip-growing pollen tubes. 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 of post-transcriptional control, with a focus on the role of stored RNPs and functionally characterized RNA-binding proteins, including the pollen-specific RNA binding protein LARP6C (collaboration with C. Bousquet-Antonelli, INRA Perpignan, France), which appears to be essential for pollen tube guidance but not pollen maturation or pollen tube growth (Biley *et al.* 2020, bioRxiv, doi: 10.1101/2020.11.27.401307; in press in Plant Cell).

Beyond pollen phosphoproteomics: nascent polypeptide-associated complex

Previously, we identified the phosphoproteome from several stages of tobacco male gametophyte (mature pollen, 5-min *in vitro* activated pollen, and 30-min *in vitro* activated pollen (Fíla *et al.* 2016, Mol Cel Proteomics 15: 1338-1350). The rapid changes of protein phosphorylation play a crucial role in regulating pollen activation. We identified 301 phosphoproteins carrying 432 phosphorylation sites, of which we studied the nascent polypeptide-associated complex (NAC complex). The NAC complex forms a dimer composed of an α- and a β-subunit, which was proven in *Arabidopsis thaliana* by several techniques, yeast two hybrid (Y2H), bimolecular fluorescence complementation (BiFC), and co-immunoprecipitation [362].

The β-subunit of the NAC complex was selected for

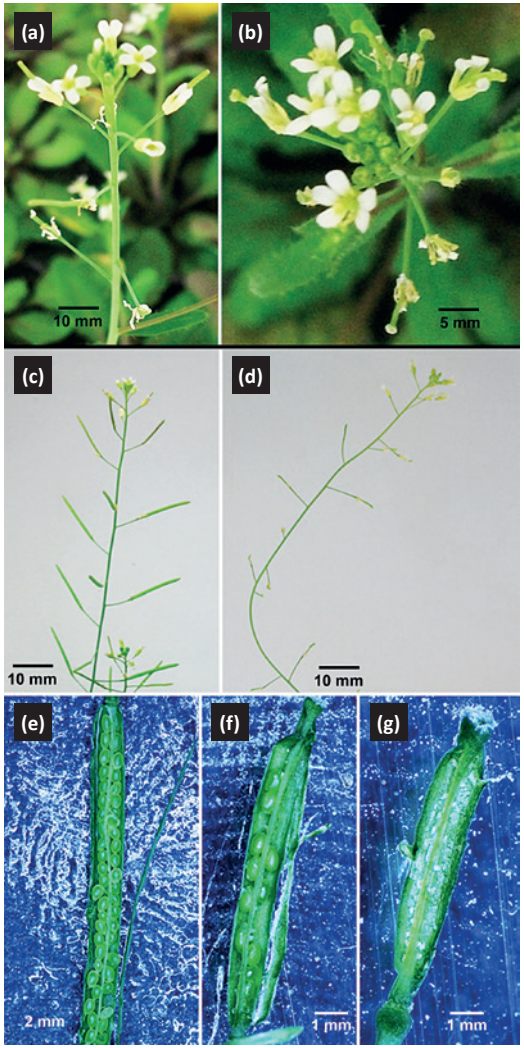

Figure 3. Phenotypic traits of the nacβ1nacβ2 mutants. **(a)** Col-0 wt inflorescence with normal-looking flowers. **(b)** *nacβ1nacβ2* inflorescence with flowers containing an abnormal number of floral organs. **(c)** Col-0 wt siliques of a normal size with a normal seed set. **(d)** *nacβ1nacβ2* siliques, which were significantly shorter. **(e)** Col-0 wt seeds inside unripe silique, most of the seeds are normal-sized and green. **(f)** *nacβ1nacβ2* seeds inside the silique of less severe phenotype, several normal-sized and green seeds are combined with aborted seeds. **(g)** *nacβ1nacβ2* seeds inside the silique of more severe phenotype where most seeds are aborted.

detailed experiments, and we studied a double NACβ homozygous mutant (*nacβ1nacβ2*). The *nacβ1nacβ2* plants were delayed in their development and their total chlorophyll content was notably lower. *nacβ1nacβ2* flowers carried an abnormal number of flower organs and produced significantly shorter siliques carrying less seeds. Our data collectively showed that both gametophytes were affected in the *nacβ1nacβ2* mutant, possibly together with the sporophyte tissues inside the flowers. NACβ localization to nuclei and cytoplasm supports the NAC role during translation. Furthermore, nine other cytoplasmatic chaperones with their role in *de novo* protein folding were present in the NACβ interactome, highlighting its role in translation and protein folding. [362].

Pollen secretomics and male-female cross-talk

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 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, University of Arizona, USA. As a joint effort with Z. Zdráhal's group (CEITEC MU, Brno), we performed gel-free LC-MS/MS for high throughput analysis of pollen-tube-secreted proteins [535]. Among them are pollen tube-secreted ligands and receptor proteins representing potential male components in perceiving ovule-emitted cues for guidance. 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, arabinogalactans, pectinases, and invertases. The pollen tube secretome was comprised vastly of a 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 (Hafidh *et al.* 2016, Genome Biol 17: 81). Our broader analyses of secretomes of *in vitro* grown pollen tubes from *Amborella*, maize, and tobacco, performed in collaboration with T. Dresselhaus, University of Regensburg, also identified novel small secreted peptides (Flores-Tornero *et al.* 2021, Plant Reprod 34: 47-60). The link between pollen tube sequestrome with the secretome is currently being evaluated.

Recently, we demonstrated the role of pre-mRNA splicing in cell-to-cell communication before double fertilization. We reported a novel function of Pre-mRNA PROCESSING factor 8 paralogs, PRP8A and PRP8B, as regulators of pollen tube attraction. Double mutant *prp8a/prp8b* ovules cannot attract pollen tubes, and *prp8a/prp8b* pollen tubes fail to sense the ovule's attraction signals. Differential exon usage and intron retention analysis revealed autoregulation of PPR8A/PRP8B splicing that facilitates pollen tube attraction via transcriptional regulation of MYB98, CRPs, and LURE pollen tube attractants [407].

DNA repair and chromosome maintenance

One of the early reactions of plants to high levels of NaCl is the generation of reactive oxygen species (ROS). Using the moss *Physcomitrium patens* we tested ROS generation and DNA degradation and showed that toxic NaCl concentrations significantly stimulate ROS production, which affects the DNA stability in a ROS-dependent manner, increasing both single (SSBs) and double (DSBs) strand DNA breaks. Surprisingly, DSBs were induced by NaCl to a lesser extent than SSBs. This is indicative of an unexpected action of NaCl on the moss genome, including induction of DSBs as

a consequence of initiated Programmed Cell Death and SSBs by hydroxyl radical-induced DNA oxidation. The research was a collaboration with V. Demidchik, BSU, Minsk, Belarus [517].

Based on previous results with J. Fajkus, CEITEC, MU Brno, we extended our interest to the roles of RAD51 and its antagonist, RTEL1, in the moss *P. patens*. In corresponding mutants, we confirmed their antagonic action in the maintenance of telomeres and rDNA, and the repair of DSBs, but not their sensitivity to DNA damage, induced by genotoxins with various modes of action. In cooperation with A. Cuming, CPS, Leeds, UK, we isolated and characterized a mutant of the *P. patens PpSOL* (SogOneLike) gene, which is a functional orthologue of a key transcription factor regulating numerous genes involved in DSB repair *AtSOG1* [174].

DNA damage generally compromises genome integrity and cell viability. However, transient induction of SSB and DSB in *P. patens* moss triggers the reprogramming of differentiated leaf cells into stem cells without cell death. After intact leaf shoots are induced by DNA breakage, some cells subsequently begin to grow at the tip and undergo asymmetric cell division to form apical chloronema stem cells and further development. We participated in this research by M. Hasabe, NIBB, Okazaki, Japan by detecting DNA breaks using the Comet assay [372].

In collaboration with J. Paleček, MU, Brno, we study the interplay within SMC5/6 complex and associated NSE1-6 components. *SMC6* and *NSE4* are essential genes of the complex, and even a slight reduction of transcript levels by dCas9 binding was enough to obtain stable lines with severe DSB repair defects and specific bleomycin sensitivity. Survival after DNA damage treatment fully depends on active SMC6, whereas attenuation of NSE4 has little or a negligible effect. Thus, circularization of SMC5/6 provided by the kleisin NSE4 is indispensable for DSB repair (Holá *et al.* 2021, Plant Mol Biol, doi: 10.1007/s11103-020-01115-7).

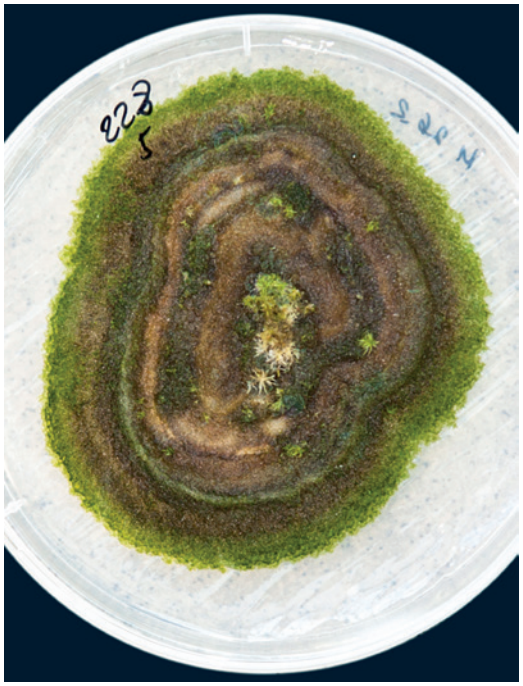

Figure 4. Annular growth of the *Physcomitrella* (*Physcomitrium patens*) line 228-5 with 50% RNAi attenuated transcription of *PpSMC6* giving the impression of a Bingham Canyon, Utah, copper mine.

In collaboration with P. Procházková Schrumpfová and J. Fajkus (CEITEC-MU Brno), we showed that *Arabidopsis* Pontin and Reptin homologues, RuvBL1 and RuvBL2a, colocalize with TERT and Telomere Repeat Binding (TRB) proteins in vivo and participate in telomerase biogenesis. Our results provide an insight into the composition and architecture of the plant telomerase complex [276].

Brief list of national and international collaborators

Dr. C. Bousquet-Antonelli, INRA Perpignan, France; Dr. P. Chaturvedi and Prof. W. Weckwerth, University of Vienna, Austria; Dr. A. Cuming, CPS, University of Leeds, UK; Prof. V. Demidchik, Belarusian State University, Minsk, Belarus; Dr. P. Doerner, University of Edinburgh, UK; Prof. T. Dresselhaus, University of Regensburg, Germany; Prof. J. Fajkus, Assoc. Prof. M. Fojtová, Assoc. Prof. J. Paleček, Dr. P. Procházková Schrumpfová, and Prof. Z. Zdráhal, CEITEC MU, Brno, Czech Republic; Drs. M. and I. Falk, and Dr. E. Sýkorová, IBP CAS, Brno, Czech Republic; Prof. U. Grossniklaus, University of Zurich, Switzerland; Prof. M. Hasabe, National Institute for Basic Biology, Okazaki, Japan; Prof. M. Johnson, Brown University, USA; Dr. C. Lafon Placette, Charles University, Prague, Czech Republic; Dr. Y. Leshem, MIGAL, Kiryat Shemona, Israel; Prof. A. A. Levy, WIS, Rehovot, Israel; Dr. J. Matoušek, Biological Center CAS, České Budějovice, Czech Republic; Dr. A. Matros, University of Adelaide, Australia; Dr. H.-P. Mock, IPK Gatersleben, Germany; Assoc. Prof. M. Mutwill, Nanyang Technological University, Singapore; Dr. F. Nogue, INRA Versailles, France; Prof. R. Palanivelu, University of Arizona, Tucson, AZ, USA; Prof. S.-K. Park, Kyungpook National University, Daegu, Korea; Dr. R. Peiman-Zahedi, ISAS Dortmund, Germany; Prof. H. Puchta, KIT Karlsruhe, Germany; Prof. E. Schleiff and Dr. Sotirios Fragkostefanakis, Goethe University Frankfurt a/Main, Germany; Prof. G. Steger, Heinrich-Heine-Universität Düsseldorf, Germany; Prof. D. Twell, University of Leicester, UK.

