Publications - Cell and Metabolic Biology

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Frey, M.; Vahabi, K.; Cankar, K.; Lackus, N. D.; Padilla-Gonzalez, F.; Ro, D.-K.; Rieseberg, L.; Spring, O.; Tissier, A.; Sesquiterpene lactones – insights into biosynthesis, regulation and signalling roles *Crit. Rev. Plant Sci.* 1-27, (2024) DOI: 10.1080/07352689.2024.2307240

Abstract
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Sesquiterpene lactones (STLs) are bitter tasting plant specialized metabolites derived from farnesyl pyrophosphate (FPP) that contain a characteristic lactone ring. STLs can be found in many plant families that are distantly related to each other and outside the plant kingdom. They are especially prevalent in the plant families Apiaceae and Asteraceae, the latter being one of the largest plant families besides the Orchidaceae. The STL diversity is especially large in the Asteraceae, which made them an ideal object for chemosystematic studies in these species. Many STLs show a high bioactivity, for example as protective compounds against herbivory. STLs are also relevant for pharmaceutical applications, such as the treatment of malaria with artemisinin. Recent findings have dramatically changed our knowledge about the biosynthesis of STLs, as well as their developmental, spatial, and environmental regulation. This review intents to update the currently achieved progress in these aspects. With the advancement of genome editing tools such as CRISPR/Cas and the rapid acceleration of the speed of genome sequencing, even deeper insights into the biosynthesis, regulation, and enzyme evolution of STL can be expected in the future. Apart from their role as protective compounds, there may be a more subtle role of STL in regulatory processes of plants that will be discussed as well.

Darwish, E.; Ghosh, R.; Bentzer, J.; Tsardakas Renhuldt, N.; Proux-Wera, E.; Kamal, N.; Spannagl, M.; Hause, B.; Sirijovski, N.; Van Aken, O.; The dynamics of touch-responsive gene expression in cereals *Plant J.* **116**, 282-302, (2023) DOI: 10.1111/tpj.16269

Abstract
Internet
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BibTeX

Wind, rain, herbivores, obstacles, neighbouring plants, etc. provide important mechanical cues to steerplant growth and survival. Mechanostimulation to stimulate yield and stress resistance of crops is of signifi-cant research interest, yet a molecular understanding of transcriptional responses to touch is largely absentin cereals. To address this, we performed whole-genome transcriptomics following mechanostimulation ofwheat, barley, and the recent genome-sequenced oat. The largest transcriptome changes occurred 25 minafter touching, with most of the genes being upregulated. While most genes returned to basal expressionlevel by 1–2 h in oat, many genes retained high expression even 4 h post-treatment in barley and wheat.Functional categories such as transcription factors, kinases, phytohormones, and Ca2+regulation wereaffected. In addition, cell wall-related genes involved in (hemi)cellulose, lignin, suberin, and callose biosyn-thesis were touch-responsive, providing molecular insight into mechanically induced changes in cell wallcomposition. Furthermore, several cereal-specific transcriptomic footprints were identified that were notobserved in Arabidopsis. In oat and barley, we found evidence for systemic spreading of touch-induced sig-nalling. Finally, we provide evidence that both the jasmonic acid-dependent and the jasmonic acid-independent pathways underlie touch-signalling in cereals, providing a detailed framework and markergenes for further study of (a)biotic stress responses in cereals.

