Epigenetic Mechanisms of Crop Adaptation To Climate Change

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GENE REGULATION BY EPIGENETICS AND DISTANT ENHANCERS

Blaise Weber1, Kathrin Lauss1, Johan Zicola2, Rurika Oka1, Rechien Bader1, Tzuu-fen Lee3, Huub Hoefsloot1, Blake Meyer3,4, Franziska Turck2 and Maike Stam1

1 University of Amsterdam, Science Park 904, 1098XH Amsterdam, The Netherlands; 2 Max Planck Institute for Plant Breeding, Carl-von-Linné 10, 50829 Cologne, Germany; 3 Department of Plant and Soil Sciences, Delaware Biotechnology Institute, University of Delaware, Newark, DE 19711; 4 Donald Danforth Plant Science Center, St. Louis, MO 63132, USA

Correspondence: m.e.stam@uva.nl

Paramutation, the transfer of heritable silencing information between two alleles, results in a susceptible allele being silenced and acquiring the epigenetic profile of the silenced, inducing allele. Paramutation requires multiple factors of the RNA-directed DNA methylation (RdDM) pathway, the hallmarks of which are 24nt small regulatory RNAs and asymmetric DNA methylation (mCHH). With paramutation at the b1 gene, a regulatory gene of the maize pigmentation pathway, the low expressed B' epiallele changes the high expressed B-I epiallele into B' in a mitotically and meiotically heritable manner with a 100% frequency. A hepta-repeat 100-kb upstream of the b1 gene are required for the in trans silencing, but also for high b1 expression. The B' repeats are DNA hypermethylated compared to the B-I repeats. Surprisingly, paramutation may be associated with more RdDM activity at the sensitive allele than the inducing allele.

The hepta-repeat at the B-I allele acts as a distal enhancer of b1 expression. This finding stimulated us to investigate the occurrence of - distal - regulatory sequences in maize, a large-genome plant. By integrating genome-wide DNA methylation, histone acetylation and chromatin accessibility data sets about 1,500 putative regulatory sequences have been identified in young seedling and husk tissue, including known and experimentally validated enhancers, such as the b1 and tb1 enhancers. About half of these were >10kb of a flanking gene. Unlike mammalian enhancers, maize enhancer candidates overlap with unmethylated (UMRs) rather than low-methylated regions (LMRs). UMRs are generally stable, consistent with maize enhancers being stably unmethylated. Currently, a number of candidate enhancers are being characterized in more detail, including Vgt1, a predicted regulatory element located about 70 kb upstream of the floral repressor gene ZmRap2.7

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HISTONE DEACETYLASE 9 CONTROL OF THERMOMORPHOGENESIS; HOW PLANTS PERFORM OPTIMALLY UNDER NON-OPTIMAL TEMPERATURE CONDITIONS

Lennard C. van der Woude1*, Giorgio Perrella2*, L. Basten Snoek3*, Eirini Kaiserli2, Martijn van Zanten1

1 Molecular Plant Physiology, Institute of Environmental Biology, Utrecht University, The Netherlands
2 Institute of Molecular, Cell & Systems Biology, College of Medical, Veterinary and Life Sciences, University of Glasgow, United Kingdom
3 Bioinformatics, Institute of Biodynamics and Biocomplexity, Utrecht University, The Netherlands

Correspondence: m.vanzanten@uu.nl, * equal contribution

Many plant species can respond to high ambient temperature conditions by adjusting their architecture. This is known as thermomorphogenesis and enables optimal plant performance under suboptimal conditions. Thermomorphogenesis includes leaf movement and elongation growth of stems and hypocotyls and allows enhanced evaporative cooling and heat flux avoidance.
We found that the chromatin modifying enzyme HISTONE DEACETYLASE 9 is required for thermomorphogenesis but not the shade avoidance response. At warm temperatures, HDA9 induces the expression of YUCCA8, a rate-limiting enzyme in auxin biosynthesis. Specifically, HISTONE DEACETYLASE 9 mediates histone deacetylation at the TSS of YUCCA8, which stimulates the eviction of the repressive histone H2A.Z variant from nucleosomes of the YUCCA8 promoter. Our work assigns a novel role to histone deacetylation in activating gene expression.

EPIGENETIC MECHANISMS IN PLANT ADAPTATION TO ENVIRONMENTAL STRESSES: A LESSON FROM THE DESERT PLANT ZYGOPHYLLUM DUMOSUM

Gideon Grafi

French Associates Institute for Agriculture and Biotechnology of Drylands, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben Gurion 84990, Israel

Plants thriving in harsh desert environments provide a suitable bio-system for unraveling novel mechanisms for survival under seasonal climate change and combination of temperature extremes, low water and nutrient availability and high salinity and radiation levels. The study of the desert plant Zygophyllum dumosum Boiss in its the natural habitat of the Negev desert revealed that stress tolerance is achieved by a plethora of mechanisms (e.g. morphological, molecular and developmental mechanisms), which are probably regulated by multiple genes that act together to bring about tolerance. Of particular interest is the finding that Z. dumosum like other Zygophyllaceae species, most of which inhabit dry and semi dry regions of the world, do not possess the repressive epigenetic markers of histone H3 di- and tri-methylated at lysine 9; yet they possess mono methyl H3K9. The adaptive value of lessening epigenetic constraints will be discussed with regard to the opportunistic behavior that makes plants most adaptable to change.