Research projects: 11, 16, 38–39, 41, 43, 53–54, 63, 73, 82, 85, 93, 97–98, 102–103


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Laboratory of Signal Transduction

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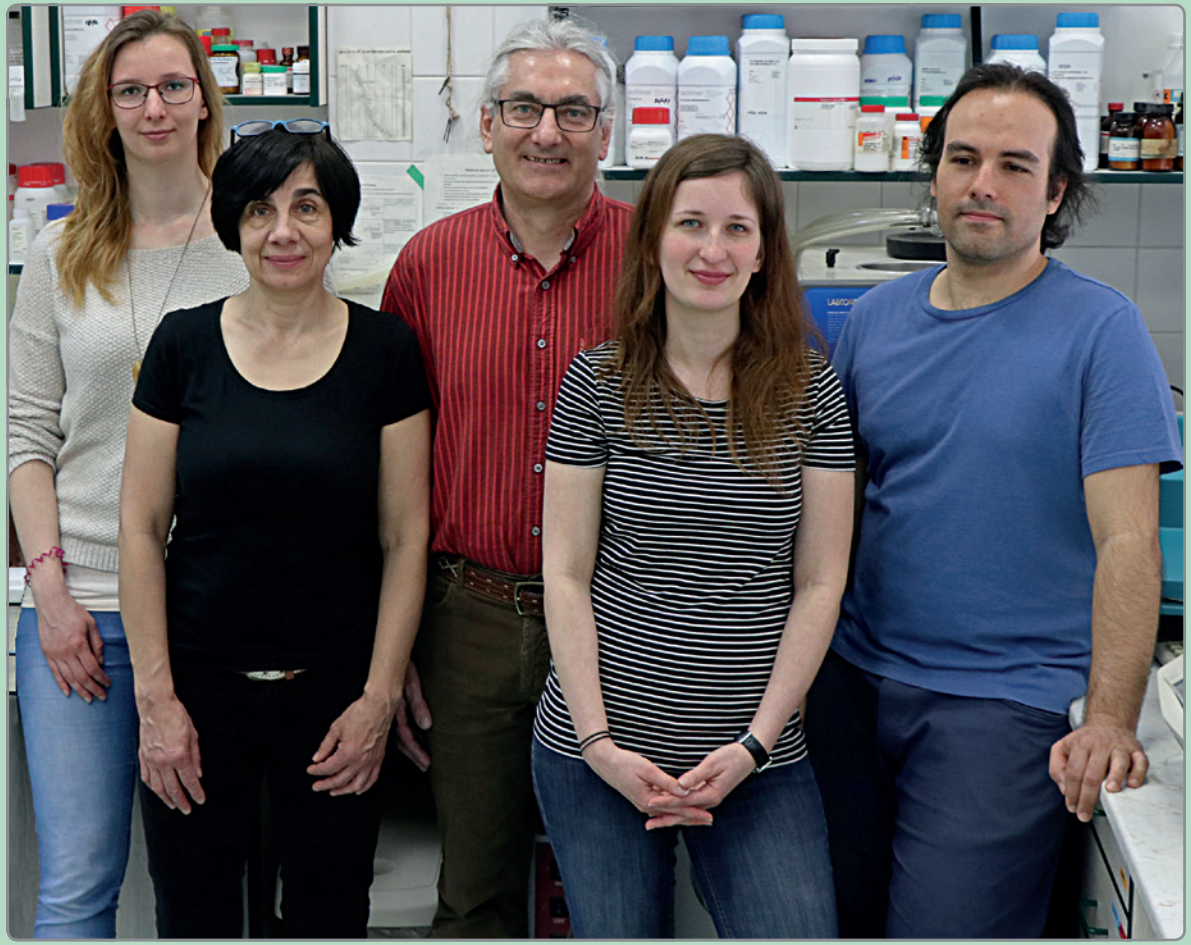
The Laboratory of Signal Transduction has been focused on developmental and stress signalling in *Arabidopsis thaliana*. Currently, the main areas of study are the roles of phospholipase D and non-specific phospholipase C protein family and flotillins in plant development and stress responses.

Phospholipase D (PLD) and non-specific phospholipase C (NPC) catalyse the hydrolysis of structural phosphoglycerolipids such as phosphatidylcholine (PC) to generate second messengers such as phosphatidic acid (PA) or diacylglycerol (DAG). Both PLD and NPC (called PC-PLC in animals) are well-known signalling proteins in animal signal transduction. However, until 2005, there was no information on the role of NPCs in plants at the gene level. In contrast, the plant PLD protein family has been characterised as an important player in plant development and stress responses.

In the years 2018–2020, we continued our series of earlier articles relating to NPCs. In an article from 2018, we reported on the role of NPC2 in the response of *Arabidopsis thaliana* to bacteria attack. NPC2 was experimentally characterised for the first time (**Fig. 1**) [61]. Heterologously expressed NPC2 possessed phospholipase C activity and was capable



In the picture (from left to right):
Mgr. Kristýna Kroumanová / research assistant, Kateřina Vltavská / technician, RNDr. Jan Martinec, CSc. / head of the laboratory, Ing. Tereza Podmanická / research assistant, Mgr. Michal Daněk, Ph.D. / postdoc.

Not pictured:
Ing. Daniela Kocourková, Ph.D. / research assistant.

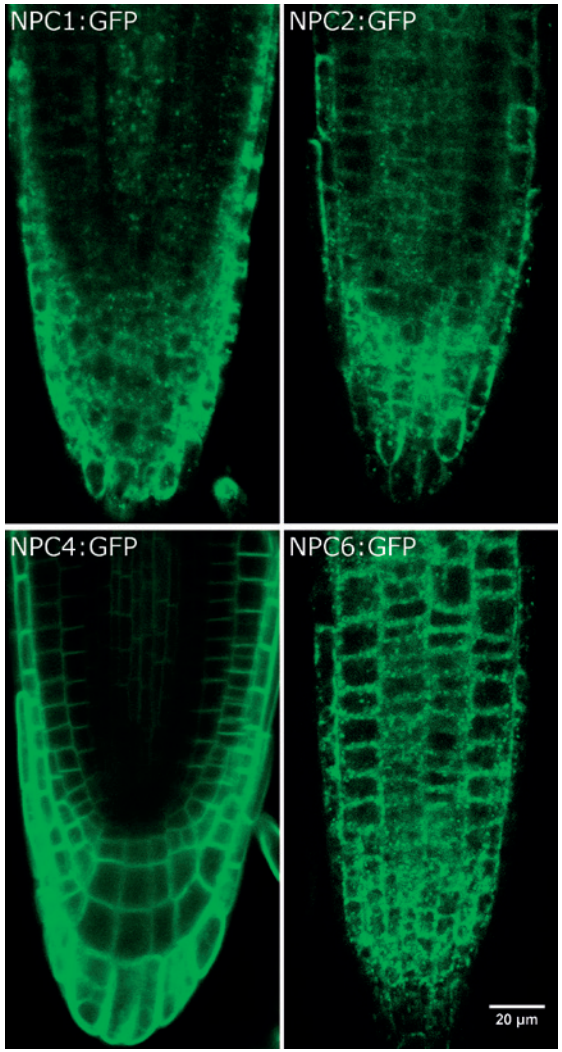


Figure 1. Individual non-specific phospholipase C isoforms exhibit distinct subcellular localisation in *Arabidopsis thaliana* seedling roots.

of hydrolysing phosphatidylcholine to diacylglycerol. GFP-tagged NPC2 was predominantly localised to the Golgi apparatus in *Arabidopsis* roots. Transcription of NPC2 decreased substantially after infiltration of the plant with *Pseudomonas syringae*, treatments with the flagellin peptide flg22 and salicylic acid, and expression of the effector molecule AvrRpm1. The decrease in NPC2 transcript levels correlated with a decrease in NPC2 enzyme activity.

In the article by Kocourková *et al.* [395], we investigated the role of phospholipase Dα1 (PLDα1) in magnesium homeostasis. Intracellular Mg^{2+} levels are highly regulated, as Mg^{2+} deficiency or excess affects normal plant growth and development. In *Arabidopsis*, we found that PLDα1 is involved in the stress response to high magnesium levels. The T-DNA insertion mutant *pldα1* was hypersensitive to elevated magnesium levels and showed reduced primary root length and fresh weight (**Fig. 2**). PLDα1 activity increased rapidly after high-Mg^{2+} treatment, and this increase was found to be dose-dependent. Two lines harbouring mutations in the HKD motif, which is essential for *PLDα1* activity, displayed the same high-Mg^{2+} hypersensitivity as *pldα1* plants. Furthermore, we showed that high concentrations of Mg^{2+} disrupt K^+ homeostasis and that transcription of the K+ homeostasis-related genes CIPK9 and HAK5 was impaired in *pldα1*. In addition, we found that the *akt1*, *hak5* double mutant is hypersensitive to high-Mg^{2+}. Thus, we conclude that in *Arabidopsis*, PLDα1 enzyme activity is vital in response to high-Mg^{2+} conditions and that PLDα1 mediates this response in part by regulating K^+ homeostasis.

In addition to the phospholipase study, we studied the role of flotillins in stress responses and development. The flotillin protein family are well-known membrane domain-forming proteins that remain poorly understood in plants. We screened knockout flotillin

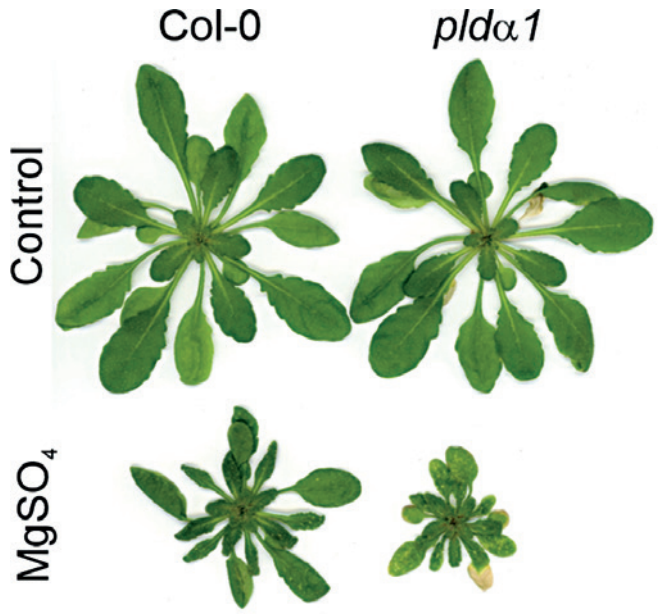


Figure 2. Knockout mutant of PLDα1 (*pldα1*) is hypersensitive to high external level of Mg^{2+}. Wild-type (Col-0) and *pldα1* plants were grown hydroponically for 3 weeks in half-strength Hoagland's media, followed by 10 days with or without 10 mM $MgSO_4$.

mutants for phenotype alteration in response to stresses [213]. To uncover the mode of action of flotillin, we identified FLOT2-interacting partners in the plasma membrane of *Arabidopsis* [52]. Finally, we showed that the cell wall contributes to the stability of the plasma membrane nanodomain organisation of *Arabidopsis* FLOT2 and HYPERSENSITIVE INDUCED REACTION1 proteins (**Fig. 3**) [347].

Another joint project with the Laboratory of Pathological Plant Physiology and the University of Chemistry

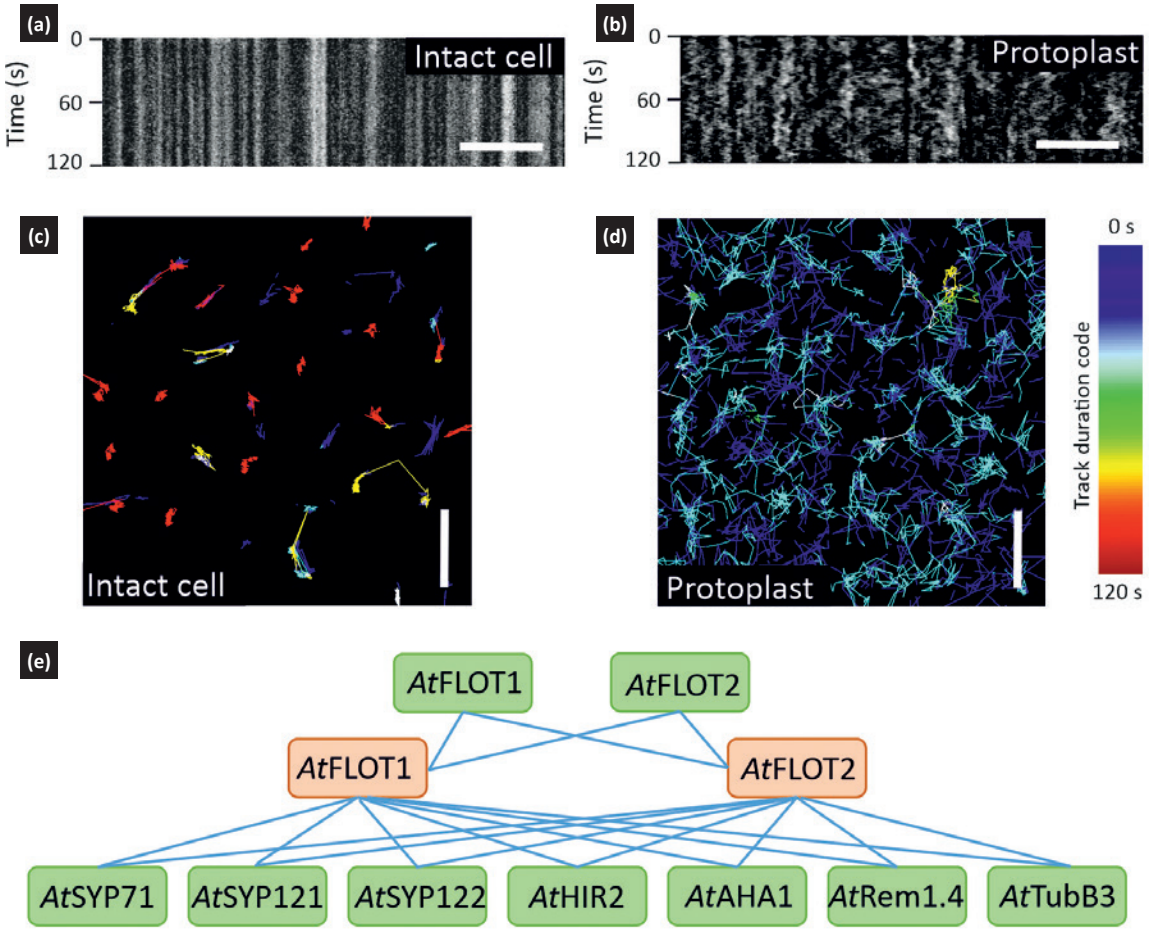


Figure 3. *Arabidopsis thaliana* FLOTILLIN 2 (*At*FLOT2) is localised in plasma membrane nanodomains stabilised by cell wall. In intact cells, *At*FLOT2-GFP nanodomains exhibit very low lateral dynamics, as shown on kymograms **(a)** and single nanodomain tracking **(c)**. Upon cell wall removal, i.e. in protoplasts, lateral mobility of the microdomain increases **(b, d)**. The kymograms and individual nanodomain tracks were constructed from time-lapse acquisitions (120 frames with acquisition interval = 1 s) obtained at the surface focal plane imaging the plasma membrane. Restricted lateral mobility of single nanodomains appears as vertical lines on kymograms in an intact cell, whereas the signal in protoplast kymograms is less steady and less connected over time. Individual trajectories in **(c)** are constrained in smaller areas and stay connected over a longer period of time, while in **(d)**, the trajectories are longer, although they last for a shorter period (color-coded). *At*FLOT1 and *At*FLOT2 share several direct membrane-associated protein interactors identified using yeast split-ubiquitin system (e). *At*FLOT1 or *At*FLOT2 were tested as bait (fused to Cub moiety, red boxes) with prey proteins (fused to Nub moiety, green boxes). The presented interactors are involved in plant-pathogen interactions, growth, intracellular trafficking, etc., which implicates the involvement of *At*FLOTs in such processes. Scale bars: 5 µm **(a, b)** and 1 µm **(c, d)**.

and Technology, Prague, deals with the effect of noble metal nanoparticles. The main objective of this study was to evaluate the potential hazard of this little-studied group of metal nanoparticles to the environment. Round-shaped gold nanoparticles had a direct but minor effect on the root development of *in vitro* grown *Arabidopsis* plants [121].