Manh, M. B.; Ost, C.; Peiter, E.; Hause, B.; Krupinska, K.;

Humbeck, K.; WHIRLY1 acts upstream of ABA-related reprogramming of drought-induced gene expression in Barley and affects stress-related histone modifications *Int. J. Mol. Sci.* **24**, 6326, (2023) DOI: 10.3390/ijms24076326

Abstract
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WHIRLY1, a small plant-specific ssDNA-binding protein, dually located in chloroplasts and the nucleus, is discussed to act as a retrograde signal transmitting a stress signal from the chloroplast to the nucleus and triggering there a stress-related gene expression. In this work, we investigated the function of WHIRLY1 in the drought stress response of barley, employing two overexpression lines (oeW1-2 and oeW1-15). The overexpression of WHIRLY1 delayed the drought-stress-related onset of senescence in primary leaves. Two abscisic acid (ABA)-dependent marker genes of drought stress, HvNCED1 and HvS40, whose expression in the wild type was induced during drought treatment, were not induced in overexpression lines. In addition, a drought-related increase in ABA concentration in the leaves was suppressed in WHIRLY1 overexpression lines. To analyze the impact of the gain-of-function of WHIRLY1 on the drought-related reprogramming of nuclear gene expression, RNAseq was performed comparing the wild type and an overexpression line. Cluster analyses revealed a set of genes highly up-regulated in response to drought in the wild type but not in the WHIRLY1 overexpression lines. Among these genes were many stress- and abscisic acid (ABA)-related ones. Another cluster comprised genes up-regulated in the oeW1 lines compared to the wild type. These were related to primary metabolism, chloroplast function and growth. Our results indicate that WHIRLY1 acts as a hub, balancing trade-off between stress-related and developmental pathways. To test whether the gain-of-function of WHIRLY1 affects the epigenetic control of stress-related gene expression, we analyzed drought-related histone modifications in different regions of the promoter and at the transcriptional start sites of HvNCED1 and HvS40. Interestingly, the level of euchromatic marks (H3K4me3 and H3K9ac) was clearly decreased in both genes in a WHIRLY1 overexpression line. Our results indicate that WHIRLY1, which is discussed to act as a retrograde signal, affects the ABA-related reprogramming of nuclear gene expression during drought via differential histone modifications.

Saadat, N. P.; van Aalst, M.; Brand, A.; Ebenhöh, O.; Tissier, A.; Matuszyńska, A. B.; Shifts in carbon partitioning by photosynthetic activity increase terpenoid synthesis in glandular trichomes *Plant J.* **115**, 1716-1728, (2023) DOI: 10.1111/tpj.16352

Abstract
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Several commercially important secondary metabolites are produced and accumulated in high amounts by glandular trichomes, giving the prospect of using them as metabolic cell factories. Due to extremely high metabolic fluxes through glandular trichomes, previous research focused on how such flows are achieved. The question regarding their bioenergetics became even more interesting with the discovery of photosynthetic activity in some glandular trichomes. Despite recent advances, how primary metabolism

contributes to the high metabolic fluxes in glandular trichomes is still not fully elucidated. Using computational methods and available multi-omics data, we first developed a quantitative framework to investigate the possible role of photosynthetic energy supply in terpenoid production and next tested experimentally the simulation-driven hypothesis. With this work, we provide the first reconstruction of specialised metabolism in Type-VI photosynthetic glandular trichomes of Solanum lycopersicum. Our model predicted that increasing light intensities results in a shift of carbon partitioning from catabolic to anabolic reactions driven by the energy availability of the cell. Moreover, we show the benefit of shifting between isoprenoid pathways under different light regimes, leading to a production of different classes of terpenes. Our computational predictions were confirmed in vivo, demonstrating a significant increase in production of monoterpenoids while the sesquiterpenes remained unchanged under higher light intensities. The outcomes of this research provide quantitative measures to assess the beneficial role of chloroplast in glandular trichomes for enhanced production of secondary metabolites and can guide the design of new experiments that aim at modulating terpenoid production.