In addition to working on NPCs, PLDs, and flotillins, we are participating in many other research projects based on collaborations with other teams, both within the Institute of Experimental Botany and from other institutes and universities in the Czech Republic. Within the institute we have been collaborating with the Laboratory of Pathological Plant Physiology for a long time [52, 188, 198, 213, 263]. We also collaborate with the Laboratory of Cell Biology and with the Laboratory of Hormonal Regulations in Plants [213, 347, 395]. Finally, we have a long-standing collaboration with the research group of Prof. Olga Valentová from the University of Chemistry and Technology, Prague [52, 61, 188, 198, 213, 263, 347].

At the international level, we also have a long-standing collaboration with the research group of Dr. Eric Ruelland from Université de Technologie de Compiègne, France [106, 198] and with the group of Dr. Volodymyr Kravets from the Institute of Bioorganic Chemistry and Petrochemistry, National Academy of Sciences of Ukraine [61, 106, 162, 198, 263]. In addition, we have established a new collaboration with a group led by Dr. Agnieszka Sirko from the Institute of Biochemistry and Biophysics, Polish Academy of Sciences, Poland, working on plant autophagy.

Research projects: 3, 11, 25, 27, 95


KONTROLA

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The research of the Laboratory of Virology is focused on several partially interconnected topics. The main factor shaping our focus in this period was the availability of funding sources. The main research topic of our laboratory is to use the potential of plants to produce valuable proteins for use in diagnostics and medicine. For this purpose, we use either modified plant viruses (viral vectors) or permanent plant transformations, using the plant pathogen Agrobacterium tumefaciens. Another topic is the detection and diagnosis of viral plant diseases and the biotechnological preparation of diagnostic enzymes. Since the summer of 2018, our laboratory has been participating in research at Centrum ExBio, a five-year program of the Ministry of Education, Youth and Sports, which aims to study both unwanted signals and synergies between climate change stresses and biotic stressors, including viruses.

In the picture (from left to right):
PharmDr. Zuzana Pobořilová, Ph.D. / postdoc, Bc. Radek Vítek / M.Sc. student, Lenka Kolčabová / technician, RNDr. Oldřich Navrátil, CSc. / researcher, Mgr. Hana Hoffmeisterová, Ph.D. / researcher, doc. RNDr. Noemi Čerovská, CSc. / researcher, Mgr. Jan Fousek, Ph.D. / technician, Ing. Jakub Dušek / Ph.D. student, Ing. Jitka Svobodová / technician, Mgr. Tomáš Moravec, Ph.D. / head of the laboratory.

Not pictured:
Ing. Jiban Kumar, Ph.D., Dr.rer.nat. Ing. Helena Plchová / researchers, RNDr. Naďa Wilhelmová, CSc. / retired researcher, Mgr. Kateřina Kratochvílová / Ph.D. student (maternity leave).

Expression of valuable proteins in plants

As a part of the transient expression of valuable proteins in plants, we arranged infectious clones of several full-length plant viruses – Bean Yellow Dwarf Virus, Tobacco Mosaic Virus, strains U1 and Cg8 (for effective *Arabidopsis thaliana* infection), Potato Virus X, Tobacco Rattle Virus, and Apple Latent Spherical Virus (ALSV) – to the GoldenBraid (GB) system. Conversion to the GB standard makes it much easier to reverse the genetic system of these viruses; deleting or replacing a gene in the viral genome is simple and straightforward. This allowed us to create more complex genetic constructs for metabolic engineering and gene editing, as well as replicative geminiviral vectors. This work resulted in two publications [355, 457].

Quick diagnostics

In addition to the expression of pharmaceutical proteins in plants, we are also interested in the diagnosis of viral diseases. Early diagnosis of a viral infection can prevent major economic losses. Modern diagnostic methods based on the detection of the viral genome (RNA, DNA) are sensitive and accurate. However, they can only be performed in centralized certified laboratories, which are usually far from the field, so most of the suspect plant material never gets properly analyzed. We are working on the development of specific methods that can be performed either directly in the field or in its vicinity without specialized equipment. The method we use is called LAMP (Loop-mediated isothermal AMPlification). Instead of a demanding thermal cycler, a thermal cell can be used, and there is no need to isolate viral RNA from a leaf sample with expensive kits. The results are available in approximately 30 minutes.

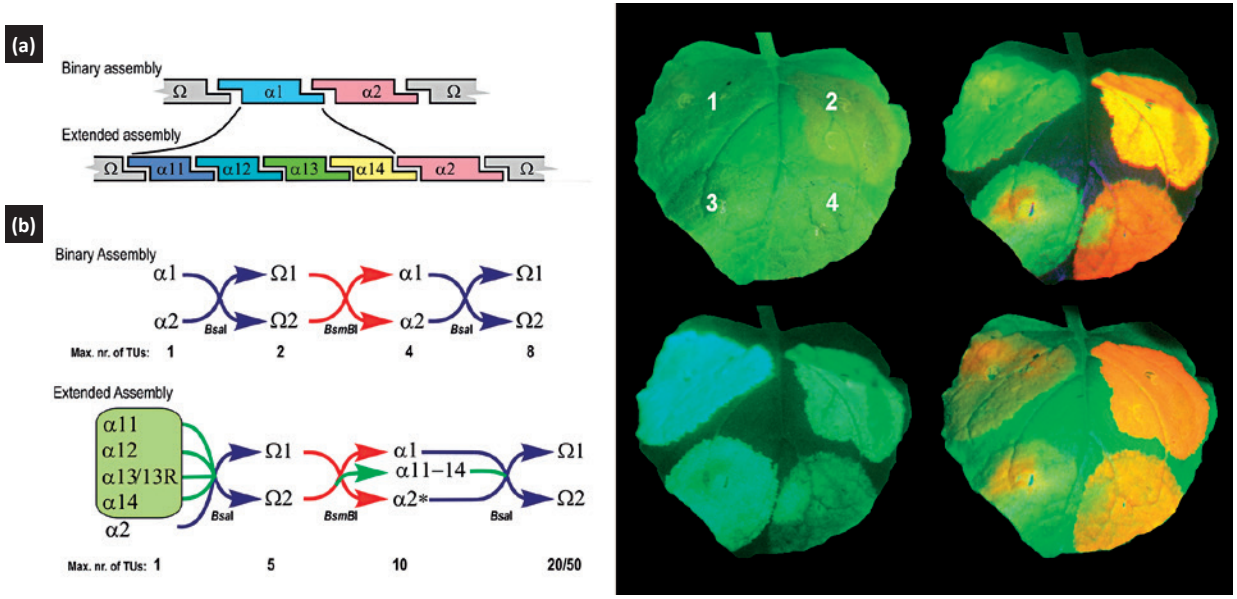

Figure 1. Left panel: Schematic representation of the original and extended GoldenBraid procedure. **(a)** In the extended assembly, the original plasmid α1 is replaced by 4 new α-plasmids. Plasmids at the Ω level are compatible with the new method. **(b)** Example of a classical binary GoldenBraid assembly versus an extended assembly with the maximum possible number of assembled transcription units [355; Sarrion-Perdigones *et al.* 2013, Plant Physiol 162: 1618-1631]. **Right panel:** Expression of two fluorescent reporters – green and red fluorescent proteins – in *Nicotiana benthamiana* leaves. Example of various combinations created using the advanced GoldenBraid method.

Influence of temperature stress on infection with plant viruses

Our research looked at whether heat shock applied before or after inoculation with Potato virus Y (PVY^{NTN} strain) affects virus multiplication in tobacco plants. Both routes of administration initially increased some isoforms of heat-shock protein 70 (HSP70) and thus facilitated virus propagation. However, some HSP70 isoforms that are induced by salicylic acid did not appear until the presence of viral RNA and viral proteins. Thus, some isoforms of HSP70 could be a part of the plant's defence responses against viral infection. This part of the research is summarized in two publications (Hýsková *et al.* 2021, Plant Biol 23: 131-141; Hýsková *et al.* 2021, Biol Plant 65: 68-79).

Foreign and domestic cooperation

The laboratory continues to work with the laboratory of Professor Ed Rybicki of the University of Cape Town, South Africa, which has resulted in joint publications. Exchange internships were not carried out due to the pandemic situation.

We also cooperate with the Crop Research Institute in Ruzyně, Prague (Dr. Jiban Kumar) and with the teams of Assoc. Prof. Lukáš Fischer and Assoc. Prof. Helena Ryšlavá from the Faculty of Science, Charles University in Prague.

Research projects: 11, 104, 111, 114

Station of Apple Breeding for Disease Resistance

Head of the laboratory:

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The station continues a long-standing tradition in breeding apple varieties resistant to scab (*Venturia inaequalis*), powdery mildew (*Podosphaera leucotricha*), and fireblight (*Erwinia amylovora*), the most widespread and harmful apple diseases. Selected IEB apple varieties find global use in organic or integrated management as well as in home gardens under conditions of concluded license agreements. The varieties are protected by Plant Variety Rights, Plant Patents, or by other plant breeding rights all over the world. The application of new varieties in practice significantly contributes to environmental and economic goals, consisting of the production of healthy fruits and a decrease in environmental load by reducing pesticides, while saving on the cost of chemical protection, which is reflected by the increasing competitiveness and profitability of the fruit growing sector. The high potential for result implementation of applied research into practice is the main domain of the world-renowned apple breeding program, from which more than 1.35 million IEB apple trees are sold worldwide per year.

In the picture (from the left):
Zdeněk Haleš, DiS. / technical assistant, Ing. Miloslav Juříček, Ph.D. / researcher, Ing. Jan Zima / graduated technical assistant, Sunee Kertbundit, Ph.D. / researcher, RNDr. Dimitrij Tyč, Ph.D. / researcher, Mgr. Veronika Janečková / graduated technical assistant, Ing. Radek Černý, Ph.D. / head of the team, Zdeněk Mikula / technical assistant, Květoslava Rabochová / technician, Dagmar Švestková / technician, Ing. Zuzana Krčková, Ph.D. / researcher.

Not pictured:
Ing. Otto Louda / graduated technical assistant.

The fungus *Venturia inaequalis* usually harms the host by making grey-black scabs on leaves and fruits. The tree is thus insufficiently nourished and the resulting damaged fruits cannot be commercially used.

The resistance to scab in some apple varieties is most often conditioned by a single gene, *Rvi6*. The first source of scab resistance was found in crab apple *Malus floribunda*, and since then it has been commonly used in breeding. The *Rvi6* gene can be transferred to the progeny simply by crossing; its presence in offspring can be evidenced by means of molecular markers. By repeated crossing for many generations, we managed to combine resistance against diseases with growing/bearing characteristics and fruit qualities to fulfil the properties required by growers and consumers.

Monogenic resistance is usually not stable in nature – in some locations it has already been overcome by new races of the fungus. Therefore, the IEB breeding program has been focused for decades on searching for new genetic sources of protection against scab by the breeding of apple varieties with a stable resistance

based on a combination of a monogenic and a polygenic basis. As new fungus races will always find ways to adapt and overcome plant defenses, the process of breeding is literally a never-ending job.

Thus, in our basic research, we are interested in the elucidating of the elemental mechanisms of the polygenic or *Riv6* gene's mediated resistance, as well as its breakdown. The completion of the second draft of the genome sequence of *Malus × domestica* 'Golden Delicious' double haploid genome (GDDH), as well as rapid advances in the next generation sequencing (NGS) technology, gave us very promising tools for studying plant pathogen interactions in difficult, non-model species such as the apple tree.

In the past, we have managed a method, developed in-house, of artificial infection by different conidia isolates allowing the monitoring of the host plant response in detail by performing a full quantitative transcriptome sequencing. We have found a great difference in gene expressions between apple cells challenged with different *Venturia isolates* (**Fig. 1**). Particularly noticeable was the enormous increase in GDSL esterase/lipase gene expression in infected plants, confirming the findings in rice that constitutive expression of GDSL esterase/lipase isoforms negatively modulates plant immunity.

On the opposite side, the most down-regulated gene expressions were found for LRR receptor-like serine threonine kinases. This disease resistance gene (R-gene) is involved in the detection of various pathogens.

The up- or down-regulated expression of these genes was also confirmed by qPCR. Their role in the defense mechanisms is now being investigated by agro-transformation to apple cells (**Fig. 2**) and their influence on scab infection.

An efficient use of the polygenic resistance in apple breeding requires the developing of reliable genetic markers. Therefore, we employed a recently published software using an apple transcriptomes approach for polymorphic SSR mining. So far, we have identified 6,742 SSR markers; 433 were found to be polymorphic.

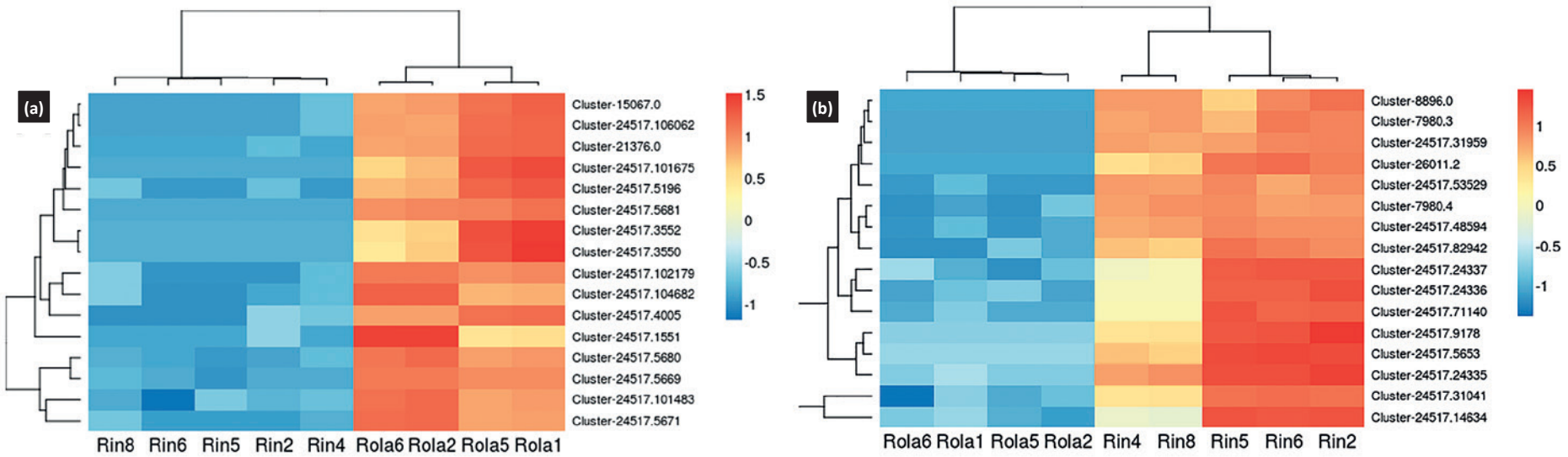

Figure 1. Relative heatmaps showing top 16 differentially upregulated genes **(a)** or downregulated genes **(b)** in the apple variety Ametyst after inoculation with *Venturia inaequalis* conidia races that can (Rola) or cannot (Rin) break *Rvi6* mediated scab resistance.

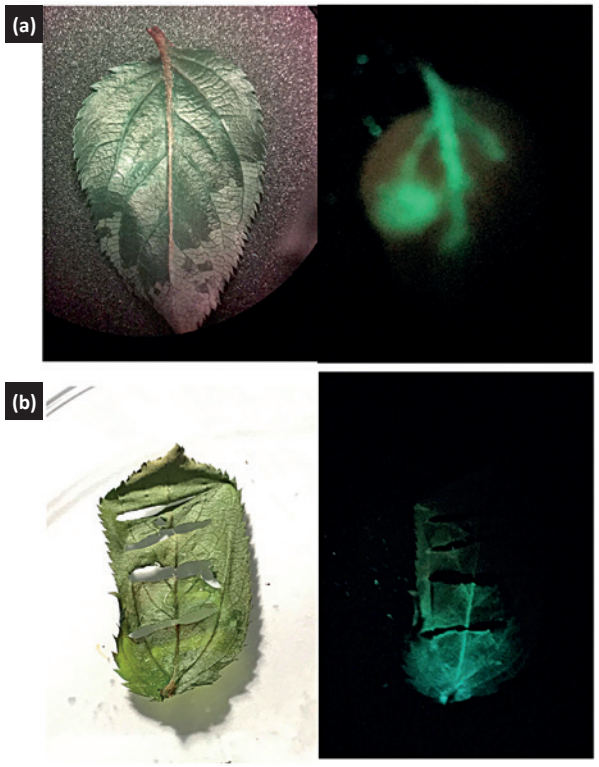

Figure 2. Agro-infection of apple cells. Green fluorescent protein is used as a reporter gene. The apple is known to be rather resilient to agro-infection.

About 20 of them were preliminarily designed for validation. The screening will continue with more apple transcriptomes and/or more precise apple transcriptomes that will be assembled. This approach, together with new resistance genes introgression, is also being applied for other important diseases like fireblight and powdery mildew.

Powdery mildew (*Podosphaera leucotricha*) occurs particularly in dry localities. The main symptoms are a whitish coating on the shoots and, indirectly, skin russeting on the fruits. That is why IEB apple newselections are subject to strict selection during testing under experimental field conditions for several years.

The third, but even more serious on a worldwide scale, is the bacterial disease fireblight (caused by *Erwinia amylovora*). It is manifested by the wilting and dying of flowers, the burning of leaves and fruits, and the drying and necrosis of vegetative shoots and branches. The consequences of attack are very destructive, often ending in the death of the entire tree. Fireblight is quite rare in the Czech Republic. However, it causes a serious economic loss in many important growing areas like the State of Washington (USA), South Tyrol (Italy), and Lake Constance (Germany). Chosen IEB newselections or varieties in an advance testing stage, showing the perspective of application in praxis, are therefore tested by the method of artificial shoot inoculation by pathogen in the international research cooperation with Agroscope Wädenswil (Switzerland) and the Julius Kühn-Institut (Germany).

Apart from disease resistance, new varieties must meet stringent growth requirements in order to be commercially successful. Among these requirements are growing characteristics, high and regular productivity, good storability, and fruit quality – like appear-

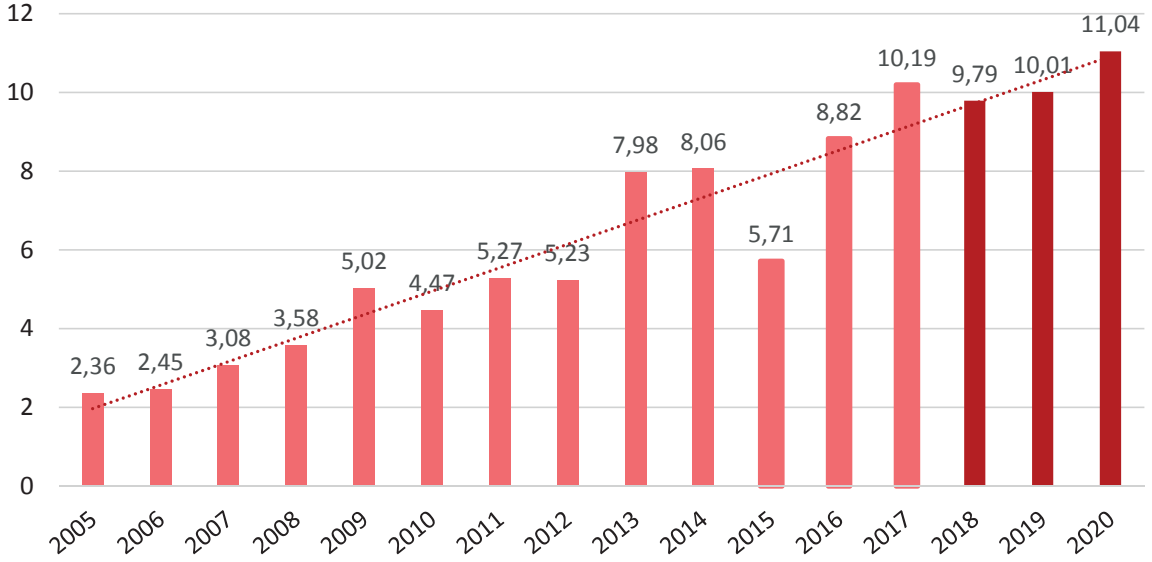

Figure 3. Income from royalties of licensed varieties of apple trees (millions of Czech crowns, CZK).

ance, flavour, firmness, the crispness and juiciness of the flesh, and durability during transfer or manipulation. Based on these aspects, chosen IEB newselections are tested in the Czech Republic, as well as in foreign research centres and by potential business partners such as nurseries, producers, and marketing companies. Commercially perspective varieties are legally protected by Community Plant Variety Rights in the EU and by the United States Plant Patent in the USA or by other plant breeding rights all over the world. In the period 2018–2020, the Station achieved 28 results of applied research, relating to 13 new IEB apple varieties. All concerned licensed varieties are traded on the market:

- 8 varieties achieved a breeding certificate of granting plant variety rights in the Czech Republic
- 1 variety achieved a national plant variety certificate in Switzerland
- 9 varieties achieved Community Plant Variety Rights in the European Union
- 8 varieties achieved a United States Plant Patent
- 1 variety achieved a Plant Patent in Ukraine
- 1 variety achieved a national breeding certificate in South Africa

These varieties are grown predominantly in organic orchards or eventually in an integrated production. Their propagation or sales are based on concluded license agreements. The great ability of the application of new IEB apple varieties in practice is demonstrated by the following in the evaluated period:

- 15 concluded license agreements (9 Czech and 6 international)
- almost 4 million trees of IEB apple varieties sold (worldwide)
- more than 30 million CZK of license income (see **Fig. 3**)

Figure 4. Demonstration of professional integrated planting of apple variety Opal® equipped with a necessary additional drip irrigation at Ralf Broetje farm in the State of Washington, USA.

One of the most commercially successful varieties of the IEB breeding program is Topaz, along with its mutation, Red Topaz. It is the most cultivated scab-resistant apple variety in the world, and at the same time, the most cultivated variety grown in organic growing conditions, planted in Europe on an area of approximately 2,000 ha, corresponding in practice to about 6 million planted trees. In the years 2018–2020, more than 1.25 million trees were sold under license all over the world. The variety is very often used worldwide as a valuable genetic source for further breeding.

Very popular, mainly in the USA, is the variety UEB 32642, known under the trademark Opal®, which is registered in more than 40 countries and is characterized by a bright yellow skin with crunchy flesh and an aromatic, sweet honey flavour. The growing of the Opal® variety is suitable mainly for warm, vineyard areas with additional irrigation. Opal® was introduced into the market according to a worldwide marketing concept managed by the companies Webfruit GmbH, Germany and Varieties International, USA. Approximately 740,000 trees were sold in the evaluated period. In total, more than 2.5 million Opal® trees have been sold worldwide, which corresponds to plantings in an area of approximately 850 ha (**Fig. 4**).

Another IEB apple variety with worldwide application is the Bonita variety. The variety name comes from Portuguese and means “pretty” or “beautiful”, which precisely represents the outstandingly attractive appearance of its bright red fruits. The variety is characterized by high and regular fruit productivity, good tree growth, and fruit quality, including a long storability. Bonita is protected in the EU, the USA, Switzerland, and South Africa. The variety is commercially applied

on the basis of an exclusive license agreement with Konsortium Südtiroler Baumschuler (KSB), Italy. This agreement allows for the control of the trademark, marketing, growing, propagation, and sales of trees and fruits. In the evaluated period, more than 600,000 Bonita trees were sold in many countries in the EU and South Africa. Since the variety was introduced on the market in 2015, more than 1.3 million Bonita trees have already been sold. Royalties were contractually agreed to be paid not only from trees sold, but also from fruits sold, i. e. from yields (**Fig. 5**).

Very advanced is a license application of the variety named UEB 6581, which will soon be distributed under trademark with a suitable fancy name. License rights for the propagation and sale of trees and trade with fruits were granted to KSB. In cooperation with the Italian sales organization Melinda, which brings together 4,000 growers, KSB set the spectacular goal of planting the variety on a remarkable area of 200 ha in the Italian region of Trentino. Although the variety was not introduced onto the market until 2018, almost 200,000 trees have already been sold

Figure 5. A professional orchard of apple variety Bonita in Vinschgau, Italy at an altitude exceeding 900 m above sea level.

Figure 6. An experimental planting of apple variety UEB 6581 in the fruit orchard of Ing. Pavel Voráček in Vlkov nad Lesy at the time of harvest in the 4th year after planting.

under license in two seasons. The fruits of UEB 6581 are characterized by an exceptionally sweet flavour, bringing to mind the tones of tropical fruit (**Fig. 6**).

Apart from dessert apple varieties, our program also includes the breeding of varieties with a compact columnar growth habit. As a result, the global marketing contract for scab-resistant varieties with this type of growth was concluded with the American company Varieties International LLC for the global territory. Released columnar varieties are legally protected in the EU and in the USA. This type of tree is suitable mainly for home gardens as a beautiful solitaire or for the planting of hedges. Columnar apple varieties may contribute to the return of fruit trees to smaller home gardens and allow for the observation of individual tree variability at the time of flowering and fruit formation, and in an interesting growth habit. In the evaluated period, almost 200,000 IEB apple trees with columnar growth were sold in selected EU countries. Considering the fact that they are usually sold in small numbers, we can find IEB columnar apple trees in tens to hundreds of thousands of home gardens.

In the evaluated period, IEB breeding was also focused on ornamental apple varieties with columnar growth intended for pollination purposes in intensively managed apple orchards. So far, there are no such apple varieties meant for pollination on the market. During the evaluated period, two new IEB apple varieties, named

Magenta (**Fig. 7**) and Lilac, were granted plant variety rights. They were introduced onto the market, and they have been subject to an advanced stage of testing, especially at Washington State University, USA.