Zeng, M.; Hause, B.; van Dam, N. M.; Uthe, H.; Hoffmann, P.; Krajinski, F.; Martínez-Medina, A.; The mycorrhizal symbiosis alters the plant defence strategy in a model legume plant *Plant Cell Environ.* **45**, 3412-3428, (2022) DOI: 10.1111/pce.14421

Abstract
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Arbuscular mycorrhizal (AM) symbiosis modulates plant-herbivore interactions. Still, how it shapes the overall plant defence strategy and the mechanisms involved remain unclear. We investigated how AM symbiosis simultaneously modulates plant resistance and tolerance to a shoot herbivore, and explored the underlying mechanisms. Bioassays with Medicago truncatula plants were used to study the effect of the AM fungus Rhizophagus irregularis on plant resistance and tolerance to Spodoptera exigua herbivory. By performing molecular and chemical analyses, we assessed the impact of AM symbiosis on herbivore-triggered phosphate (Pi)- and jasmonate (JA)-related responses. Upon herbivory, AM symbiosis led to an increased leaf Pi content by boosting the mycorrhizal Pi-uptake pathway. This enhanced both plant tolerance and herbivore performance. AM symbiosis counteracted the herbivore-triggered JA burst, reducing plant resistance. To disentangle the role of the mycorrhizal Pi-uptake pathway in the plant\'s response to herbivory, we used the mutant line ha1-2, impaired in the H+-ATPase gene HA1, which is essential for Pi-uptake via the mycorrhizal pathway. We found that mycorrhiza-triggered enhancement of herbivore performance was compromised in ha1-2 plants. AM symbiosis thus affects the defence pattern of M. truncatula by altering resistance and tolerance simultaneously. We propose that the mycorrhizal Pi-uptake pathway is involved in the modulation of the plant defence strategy.

Vendemiatti, E.; Therezan, R.; Vicente, M.; Pinto, M.; Bergau, N.; Yang, L.; Bernardi, W.; Alencar, S.; Zsögön, A.; Tissier, A.; Benedito, V.; Peres, L.; The genetic complexity of type-IV trichome development reveals the steps towards an insect-resistant tomato *Plants* **11**, 1309, (2022) DOI: 10.3390/plants11101309

Abstract
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The leaves of the wild tomato Solanum galapagense harbor type-IV glandular trichomes (GT) that produce high levels of acylsugars (AS), conferring insect resistance. Conversely, domesticated tomatoes (S. lycopersicum) lack type-IV trichomes on the leaves of mature plants, preventing high AS production, thus rendering the plants more vulnerable to insect predation. We hypothesized that cultivated tomatoes engineered to harbor type-IV trichomes on the leaves of adult plants could be insect-resistant. We introgressed the genetic determinants controlling type-IV trichome development from S. galapagense into cv. Micro-Tom (MT) and created a line named "Galapagos-enhanced trichomes" (MT-Get). Mapping-by-sequencing revealed that five chromosomal regions of S. galapagense were present in MT-Get. Further genetic mapping showed that S. galapagense alleles in chromosomes 1, 2, and 3 were sufficient for the presence of type-IV trichomes on adult organs but at lower densities. Metabolic and gene expression analyses demonstrated that type-IV trichome density was not accompanied by the AS production and exudation in MT-Get. Although the plants produce a significant amount of acylsugars, those are still not enough to make them resistant to whiteflies. We demonstrate that type-IV glandular trichome development is insufficient for high AS accumulation. The results from our study provided additional insights into the steps necessary for breeding an insect-resistant tomato.

Mittelberger, C.; Hause, B.; Janik, K.; The 'Candidatus Phytoplasma mali' effector protein SAP11CaPm interacts with MdTCP16, a class II CYC/TB1 transcription factor that is highly expressed during phytoplasma infection *PLOS ONE* **17**, e0272467, (2022) DOI: 10.1371/journal.pone.0272467