The modernization of the IEB Station of Apple Breeding in Střížovice made it possible to start the year 2018 with the use of new breeding technologies, with the aim of making the selection process of the most promising newselections more efficient, faster, and more refined.

Figure 7. Ornamental apple variety Magenta with columnar growth type at the time of flowering, meant for pollination in apple orchards.

Figure 8. Demonstration of new experimental planting of apple newselections at the IEB Station in Střížovice.

A new greenhouse enables a pre-selection of plants after a previous intentional scab inoculation. Consequently, the team tests only the most resistant individuals in the field. Grafting those onto M9 rootstocks allows for the evaluating of the fruit characteristics of new varieties at the latest in the fourth year after crossing, or in the second year after planting. The construction of a new cold storage, including equipment with ULO technology (Ultra Low Oxygen), enables the research of optimal storing conditions for new varieties and at the same time, it preserves fruits at a good quality level for their promotion and presentation in organoleptic evaluations in the late spring. Moreover, a new support system with intensive tree planting was built in an experimental orchard (**Fig. 8**). Starting in 2021, the support system is expected to be supplemented by a drip irrigation in order to prevent drought risks and a top irrigation to prevent damage from late frosts, and there is also a possibility of the future installation of anti-hail nets.

Research projects: 11, 111–112

Additional figures of some apple varieties bred by the station: **1.** Apple variety named ´Barby´. **2.** Apple variety ´Ghiva´. **3.** Pilot planting of the variety ´Bonita´ in Research Centre Laimburg, Italy. **4.** Apple variety ´Telse´. **5.** Apple variety ´UEB 6581´. **6.** Promotion of the variety ´Bonita´ at Fruitlogistica 2020 international fair, Berlin, Germany. **7.** Harvest of the variety Opal® at Ralph Broetje farm, The State of Washington, USA. **8.** Experimental bio orchard of the variety ´Ghiva´ in Competence Centre for Fruit Growing, Bavendorf, Germany. **9.** Professional orchard of the variety Opal®, The State of Washington, USA. **10.** The sale of the variety Opal® in a Czech supermarket.


Bonita
FERTENIA
Dalla natura... alla natura
Rubelit
Bonita
UEB 6581


BROETJE
2014


AKCE Z LETÁKU
opal
36,90

Science Outreach

The institute actively promotes its work, and plant biology in general, among the Czech public of all ages. Public relations and science outreach are coordinated by three professionals:

- **Mgr. Jan Kolář, Ph.D.** (press releases, media relations, web pages for the public, social media, and other PR services),
- **Mgr. Markéta Fílová** (events, workshops, science club for young children, social media, web pages),
- **Ing. Radoslava Kvasničková** (PR services and events for the Centre of Plant Structural and Functional Genomics).

These specialists are assisted by a group of researchers and students who act as presenters at public events and help with event management. Many scientists and other employees also participate in the annual Open Door Days or give public lectures on various topics.

A complete list of our activities would be rather long; therefore we will just review some important examples.

Online communication

The institute's website has a section for journalists and the general public. Here we let them know about new discoveries, interesting research projects, upcoming events, media coverage of our work, etc. We also operate social media accounts on Facebook and Twitter that had approximately 4,600 and 1,000 followers, respectively, at the end of 2020.

Major events

We also participate in several annual events that promote public interest in science. The largest one is the Science and Technology Week, organized by the Czech Academy of Sciences (CAS). Our researchers contribute by presenting lectures and interactive exhibitions.

Figure 1. As a part of our day camp activities, children learn the basics of plant *in vitro* cultivation. Here they work in tissue culture hoods and sow seeds on sterile growth media.

During this week, the institute also holds its Open Door Days. School groups, university students, and individuals interested in plant biology visit our laboratories and get involved in hands-on activities. We attract about 1,000 visitors every year.

The Czech Academy of Sciences also organizes the Science Fair – a large three-day event at a fairground in Prague, which involves almost all CAS institutes. Our program typically features microscopes, (bio)chemical experiments, *in vitro* plants, and workshops where visitors can learn how to work with laboratory equipment.

Other annual activities include the Science Festival in Prague, the Researchers' Night in Olomouc, and Prague Museum Night. We also participate in the Fascination of Plants Day, held biennially by the European Plant Science Organisation.

Activities in Olomouc

Our Centre of Plant Structural and Functional Genomics is located in the city of Olomouc. The head of the centre, Professor Jaroslav Doležel, received the country's highest scientific award, the National Government Prize Česká hlava (meaning "Czech head") in 2018. The achievement had a broad media impact and greatly increased public recognition of plant biology.

This team from Olomouc is very active in science outreach. It coordinates the CAS programme Food for the Future, which has science communication as one of its main goals. Most importantly, the centre opened the Application Laboratory for Agricultural Research – the first facility in Czechia that enables a quick transfer of scientific knowledge to agricultural applications. This laboratory cooperates with breeders, seed producers, farmers, government agencies, and non-profit organizations.

The centre, as well as the Food for the Future programme that it coordinates, promote their work

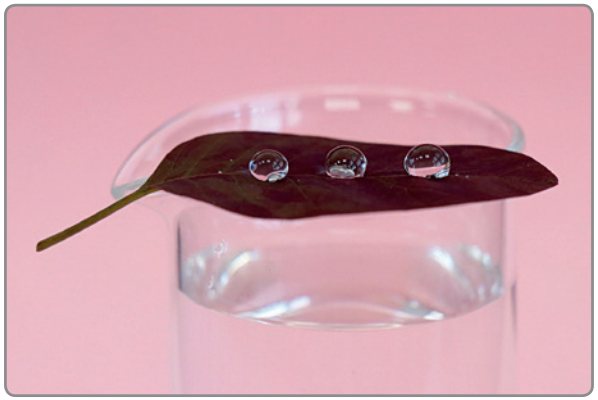

Figure 2. One of the "science-at-home" experiments that we published online during the covid-19 pandemic dealt with superhydrophobic properties of some leaf surfaces. The image shows water droplets on a smoke tree (*Cotinus coggygria*) leaf.

at several large events. These include Flora Olomouc, an exhibition of ornamental plants and crops, and Academia Film Olomouc, an international festival of science documentary films. In 2018, they organized a special section at this festival that addressed issues of sustainability, food production, and agriculture.

Our genomics facility also cooperates with Fort Science, an interactive science centre of Palacký University in Olomouc. Together they prepared a permanent exhibition which explains genetics, DNA, and related topics. Our scientists also participate in various events held at Fort Science. Science Camps for children that include visits to our laboratories are another joint project.

In 2019, the centre contributed to two exhibitions. Nature–Future showed efforts to preserve crop biodiversity and ensure sufficient food supply. It combined information about genomics with photographs by the Swiss author Mario del Curto. The exhibition Top Research in Public Interest took place in the Czech parliament and presented important CAS programmes to the lawmakers.

The scientists from Olomouc also give numerous public lectures and seminars and have authored an award-winning article series on plant genetics for a popular science magazine. Frequent topics of their lectures and texts are genetic modifications, gene editing, and the potential benefits of these technologies for breeding better crop varieties.

Science for the "youngest researchers"

In order to give children a direct, personal experience with science, we offer hands-on workshops in our laboratories. Their most popular topics are plant *in vitro* cultivation and light or fluorescent microscopy.

In 2017, we started a successful science club for children aged 6–12. Through hands-on activities, simple experiments, and games, they learn about plant biology in a playful way. Since 2020, the children of our employees have been able to participate in summer day camps where they work with lab equipment, grow plants, and enjoy sports activities.

Figure 3. The exhibition Nature–Future focused on the importance of gene banks, genomics and plant biology for the preservation of crop biodiversity and breeding of new crop varieties.

Figure 4. Young participants of a science camp visited our Olomouc laboratories in the summer of 2020.

Covid-19 pandemic

During the covid-19 pandemic in 2020, public events and group activities were banned or severely limited for many months. We therefore launched several online projects. When the pandemic hit Czechia in March, schools closed and switched to distance learning. At this time we started to publish instructions for simple experiments on our website so that children could try these experiments while they were at home during the lockdown.

We also organized online contests for both children and adults via our social media channels. The participants had to fulfil several tasks or answer questions. In the autumn, they made decorations from leaves and fruits. In the winter, they determined tree species according to their buds. These activities continued in 2021 during a further lockdown.

Journals

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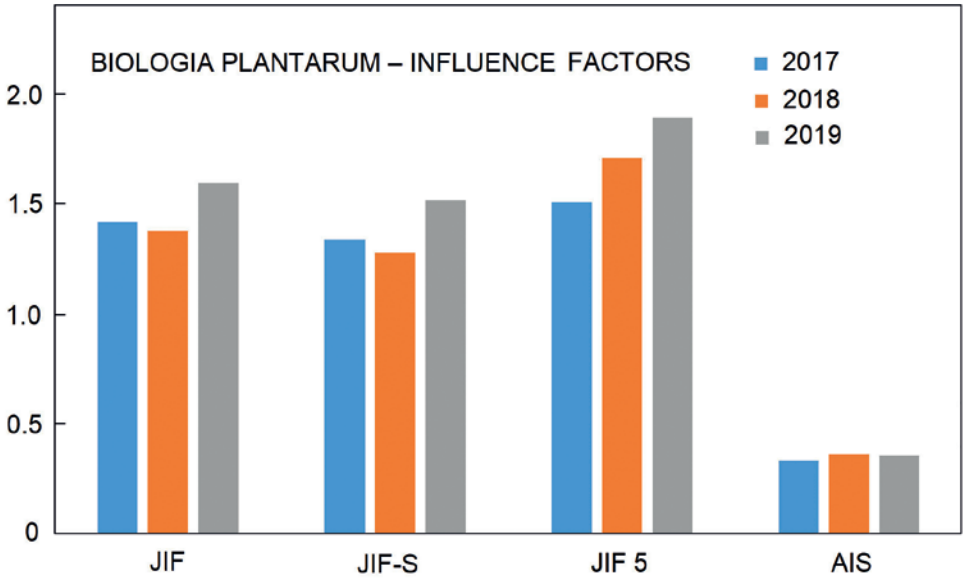
The Institute of Experimental Botany publishes two scientific journals, both with an impact factor. The journals were distributed by Springer Nature until the end of 2018, but since 2019, they have been published electronically in an open-science mode.



Biologia Plantarum, an international journal of experimental botany founded in 1959, publishes-- in English-- original scientific papers, reviews on specialized topics, brief communications and book reviews across all fields of plant physiology, plant biochemistry, and biophysics, physiological anatomy, ecophysiology, genetics, molecular biology, biotechnology, cell biology, evolution, and pathophysiology. The journal focuses on model and crop plants, as well as on under-investigated species.

Since 2019, *Biologia Plantarum* has been an open access journal. It is available only in its electronic online version on our website. All articles are open-access articles distributed under the terms of the Creative Commons BY-NC-ND License (creativecommons.org/licenses/by/4.0/). *Biologia Plantarum* is directed by an international Editorial Board.

In 2020 the journal published two special issues. The first Special Issue focused on gasotransmitters, gaseous signalling molecules (nitric oxide, hydrogen sulfide, and carbon monoxide), and their roles in plant developmental processes and plant responses to abiotic stresses. This issue consisted of six articles and was edited by Prof. Vijay Pratap Singh.

The second Special Issue, entitled "Festulolium – from nature to modern breeding", was compiled for the 100th anniversary of the first reported artificial crossing of fescues and ryegrasses and the development of the first artificial hybrid, later named Festulolium. The issue consisted of 14 articles and was edited by Assoc. Prof. David Kopecký and Prof. Arkadiusz Kosmala.

From 2021, the journal is going to implement many changes concerning the design of its articles, the improvement of information on the website, and the publication process.

Up until September 2020 the Editor-in-Chief was RNDr. Jana Pospíšilová, CSc., from the Institute of Experimental Botany, Czech Academy of Sciences. Since September 2020, the new Editor-in-Chief has been Dr. rer. nat. Ing. Helena Plchová, from the same institute.

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Photosynthetica publishes original scientific papers and brief communications, reviews on specialized topics, book reviews, and announcements and reports covering a wide range of photosynthesis research or research including photosynthetic parameters of both an experimental and theoretical nature, and dealing with physiology, biophysics, biochemistry, and molecular biology on one side and leaf optics, stress physiology, and ecology of photosynthesis on the other side.

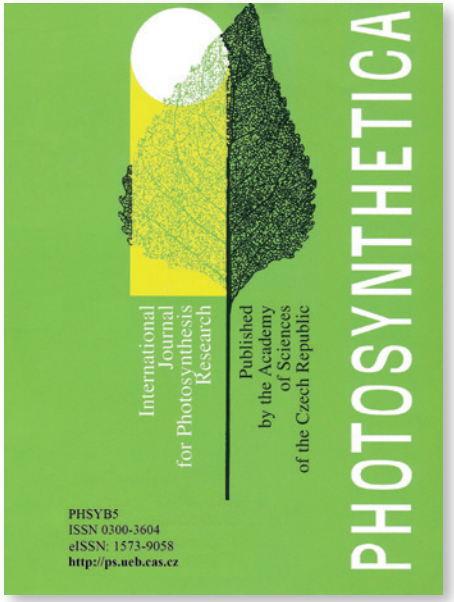
We are committed to the goals of open research; therefore, our journal publishes all research as Open Access. The articles are written in English. Four issues per year are produced.