Abstract
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'Candidatus Phytoplasma mali', is a bacterial pathogen associated with the so-called apple proliferation disease in Malus × domestica. The pathogen manipulates its host with a set of effector proteins, among them SAP11CaPm, which shares similarity to SAP11AYWB from 'Candidatus Phytoplasma asteris'. SAP11AYWB interacts and destabilizes the class II CIN transcription factors of Arabidopsis thaliana, namely AtTCP4 and AtTCP13 as well as the class II CYC/TB1 transcription factor AtTCP18, also known as BRANCHED1 being an important factor for shoot branching. It has been shown that SAP11CaPm interacts with the Malus × domestica orthologues of AtTCP4 (MdTCP25) and AtTCP13 (MdTCP24), but an interaction with MdTCP16, the orthologue of AtTCP18, has never been proven. The aim of this study was to investigate this potential interaction and close a knowledge gap regarding the function of SAP11CaPm. A Yeast two-hybrid test and Bimolecular Fluorescence Complementation in planta revealed that SAP11CaPm interacts with MdTCP16. MdTCP16 is known to play a role in the control of the seasonal growth of perennial plants and an increase of MdTCP16 gene expression has been detected in apple leaves in autumn. In addition to this, MdTCP16 is highly expressed during phytoplasma infection. Binding of MdTCP16 by SAP11CaPm might lead to the induction of shoot proliferation and early bud break, both of which are characteristic symptoms of apple proliferation disease.

Jäckel, L.; Schnabel, A.; Stellmach, H.; Klauß, U.; Matschi, S.; Hause, G.; Vogt, T.; The terminal enzymatic step in piperine biosynthesis is co-localized with the product piperine in specialized cells of black pepper (Piper nigrum L.) *Plant J.* **111**, 731–747, (2022) DOI: 10.1111/tpj.15847

Abstract
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Piperine (1-piperoyl piperidine) is responsible for the pungent perception of dried black pepper (Pipernigrum) fruits and essentially contributes to the aromatic properties of this spice in combination with ablend of terpenoids. The final step in piperine biosynthesis involves piperine synthase (PS), which catalyzesthe reaction of piperoyl CoA and piperidine to the biologically active and pungent amide. Nevertheless, experimental data on the cellular localization of piperine and the complete biosynthetic pathway are missing. Not only co-localization of enzymes and products, but also potential transport of piperamides to thesink organs is a possible alternative. This work, which includes purification of the native enzyme, immunolocalization, laser microdissection, fluorescence microscopy, and electron microscopy combinedwith liquid chromatography electrospray ionization tandem mass spectrometry (LC-ESI-MS/MS), providesexperimental evidence that piperine and PS are co-localized in specialized cells of the black pepper fruit peri-sperm. PS accumulates during early stages of fruit development and its level declines before the fruits arefully mature. The product piperine is co-localized to PS and can be monitored at the cellular level by itsstrong bluish fluorescence. Rising piperine levels during fruit maturation are consistent with the increasingnumbers of fluorescent cells within the perisperm. Signal intensities of individual laser-dissected cells whenmonitored by LC-ESI-MS/MS indicate molar concentrations of this alkaloid. Significant levels of piperineand additional piperamides were also detected in cells distributed in the cortex of black pepper roots. Insummary, the data provide comprehensive experimental evidence of and insights into cell-specific biosyn-thesis and storage of piperidine alkaloids, specific and characteristic for the Piperaceae. By a combination offluorescence microscopy and LC-MS/MS analysis we localized the major piperidine alkaloids to specific cellsof the fruit perisperm and the root cortex. Immunolocalization of native piperine and piperamide synthasesshows that enzymes are co-localized with high concentrations of products in these idioblasts.