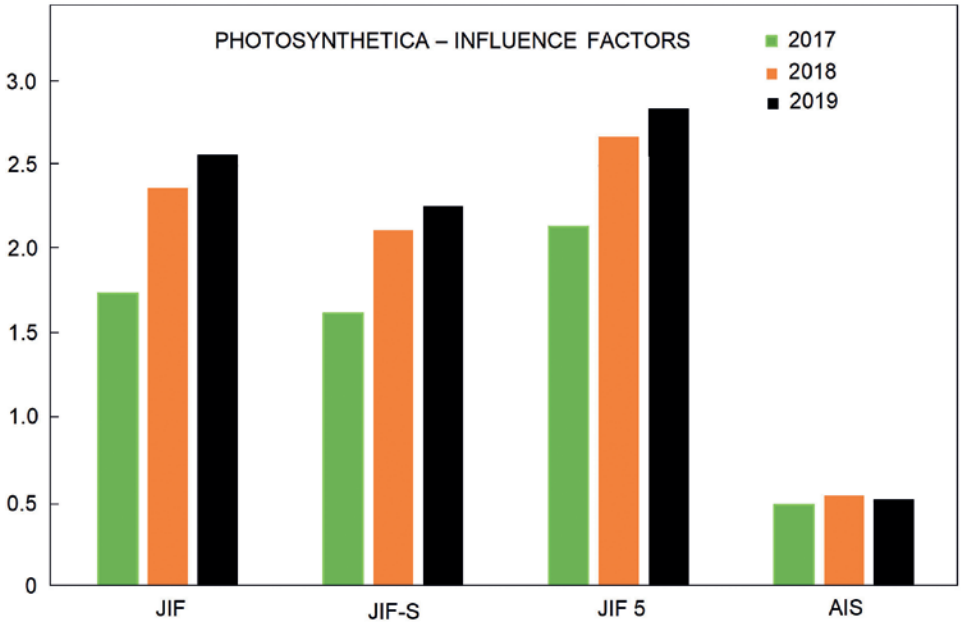
The publisher is the Institute of Experimental Botany, Czech Academy of Sciences. Springer Nature served as the distributor of the printed and electronic versions of the journal until the end of 2018. Since then, the journal has been published online only in an electronic version under the Open Access agreement. In 2019, the new Actavia online submission and review system was adopted.

Apart from four regular issues, special issues are also published. In 2018, a Special Issue in honour of Prof. Govindjee's 85th birthday was published under the guidance of a guest editor, Prof. Julian Eaton-Rye. In 2020, a Special Issue in honour of Prof. Reto J. Strasser's 75th birthday was produced under the guidance of Prof. H. Kalaji.

Changes in article design and content (e.g. interactive references) are slated to start in 2021.

Photosynthetica is directed by an international editorial board composed of Associated Editors. The Editor-in-Chief is RNDr. Helena Synková, CSc., from the Institute of Experimental Botany, Czech Academy of Sciences.





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Research Projects 2018–2020

1. ‘AEGILWHEAT‘-H2020-MSCA-IF-2016-746253, Widening the gene pool of bread wheat by interspecific variation from *Aegilops biuncialis* using advanced genetic and chromosome-genomic resourches and tools (AEGILWHEAT)
2. ‘COPE50‘-H2020-MSCA-IF-2016-747718, Global Climate change impact on phenOtype and ePigenomE stability: Accessing plant adaptability through a 2050 simulation model (COPE-50)
3. 7AMB17FR005, Role of plasma membrane microdomains and flotillins in the control of the dynamics of the IRT1 iron transporter in *Arabidopsis*
4. 7AMB17FR006, Selection of rhizobacterial communities associated with differences in plant resistance to pathogens
5. 8G15003, Uptake of engineered nanoparticles (ENPS) by plants and its implications for potential remediation of contaminated water and soil
6. 8J18AT020, Wheat with decreased coeliac reactivity
7. 8J19AT004, SIGNALS – The role of anionic phospholipids in the regulation of endocytosis in tip-growing plant cells
8. 8J19FR001, “ImmuneWall“ – plant immunity, cell wall and exocyst
9. 8J20FR032, Role of diacylglycerol kinases in the plant unfolded protein response
10. EF16_013/0001775, Modernization and support of research activities of the national infrastructure for biological and medical imaging Czech-BioImaging
11. EF16_019/0000738, Centre for Experimental Plant Biology
12. EF16_019/0000827, Plants as a tool for sustainable global development
13. EF18_046/0016045, Modernization of the National Infrastructure for Biological and Medical Imaging Czech-BioImaging
14. FV10599, Gels based on plant triterpenoid acids
15. GA15-24711S, Regulation of pollen tube growth by the exocyst vesicle-tethering complex: functions of multiple isoforms of the EXO70 exocyst subunit
16. GA16-01137S, Factors of genome stability in moss and flowering plants
17. GA16-04184S, Study of the intracellular distribution of cytokinins and their transport to vacuoles
18. GA16-07193S, Anti-inflammatory activity of selected stilbenoids, 2-arylbenzofuranes and their metabolites
19. GA16-08698S, Origin and evolution of sex chromosomes in the dioecious plant *Rumex acetosa*
20. GA16-09220S, Tower of Babel: Mitochondrial-nuclear interactions in the gynodioecious species Silene vulgaris investigated with transcriptomics
21. GA16-10948S, Establishment and regulation of auxin homeostasis on a single cell level: Metabolic and transport processes
22. GA16-14649S, Inactivation of cytokinin-type phytohormones via N- and O-glucosylation – phylogeny and significance in evolution of hormonal homeostatic mechanism
23. GA16-16992S, Chromosome genomics of *Agropyron cristatum*, a wild relative of wheat
24. GA16-19557S, Specificity and regulation of auxin transport by nitrate transceptor NRT1.1 in plants
25. GA17-00522S, A new insight into the role of phospholipase in leaf senescence
26. GA17-04607S, Light-cytokinin interactions in contrasting *Arabidopsis thaliana* ecotypes during cold acclimation and their impact on freezing stress responses

27. GA17-05151S, Phospholipid metabolizing enzymes as new components of salicylic acid signalling pathway
28. GA17-05341S, Physical map of Ph2 region in hexaploid wheat
29. GA17-06548S, Foreign DNA in barley (*Hordeum* spp.) – are there any genomic enablers of horizontal gene transfer in grasses?
30. GA17-06613S, Phytohormone cross-talk during sub-zero acclimation
31. GA17-10280S, Variability in plant traits as a tool to cope with climate change – from phenotypes to genes and back again
32. GA17-10591S, Definition of physiological, metabolic and adaptation processes in the fern Pteris cretica growing on soils contaminated with arsenic
33. GA17-10907S, Environmental impact of noble metal nanoparticles
34. GA17-13853S, Nuclear architecture in interspecific plant hybrids
35. GA17-14007S, Modulation of CDK and related molecular targets in aggressive non-Hodgkin lymphomas
36. GA17-14048S, Spatial and temporal characterization of DNA replication in phylogeneticaly related plant species with contrasting genome sizes
37. GA17-17564S, Dynamics and evolution of multigene ribosomal RNA loci in *Triticeae*
38. GA17-23183S, Revealing pollen bZIP transcriptional regulons in *Arabidopsis thaliana*
39. GA17-23203S, mRNA inheritance as a mechanism of parental control over zygotic development
40. GA17-27477S, Multifaceted analysis of diacylglycerol kinase family in plants
41. GA18-02448S, The role of translation initiation factors in transcripts sequestration and activation in the male germline of angiosperm plants
42. GA18-06147S, Y chromosome dynamics in dioecious plants: intra- and interspecies genomic analysis of *Silene latifolia* and *S. dioica*
43. GA18-07027S, Involvement of telomerase in the cell interactome
44. GA18-07563S, Functional and stuctural study on plant enzymes involved in cytokinin degradation and aldehyde detoxification
45. GA18-07724S, Circulation of anthelmintics in the environment – does it contribute to drug resistance development in parasitic nematodes?
46. GA18-08452S, Anthelmintics in plants – interactions with polyphenols biosynthesis and antioxidant defence
47. GA18-10349S, Gibberellin biosynthesis and signal transduction – identification of novel targets for plant growth regulation
48. GA18-11688S, Identification and characterization of *T. militinae* gene responsible for wheat APR resistance against powdery mildew
49. GA18-12178S, Unusual light management strategies of photosystem II in Norway spruce
50. GA18-12197S, Analysis of nuclear organization and dynamics in endosperm tissues of barley
51. GA19-01383S, Modulation of steroid receptors in human cancer cells by brassinosteroids
52. GA19-01639S, Diamonds in the dust. Genetic basis of floral induction in the *Chenopodium* representatives with the contrasting photoperiodic response
53. GA19-01723S, Revealing the role of the nascent polypeptide associated complex during flower and fruit development of A*rabidopsis thaliana*
54. GA19-02699S, Transcriptome and hormonome of male gametophyte in the evolutionary context
55. GA19-05445S, Study of molecular mechanisms of vernalization in wheat
56. GA19-12262S, Physiological, biochemical, molecular and phylogenic characterization of metabolic pathways and mechanisms of cytokinin down-regulation in plants
57. GA19-13103S, Anatomical and physiological constraints as key factors governing plant vegetative regeneration
58. GA19-13848S, Analyzing repair of DNA-protein crosslinks in *Arabidopsis*
59. GA19-15609S, Sex-specific proliferation of transposable elements in plants
60. GA19-20303S, Karyotype structure and evolution in the banana family (*Musaceae*)
61. GA19-21758S, Good-Cop/Bad-Cop: Distinct roles of anionic phospholipids in plant endocytosis
62. GA19-23773S, PIN transporter-mediated auxin sinks in plant development
63. GA20-05095S, Role of the SMC5/6 complex and its interaction partners in DNA damage repair
64. GA20-10019S, Genomic dominance as a force shaping evolution of plant wide hybrids
65. GA20-11642S, Exocyst complex in moss secretory pathway and development
66. GA20-13587S, The evolutionary origin and significance of auxin transport
67. GA20-15621S, Natural agents and their derivatives for the neuroprotective therapy of Parkinson's disease
68. GA20-17984S, Molecular mechanisms of hormone and light signalling in shoots and roots in responses to abiotic stress
69. GA20-21547S, There and back again: the role of phosphatidic acid in the protein transport to and from the nucleus in plant cells
70. GA20-22875S, Organelle-specific gene expression and hormone dynamics during heat stress and high light responses
71. GA20-25308S, Modulation of cyclin-dependent kinases for targeted treatment of tumors with molecularly defined deregulation G1/S phase of cell cycle

72. GBP501/12/G090, Evolution and function of complex plant genomes
73. GC18-10515J, Mechanisms of parasitic RNA propagation and elimination in male germline studied on economically important viroid species
74. GC18-14450J, MITOCHROM: Three-dimensional organization of nuclear chromatin in plants across the cell cycle
75. GC18-18290J, Control of plant exocyst function by protein phosphorylation in root hairs and pollen tubes – role of unconventional exocyst complex subunits EXO70C
76. GJ17-21581Y, Auxin homeostasis on subcellular level
77. GJ18-12338Y, B chromosome evolution in the tribe *Andropogoneae*
78. GJ19-13375Y, The role of actin cytoskeleton in lytic degradation of auxin plasma membrane carriers
79. LM2015062, National Infrastructure for Biological and Medical Imaging
80. LM2018129, Czech-BioImaging / National Research Infrastructure for Biological and Medical Imaging
81. LO1204, Sustainable development of research in the Centre of the Region Haná
82. LTAIN19030, A study on pollen competition in *Arabidopsis thaliana* hybrids
83. LTAUSA17081, Hormonal mechanisms of plant acclimation to heat and cold stresses
84. LTAUSA18004, Evolution of diploid-polyploid complex of *Chenopodium album* agg. Joint or parallel evolution of North American and Eurasian species?
85. LTAUSA18115, The role of *Arabidopsis* Lorelei-like GPI anchored proteins (LLGs) in pollen tube reception by the female gametophyte
86. LTC17013, Plant defence system in multiple parallel biotic stresses on the model interaction: *Brassica napus* – *Leptosphaeria maculans* – insect pests
87. LTC17030, Contribution of superresolution microscopy and image analysis to the study of plant in vitro cultures with the emphasis on somatic embryogenesis of conifers
88. LTC17033, Differences between conifers and deciduous trees in metabolomic and physiological responses to selected pesticides and their utilization for environment protection
89. LTC17034, The profile of carotenoids in selected apple varieties in relation to storage conditions
90. LTC17035, Search for new sources of valuable and biologically active carotenoids in rarely used plant species
91. LTC17036, The role of polyamines in the process of plant autophagy
92. LTC17046, Possibilities of phytosorption and phytoextraction of REE from contaminated water and soil by plants
93. LTC17047, The use of plants in monitoring of human DNA damage
94. LTC17048, Synthesis of kinase inhibitors aiming at autophagy
95. LTC17084, The role of lipids and lipid-metabolizing enzymes in plant autophagy
96. LTC18026, Analysis of 3D organization of nuclear genome in plants with contrasting amount of DNA
97. LTC18034, Characterization of nuclear proteomes in the male germline and their implications under standard and stress conditions
98. LTC18043, The application of modern imaging techniques to reveal flower and male gametophyte development of *Arabidopsis thaliana*
99. LTC18047, Analysis of specificity and efficacy of RNAi in tobacco BY-2 cell line
100. LTC18065, Selective COX-1 inhibition as cardioprotective therapeutical target
101. LTC18073, RNA maturation and auxin response – a spot for mRNA methylation
102. LTC20028, Nuclear regulatory landscape of bZIP transcription factors in plant reproductive development (REPROZIP)
103. LTC20050, The application of CRISPR-Cas9 for the creation of multiple mutants in the genes coding for the nascent polypeptide associated complex
104. LTC20066, Genome editing in plants – IEB CAS contribution
105. LTT19007, Collaboration with CIMMYT on the study of diversity and evolution of maize B chromosome
106. LTT19009, Collaboration with the International Institute of Tropical Agriculture on comparative genetic and epigenetic analysis of plantains (AAB bananas)
107. LTV17010, Participation at EPSO meetings
108. QK1710302, Improvement of common wheat tolerance to drought, frost, *Phytophthora infestans* and *Fusarium* head blight using genomics and proteomics approaches
109. QK1710397, Characterization of compatibility of relations between agents causing blackleg and oilseed rape varieties as a basis for increasing of growing rentability of this crop in the Czech Republic
110. QK1910290, Development and application of molecular genetic methods for the rationalization of sweet cherry breeding practices (*Prunus avium L.*)
111. TG03010009, Support for the process of commercializing the results of research and development at the Institute of Experimental Botany AS CR v. v. i.
112. TJ04000490, New apple varieties suitable not only for organic production
113. TN01000062, Biotechnological centre for plant genotyping
114. TP01010037, Support for the process of commercializing the results of research and development at the Institute of Experimental Botany AS CR v. v. i. from 2020
115. UH0109, Technological transfer and commercialization of R & D outputs in the Institute of Experimental Botany AS CR

Publications 2018–2020

Authors in **bold** are from the Institute of Experimental Botany, Czech Academy of Sciences. Corresponding authors are marked with an asterisk.