El Amerany, F.; Rhazi, M.; Balcke, G.; Wahbi, S.; Meddich, A.; Taourirte, M.; Hause, B.; The effect of chitosan on plant physiology, wound response, and fruit quality of tomato *Polymers* **14**, 5006, (2022) DOI: 10.3390/polym14225006

Abstract
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In agriculture, chitosan has become popular as a metabolic enhancer; however, no deep information has been obtained yet regarding its mechanisms on vegetative tissues. This work was conducted to test the impact of chitosan applied at different plant growth stages on plant development, physiology, and response

to wounding as well as fruit shape and composition. Five concentrations of chitosan were tested on tomato. The most effective chitosan doses that increased leaf number, leaf area, plant biomass, and stomatal conductance were 0.75 and 1 mg mL−1. Chitosan (1 mg mL−1) applied as foliar spray increased the levels of jasmonoyl–isoleucine and abscisic acid in wounded roots. The application of this dose at vegetative and flowering stages increased chlorophyll fluorescence (Fv/Fm) values, whereas application at the fruit maturation stage reduced the Fv/Fm values. This decline was positively correlated with fruit shape and negatively correlated with the pH and the content of soluble sugars, lycopene, total flavonoids, and nitrogen in fruits. Moreover, the levels of primary metabolites derived from glycolysis, such as inositol phosphate, lactic acid, and ascorbic acid, increased in response to treatment of plants with 1 mg mL−1- chitosan. Thus, chitosan application affects various plant processes by influencing stomata aperture, cell division and expansion, fruit maturation, mineral assimilation, and defense responses.

Asfaw, K. G.; Liu, Q.; Eghbalian, R.; Purper, S.; Akaberi, S.; Dhakarey, R.; Münch, S. W.; Wehl, I.; Bräse, S.; Eiche, E.; Hause, B.; Bogeski, I.; Schepers, U.; Riemann, M.; Nick, P.;
The jasmonate biosynthesis Gene OsOPR7 can mitigate salinity induced mitochondrial oxidative stress *Plant Sci.* **316**, 111156, (2022) DOI: 10.1016/j.plantsci.2021.111156

Abstract
Internet
RIS
BibTeX

Salinity poses a serious threat to global agriculture and human food security. A better understanding of plant adaptation to salt stress is, therefore, mandatory. In the non-photosynthetic cells of the root, salinity perturbs oxidative balance in mitochondria, leading to cell death. In parallel, plastids accumulate the jasmonate precursor cis (+)12-Oxo-Phyto-Dienoic Acid (OPDA) that is then translocated to peroxisomes and has been identified as promoting factor for salt-induced cell death as well. In the current study, we probed for a potential interaction between these three organelles that are primarily dealing with oxidative metabolism. We made use of two tools: (i) Rice OPDA Reductase 7 (OsOPR7), an enzyme localised in peroxisomes converting OPDA into the precursors of the stress hormone JA-Ile. (ii) A Trojan Peptoid, Plant PeptoQ, which can specifically target to mitochondria and scavenge excessive superoxide accumulating in response to salt stress. We show that overexpression of OsOPR7 as GFP fusion in tobacco (Nicotiana tabacum L. cv. Bright Yellow 2, BY-2) cells, as well as a pretreatment with Plant PeptoQ can mitigate salt stress with respect to numerous aspects including proliferation, expansion, ionic balance, redox homeostasis, and mortality. This mitigation correlates with a more robust oxidative balance, evident from a higher activity of superoxide dismutase (SOD), lower levels of superoxide and lipid peroxidation damage, and a conspicuous and specific upregulation of mitochondrial SOD transcripts. Although both, Plant PeptoQ and ectopic OsOPR7, were acting in parallel and mostly additive, there are two specific differences: (i) OsOPR7 is strictly localised to the peroxisomes, while Plant PeptoQ found in mitochondria. (ii) Plant PeptoQ activates transcripts of NAC, a factor involved in retrograde signalling from mitochondria to the nucleus, while these transcripts are suppressed significantly in the cells overexpressing OsOPR7. The fact that overexpression of a peroxisomal enzyme shifting the jasmonate pathway from the cell-death signal OPDA towards JA-Ile, a hormone linked with salt adaptation, is accompanied by more robust redox homeostasis in a different organelle, the mitochondrion, indicates that cross-talk between peroxisome and mitochondrion is a crucial factor for efficient adaptation to salt stress.

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