Impacted Publications

2018

1. Ajani H, Jansa J, Köprülüoglu C, Hobza P, **Kryštof V**, Lyčka A, Lepšík M* (2018) Imidazo[1,2-c]pyrimidin-5(6H)-one as a novel core of cyclin-dependent kinase 2 inhibitors: Synthesis, activity measurement, docking, and quantum mechanical scoring. JOURNAL OF MOLECULAR RECOGNITION 31: E2720.
2. Akpinar BA, Biyiklioglu S, Alptekin B, **Havránková M**, **Vrána J**, **Doležel J**, Distelfeld A, Hernandez P, The IWGSC, Budak H* (2018) Chromosome-based survey sequencing reveals the genome organization of wild wheat progenitor *Triticum dicoccoides*. PLANT BIOTECHNOLOGY JOURNAL 16: 2077-2087.
3. Angelini J*, Vosolsobě S, **Skůpa P**, Ho AYY, Bellinvia E, Valentová O, Marc J (2018) Phospholipase D delta assists to cortical microtubule recovery after salt stress. PROTOPLASMA 255: 1195-1204.
4. Appels R*, Eversole K*, Stein N*; International Wheat Genome Sequencing Consortium (IWGSC) 202 authors: from IEB: Šimková H, **Abrouk M**, **Bartoš J**, **Doležel J**, **Valárik M**, **Čihalíková J**, **Toegelová H**, **Vrána J**, Čížková J, **Kubaláková M**, **Šafář J**, **Holušová K**, **Balcárková B**, **Tulpová Z** (2018) Shifting the limits in wheat research and breeding using a fully annotated reference genome. SCIENCE 361: eaar7191.
5. Bahaji A, Almagro G, Ezquer I, Gamez-Arcas S, Sanchez-Lopez AM, Munoz FJ, Barrio RJ, Sampedro MC, De Diego N, Spíchal L, **Doležal K**, **Tarkowská D**, Caporali E, Mendes MA, Baroja-Fernandez E, Pozueta-Romero J* (2018) Plastidial phosphoglucose isomerase is an important determinant of seed yield through its involvement in gibberellin-mediated reproductive development and storage reserve biosynthesis in *Arabidopsis*. PLANT CELL 30: 2082-2098.
6. **Balarynová J**, Danihlík J, **Fellner M*** (2018) Changes in plasma membrane aquaporin gene expression under osmotic stress and blue light in tomato. ACTA PHYSIOLOGIAE PLANTARUM 40: 27.
7. Barbuščáková Z, Kozubíková H, Zálešák B, **Doležal K**, **Pospíšil J*** (2018) General approach to neolignan-core of the boehmenan natural product family. MONATSHEFTE FÜR CHEMIE 149: 737-748.
8. Béres T*, Dragull K, **Pospíšil J**, **Tarkowská D**, Dančák M, **Bíba O**, Tarkowski P, Doležal K, **Strnad M** (2018) Quantitative analysis of ingenol in *Euphorbia* species via validated isotope dilution ultra-high performance liquid chromatography tandem mass spectrometry. PHYTOCHEMICAL ANALYSIS 29: 23-29.
9. **Bildziukevich U**, Rárová L, Šaman D, **Wimmer Z*** (2018) Picolyl amides of betulinic acid as antitumor agents causing tumor cell apoptosis. EUROPEAN JOURNAL OF MEDICINAL CHEMISTRY 145: 41-50.
10. Bon DJYD, Kováč O, Ferugová V, Zálešák F, **Pospíšil J*** (2018) One and two-carbon homologation of primary and secondary alcohols to corresponding carboxylic esters using β-carbonyl BT sulfones as a common intermediate. JOURNAL OF ORGANIC CHEMISTRY 83: 4990-5001.
11. Buček J*, Zatloukal M, **Havlíček L**, **Plíhalová L**, Pospíšil T, **Novák O**, **Doležal K**, **Strnad M** (2018) Total synthesis of [N-15]-labelled C6-substituted purines from [N-15]-formamide – easy preparation of isotopically labelled cytokinins and derivatives. ROYAL SOCIETY OPEN SCIENCE 5: 181322.
12. Cucinotta M, Manrique S, Cuesta C, Benková E, **Novák O**, Colombo L* (2018) CUP-SHAPED COTYLEDON1 (CUC1) and CUC2 regulate cytokinin homeostasis to determine ovule number in *Arabidopsis*. JOURNAL OF EXPERIMENTAL BOTANY 69: 5169-5176.
13. Danova K*, **Motyka V***, Todorova M, Trendafilova A, Krumova S, **Dobrev P**, Andreeva T, Oreshkova T, Taneva S, Evstatieva L (2018) Effect of cytokinin and auxin treatments on morphogenesis, terpenoid biosynthesis, photosystem structural organization, and endogenous isoprenoid cytokinin profile in *Artemisia alba* Turra *in vitro*. JOURNAL OF PLANT GROWTH REGULATION 37: 403-418.
14. de la Fuente AG, Traldi F, Široká J, Kretowski A, Ciborowski M, Otero A, Barbas C, Godzien J* (2018) Characterization and annotation of oxidized glycerophosphocholines for non-targeted metabolomics with LC-QTOF-MS data. ANALYTICA CHIMICA ACTA 1037: 358-368.
15. Dhandapani P, Song J, **Novák O**, Jameson PE* (2018) Both epiphytic and endophytic strains of *Rhodococcus fascians* influence transporter gene expression and cytokinins in infected *Pisum sativum* L. seedlings. PLANT GROWTH REGULATION 85: 231-242.
16. **Diaz M**, **Pečinka A*** (2018) Scaffolding for repair: Understanding molecular functions of the SMC5/6 complex. GENES 9: 36.
17. Do D, **Záveská Drábková L*** (2018) Herbarium tale: the utility of dry specimens for DNA barcoding *Juncaceae*. PLANT SYSTEMATICS AND EVOLUTION 304: 281–294.
18. Dokládal L, Benková E, **Honys D**, **Dupľáková N**, Lee LY, Gelvin SB, Sýkorová E* (2018) An armadillo-domain protein participates in a telomerase interaction network. PLANT MOLECULAR BIOLOGY 97: 407-420.
19. **Doležel J***, Čížková J, **Šimková H**, **Bartoš J** (2018) One major challenge of sequencing large plant genomes is to know how big they really are. INTERNATIONAL JOURNAL OF MOLECULAR SCIENCES 19: 3554.
20. Dube L, Naidoo KK, Arthur GD, Aremu AO*, **Grúz J**, **Šubrtová M**, Jarošová M, Tarkowski P, **Doležal K** (2018) Regulation of growth, nutritive, phytochemical and antioxidant potential of cultivated *Drimiopsis maculata* in response to biostimulant (vermicompost leachate, VCL) application. PLANT GROWTH REGULATION 86: 433-444.
21. **Dvořáková M**, Hýlová A, **Soudek P**, **Retzer K**, Spíchal L, **Vaněk T*** (2018) Resorcinol-type strigolactone mimics as potent germinators of the parasitic plants *Striga hermonthica* and *Phelipanche ramosa*. JOURNAL OF NATURAL PRODUCTS 81: 2321-2328.
22. Edwards KD, Takata N, Johansson M, Jurča M, **Novák O**, Hényková E, Liverani S, Kozarewa I, **Strnad M**, Millar AJ, Ljung K, Eriksson ME* (2018) Circadian clock components control daily growth activities by modulating cytokinin levels and cell division-associated gene expression in *Populus* trees. PLANT, CELL AND ENVIRONMENT 41: 1468-1482.

23. **Eliášová K**, **Vondráková Z**, **Gemperlová L**, Neděla V, Runštuk J, **Fischerová L**, **Malbeck J**, **Trávníčková A**, **Cvikrová M**, Vágner M* (2018) The response of *Picea abies* somatic embryos to UV-B radiation depends on the phase of maturation. FRONTIERS IN PLANT SCIENCE 9: 1736.

24. Fan L, Zhao L, Hu W, Li W, **Novák O**, **Strnad M**, Simon S, Friml J, Shen J, Jiang L, Qiu QS* (2018) Na^+, K^+/H^+ antiporters regulate the pH of endoplasmic reticulum and auxin-mediated development. PLANT, CELL AND ENVIRONMENT 41: 850-864.

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27. Filiault DL, Ballerini ES, Mandáková T, Aköz G, Derieg NJ, Schmutz J, Jenkins J, Grimwood J, Shu S, Hayes RD, Hellsten U, Barry K, Yan J, Mihaltcheva S, **Karafiátová M**, Nizhynska V, Kramer EM, Lysák MA, Hodges SA*, Nordborg M* (2018) The *Aquilegia* genome provides insight into adaptive radiation and reveals an extraordinarily polymorphic chromosome with a unique history. eLIFE 7: e36426.

28. Florencio-Ortiz V*, **Novák O**, Casas JL (2018) Local and systemic hormonal responses in pepper (*Capsicum annuum* L.) leaves under green peach aphid (*Myzus persicae* Sulzer) infestation. JOURNAL OF PLANT PHYSIOLOGY 231: 356-363.

29. Ford BA, Foo E, Sharwood R, **Karafiátová M**, **Vrána J**, MacMillan C, Nichols DS, Steuernagel B, Uauy C, **Doležel J**, Chandler PM, Spielmeyer W* (2018) Rht18 semidwarfism in wheat is due to increased GA 2-oxidaseA9 expression and reduced GA content. PLANT PHYSIOLOGY 177: 168-180.

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33. Gelová Z, ten Hoopen P, **Novák O**, **Motyka V**, Pernisová M, Dabravolski S, Didi V, Tillack I, **Oklešťková J**, **Strnad M**, Hause B, Haruštiaková D, Conrad U, Janda L*, Hejátko J* (2018) Antibody-mediated modulation of cytokinins in tobacco: Organ-specific changes in cytokinin homeostasis. JOURNAL OF EXPERIMENTAL BOTANY 69: 441-454.

34. Gigli-Bisceglia N, Engelsdorf T, **Strnad M**, Vaahtera L, Khan GA, Yamoune A, Alipanah L, **Novák O**, Persson S, Hejátko J, Hamann T* (2018) Cell wall integrity modulates *Arabidopsis thaliana* cell cycle gene expression in a cytokinin- and nitrate reductase-dependent manner. DEVELOPMENT 145: dev166678.

35. Gucký T, Řezníčková E, Radošová Muchová T, **Jorda R**, Klejová Z, Malínková V, Berka K, Bazgier V, Ajani H, Lepšík M, Divoký V, **Kryštof V*** (2018) Discovery of N-2-(4-amino-cyclohexyl)-9-cyclopentyl-N-6-(4-morpholin-4-ylmethyl-phenyl)-9H-purine-2,6-diamine as a potent FLT3 kinase inhibitor for acute myeloid leukemia with FLT3 mutations. JOURNAL OF MEDICINAL CHEMISTRY 61: 3855-3869.

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37. Holubová K, Hensel G*, Vojta P, **Tarkowski P**, Bergougnoux V, Galuszka P (2018) Modification of barley plant productivity through regulation of cytokinin content by reverse-genetics approaches. FRONTIERS IN PLANT SCIENCE 9: 1676.

38. Himmelbach A, Ruban AV, Walde I, Šimková H, **Doležel J**, Hastie A, Stein N*, Mascher M* (2018) Discovery of multi-megabase polymorphic inversions by chromosome conformation capture sequencing in large-genome plant species. PLANT JOURNAL 96: 1309-1316.

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40. **Hönig M**, **Plíhalová L***, Spíchal L, **Grúz J**, **Kadlecová A**, **Voller J**, Rajnochová Svobodová A, Vostálová J, Ulrichová J, **Doležal K**, **Strnad M** (2018) New cytokinin derivatives possess UVA and UVB photoprotective effect on human skin cells and prevent oxidative stress. EUROPEAN JOURNAL OF MEDICINAL CHEMISTRY 150: 946-957.

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42. Cherukupalli S, Chandrasekaran B, **Kryštof V**, Aleti RR, Sayyad N, Merugu SR, Kushwaha ND, Karpoormath R* (2018) Synthesis, anticancer evaluation, and molecular docking studies of some novel 4,6-disubstituted pyrazolo[3,4-d]pyrimidines as cyclin-dependent kinase 2 (CDK2) inhibitors. BIOORGANIC CHEMISTRY 79: 46-59.

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Patents 2018–2020

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   Issue date: 01.05.2018. **Patent No. US9957273**
2. **Nisler J**, Zatloukal M, Spíchal L, Koprna R, **Doležal K, Strnad M**. 1,2,3-thidiazol-5yl-urea derivatives, use thereof for regulationg plant senescence and preparations containing these derivatives.
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    Issue date: 16.10.2019. **Patent No. CZ308056**
11. **Moravec T**, **Navrátil O**, **Čeřovská N**, **Plchová H**, **Vaculík P**, **Oklešťková J**. Expression system and method of protein expression in plants.
    Issue date: 11.12.2019. **Patent No. CZ308137**
12. **Dvořáková M**, **Soudek P**, **Vaněk T**. Strigolactone derivatives for controlling parasitic plants seed germination.
    Issue date: 11.12.2019. **Patent No. CZ308139**

2020

13. **Soudek P**, **Vaněk T**, Hudcová T. A process for removing contaminants and nitrogen and phosphorus compounds from waste water and a root treatment plant for carrying out the proces.
    Issue date: 18.03.2020. **Patent No. CZ308297**
14. **Nisler J**, Zatloukal M, Spíchal L, Koprna R, **Doležal K**, **Strnad M**. 1,2,3-thiadiazol-5yl-urea derivatives, use therof for regulation plant senescence and preparations containing these derivatives.
    Issue date: 12.05.2020. **Patent No. CA2991519**
15. **Havlíček L**, Šturc A, **Řezníčková E**, Jorda R, **Kryštof V**, **Strnad M**. 5-Alkylthio-7-[(4-arylbenzyl) amino]-1(2)H-pyrazolo[4,3-d]pyrimidines for the treatment of lymphomas.
    Issue date: 05.08.2020. **Patent No. CZ308484**

Apple Varieties 2018–2020

2018

1. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Variety of *Malus domestica* Borkh., **UEB 6581**.
   Issue date: 09.01.2018. Identification No. CZ 1/2018.
   A new and distinct, late dessert apple variety with *Vf* resistance against scab, characterized by weaker vigor, good extensive branching and medium sized, globose, dark red fruits with rare russet. Flavor of fruits is very sweet with low content of acids and it reminds the taste of tropical fruits. Thinning is recommended for regular crop.
2. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Variety of *Malus domestica* Borkh., **UEB 6581**.
   Issue date: 05.02.2018. Identification No. EU 48317.
   A new and distinct, late dessert apple variety with *Vf* resistance against scab, characterized by weaker vigor, good extensive branching and medium sized, globose, dark red fruits with rare russet. Flavor of fruits is very sweet with low content of acids and it reminds the taste of tropical fruits. Thinning is recommended for regular crop.
3. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Variety of *Malus domestica* Borkh., **LAMBADA**.
   Issue date: 07.05.2018. Identification No. EU 49213.
   A new and distinct medium to late apple variety characterized by a columnar tree type, presence of *Vf* resistance against scab and yellow fruits of a very good taste, with eating maturity immediately or shortly after picking. The variety is suitable for home gardens in narrow hedges and for production of dessert apples.
4. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Variety of *Malus domestica* Borkh., **RUMBA**.
   Issue date: 07.05.2018. Identification No. EU 49214.
   A new and distinct late apple variety characterized by a very narrow columnar tree type, presence of *Vf* resistance against scab and attractive bright red fruits of a good quality and storability. The variety is suitable for home gardens as a solitaire or for narrow hedges, as well as for dessert apples production and juice industry.
5. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Variety of *Malus domestica* Borkh., **UEB 6581**.
   Issue date: 31.10.2018. Identification No. CH 18.2769.
   A new and distinct, late dessert apple variety with *Vf* resistance against scab, characterized by weaker vigor, good extensive branching and medium sized, globose, dark red fruits with rare russet. Flavor of fruits is very sweet with low content of acids and it reminds the taste of tropical fruits. Thinning is recommended for regular crop.
6. **Černý R**, **Tupý J**, **Louda O**, **Zima J**. Variety of *Malus domestica* Borkh., **UEBI 406/1**.
   Issue date: 11.12.2018. Identification No. US PP29,959 P3.
   A new and distinct late dessert apple variety with good growing characteristics, heavy and regular crop without necessity of thinning. It has a very attractive bright red fruits of good

shape and size with a good acidic taste. This variety is suitable particularly for intensive production.

7. **Tupý J**, **Černý R**, **Louda O**, **Zima J**. Variety of *Malus domestica* Borkh., **UEB 38026**.
   Issue date: 11.12.2018. Identification No. US PP29,960 P3.
   A new and distinct, healthy, early ripening apple variety with attractive bicolor appearance, good fruits quality, sweet taste and resistance against scab on assumed polygenic basis, the variety is suitable for organic production as a home garden.
8. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Variety of *Malus domestica* Borkh., **NUBIA**.
   Issue date: 13.12.2018. Identification No. CZ 60/2018.
   A new and distinct early winter variety with *Vf* resistance against scab, characterized by bigger globose fruits of purple to dark red color and medium firm flesh of aromatic, rather sweet flavor. The variety is particularly suitable for home gardens.
9. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Variety of *Malus domestica* Borkh., **BARBY**.
   Issue date: 13.12.2018. Identification No. CZ 61/2018.
   A new and distinct late dessert apple variety with resistance against scab on assumed polygenic basis, characterized by globose, medium sized fruits with red blush on yellow background and with crunchy and juicy flesh of very good taste which is highly appreciated mainly by children. The variety is suitable for intensive apple tree production as well as for home gardens.
10. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Variety of *Malus domestica* Borkh., **MAGENTA**.
    Issue date: 13.12.2018. Identification No. CZ 62/2018.
    A new and distinct ornamental apple variety with narrow columnar growth, attractive purple-red color of flowers, greyish-purple, later green leaves and on average 25 mm, broadly globose, purple-red fruits. These ornamental fruits remain on the tree over the winter and are a valuable food for birds. The variety is, apart from ornamental purposes, suitable for pollination of apple tree plantings with early to medium time of flowering.
11. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Variety of *Malus domestica* Borkh., **LILAC**.
    Issue date: 13.12.2018. Identification No. CZ 63/2018.
    A new and distinct ornamental apple variety with columnar growth, characterized by pink to light purple color of flowers and greyish-purple, later green leaves. Ornamental fruits with mean size of 33 mm are flat globose, slightly ribbed, with red over color on yellow background. Fruits of this variety remain on the tree over the winter as a food for birds. Apart from ornamental purposes this variety is suitable for pollination of apple tree plantings with early time of flowering.
12. **Tupý J**, **Černý R**, **Louda O**, **Zima J**. Variety of *Malus domestica* Borkh., **UEB 1813**.
    Issue date: 18.12.2018. Identification No. US PP29,987 P3.
    A new and distinctive late dessert apple variety with *Vf* resistance against scab, medium vigor, drooping tree habit and medium sized globose dark red fruits with weak defined stripes. Fruits have an aromatic sweet-sour flavor. Thinning to achieve regular crop is recommended.
13. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Variety of *Malus domestica* Borkh., **ALLEGRO**.
    Issue date: 10.05.2018. Identification No. Patent No. 180920.
    A new and distinct, healthy and friendly, early ripening apple variety with attractive bicolor appearance, good fruits quality, sweet taste and resistance against scab on assumed polygenic basis, the variety is suitable for organic production as a home garden.

2019

14. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Variety of *Malus domestica* Borkh., **TELSE**.
    Issue date: 05.02.2019. Identification No. CZ 8/2019.
    A new and distinct autumn apple variety with *Vf* resistance against scab, characterized by orange red fruits of very good flavor, meant for direct consumption or for medium long storing. The variety is particularly suitable for home gardens or for intensive production as an alternative to variety Elstar.
15. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Variety of *Malus domestica* Borkh., **GHIVA**.
    Issue date: 05.02.2019. Identification No. CZ 9/2019.
    A new and distinct late winter apple variety with resistance to fire blight, characterized by very firm, conic, pink red fruits of sweet flavor and long storability. The variety is particularly suitable for intensive apple productions managed in mode of integrated production.
16. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Variety of *Malus domestica* Borkh., **LILAC**.
    Issue date: 25.02.2019. Identification No. EU 51496.
    A new and distinct ornamental apple variety with columnar growth, characterized by pink to light purple color of flowers and greyish-purple, later green leaves. Ornamental fruits with mean size of 33 mm are flat globose, slightly ribbed, with red over color on yellow background. Fruits of this variety remain on the tree over the winter as a food for birds. Apart from ornamental purposes this variety is suitable for pollination of apple tree plantings with early time of flowering.
17. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Variety of *Malus domestica* Borkh., **MAGENTA**.
    Issue date: 25.02.2019. Identification No. EU 51497.
    A new and distinct ornamental apple variety with narrow columnar growth, attractive purple-red color of flowers, greyish-purple, later green leaves and on average 25 mm, broadly globose, purple-red fruits. These ornamental fruits remain on the tree over the winter and are a valuable food for birds. The variety is, apart from ornamental purposes, suitable for pollination of apple tree plantings with early to medium time of flowering.

18. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Variety of *Malus domestica* Borkh., **BARBY**.
Issue date: 25.02.2019. Identification No. EU 51498.
A new and distinct late dessert apple variety with resistance against scab on assumed polygenic basis, characterized by globose, medium sized fruits with red blush on yellow background and with crunchy and juicy flesh of very good taste and long storability. The variety is suitable for intensive apple tree production as well as for home gardens.

19. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Variety of *Malus domestica* Borkh., **NUBIA**.
Issue date: 25.02.2019. Identification No. EU 51499.
A new and distinct early winter variety with *Vf* resistance against scab, characterized by bigger globose fruits of purple to dark red color and medium firm flesh of aromatic, rather sweet flavor. The variety is particularly suitable for home gardens.

20. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Variety of *Malus domestica* Borkh., **BONITA**.
Issue date: 09.07.2019. Identification No. ZA 20196876.
A new and distinct late dessert apple variety with good growing characteristics, heavy and regular crop without necessity of thinning. It has a very attractive bright red fruits of good shape and size with a good acidic taste. This variety is suitable particularly for intensive production.

21. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Apple tree named `**UEB 43054**`.
Issue date: 27.08.2019. Identification No. US PP30,847 P3.
A new and distinct late apple variety characterized by a very narrow columnar tree type, presence of *Vf* resistance against scab and attractive bright red fruits of a good quality and storability. The variety is suitable for home gardens as a solitaire or for narrow hedges, as well as for dessert apples production and juice industry.

22. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Apple tree named `**UEB 6581**`.
Issue date: 27.08.2019. Identification No. US PP30,848 P3.
A new and distinct, late dessert apple variety with *Vf* resistance against scab, characterized by weaker vigor, good extensive branching and medium sized, globose, dark red fruits with rare russet. Flavor of fruits is very sweet with low content of acids and it reminds the taste of tropical fruits. Thinning is recommended for regular crop.

23. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Apple tree named `**UEB 42723**`.
Issue date: 27.08.2019. Identification No. US PP30,849 P3.
A new and distinct ornamental apple variety with columnar growth, characterized by pink to light purple color of flowers and greyish-purple, later green leaves. Ornamental fruits with mean size of 33 mm are flat globose, slightly ribbed, with red over color on yellow background. Fruits of this variety remain on the tree over the winter as a food for birds. Apart from ornamental purposes this variety is suitable for pollination of apple tree plantings with early time of flowering.

24. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Apple tree named `**UEB 42721**`.
Issue date: 03.09.2019. Identification No. US PP30,861 P3.
A new and distinct ornamental apple variety with narrow columnar growth, attractive purple-red color of flowers, greyish-purple, later green leaves and on average 25 mm, broadly globose, purple-red fruits. These ornamental fruits remain on the tree over the winter and are a valuable food for birds. The variety is, apart from ornamental purposes, suitable for pollination of apple tree plantings with early to medium time of flowering.

25. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Apple tree named `**UEB 41811**`.
Issue date: 03.09.2019. Identification No. US PP30,864 P3.
A new and distinct medium to late apple variety characterized by a columnar tree type, presence of *Vf* resistance against scab and yellow fruits of a very good taste, with eating maturity immediately or shortly after picking. The variety is suitable for home gardens in narrow hedges and for production of dessert apples.

2020

26. **Černý R**, **Zima J**. Variety of *Malus domestica* Borkh., **ACROBAT**.
Issue date: 27.01.2020. Identification No. CZ 3/2020.
A new and distinct columnar apple variety with autumn term of harvest maturity and resistance to scab and powdery mildew. It is characterized by orange red fruits of a very good balanced acid/sugar flavor. Fruits are meant for direct consumption or for medium long storing. The variety is particularly suitable for home gardens as a solitaire or for narrow hedges. It does not have any special growing demands.

27. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Variety of *Malus domestica* Borkh., **TELSE**.
Issue date: 06.04.2020. Identification No. EU 54899.
A new and distinct autumn apple variety with *Vf* resistance against scab, characterized by orange red fruits of very good flavor, meant for direct consumption or for medium long storing. The variety is particularly suitable for home gardens or for intensive production as an alternative to variety Elstar.

28. **Černý R**, **Zima J**, **Tupý J**, **Louda O**. Variety of *Malus domestica* Borkh., **GHIVA**.
Issue date: 06.04.2020. Identification No. EU 54900.
A new and distinct late winter apple variety with resistance to scab, powdery mildew and fire blight. It is characterized by very firm, conic, pink red fruits of sweet flavor and long storability. The variety is particularly suitable for intensive apple productions managed in a mode of integrated or organic production.


CAUTION
Deflection Plates
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Scientific Report
2018–2020

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