THE REGULATORY LANDSCAPE OF EARLY MAIZE INFLORESCENCE DEVELOPMENT

Edoardo Bertolini

Danforth Center, USA
EBertolini@danforthcenter.org

The functional genome of agronomically important plant species remains largely unexplored, yet presents a virtually untapped resource for targeted crop improvement.

Functional elements of regulatory DNA revealed through profiles of chromatin accessibility can be harnessed for fine-tuning gene expression to optimal phenotypes in specific environments. Here, we investigate the non-coding regulatory space in the maize (Zea mays) genome during early reproductive development of pollen-and grain-bearing inflorescences. Using an assay for differential sensitivity of chromatin to micrococcal nuclease (MNase) digestion, we profile accessible chromatin and nucleosome occupancy in these largely undifferentiated tissues and classify at least 1.6% of the genome as accessible, with the majority of MNase hypersensitive sites marking proximal promoters, but also 3′ ends of maize genes.

Integration of complementary transcriptome profiles and transcription factor occupancy data are used to annotate regulatory factors, such as combinatorial transcription factor binding motifs and long non-coding RNAs, that potentially contribute to organogenesis, including tissue-specific regulation between male and female inflorescence structures. Finally, genome-wide association studies for inflorescence architecture traits based solely on functional regions delineated by MNase hypersensitivity reveals new SNP-trait associations in known regulators of inflorescence development as well as new candidates.

These analyses provide a comprehensive look into the cis-regulatory landscape during inflorescence differentiation in a major cereal crop, which ultimately shapes architecture and influences yield potential.

EPIGENETIC ANALYSIS IN POTATO MANURED WITH COMPOST OR MINERAL FERTILIZERS.

Angela Cicatelli, Stefano Castiglione.

University of Salerno

Composting of the solid waste organic fraction of Municipality and its utilization in agriculture would be a possible approach to solve the problem of the low organic matter content found in several agricultural soils, prevalently due to the massive use of chemical fertilizers and by the intensive agriculture. Benefits of compost application are well recognized: recycling of nutrient elements; increasing of soil fertility, porosity, structural stability, moisture and nutrient availability, biological activity and root aeration; low disposal costs.
The aim of our study was to evaluate the effects of soil amendment with compost in comparison with traditional chemical fertilization practices on potato (Solanum tuberosum L.) cultures. Molecular characterization of 54 registered potato cultivars was performed, and the five most genetically biodiverse (King Edward, Pentland Dell, Maris piper, , Wilja and Kingston) cultivars (together with Reference samples) were selected and employed to establish an experimental field in Southern Italy (particularly suitable for potato culture). The field area was divided into two portions of about thousand square meter each and one portion of the field was amended with compost at 20 tons per hectare, while the other one was supplemented with ammonium sulphate at 200.00 Kg per hectare, on the basis of the soil chemical analysis previously carried out. Epigenetic analysis by means of MSAP (methylation sensitive amplified polymorphism) tool was performed on both leaves and tubers of selected cultivars to estimate if any epigenetic modifications were induced by the two kinds of fertilization. The results achieved in the present study demonstrated that mineral fertilizers and compost amendment did not cause any significant modification in epigenome profiles in both analyzed potato organs and at two collection times, suggesting a comparable situation in terms of quality and nutraceutical characteristics of potato tubers produced by means of different soil fertilization strategy.

HISTONE H3.3 INCORPORATION IN ARABIDOPSIS

Sylvain Bischof

University of Zurich

Nucleosomes constitute the basic unit of chromatin and are composed of two tetramers of histone proteins H2A, H2B, H3 and H4. The position and stability of nucleosomes control the accessibility of regulatory factors that need to access DNA to regulate transcription and maintain genomic integrity. Two main variants exist for histone H3 that differ only by a few amino acids. Canonical H3.1 is expressed and incorporated into chromatin during DNA replication and is marking silent heterochromatin. In contrast, H3.3 is expressed throughout the cell cycle and is incorporated into active chromatin. Two chaperone complexes, HIRA and ATRX, were shown to bind and incorporate H3.3. To date, it remains not exactly understood where these complexes localize on chromatin and how they incorporate H3.3. Genetic analyses suggest that HIRA and ATRX have independent but also redundant functions, pointing towards a loci-specific mode-of-action. Here, we discuss the relationship between HIRA and ATRX, their role in H3.3 deposition and their implication to activate and repress transcription.

TARGETED MANIPULATION OF DNA METHYLATION IN PLANTS

Javier Gallego-Bartolomé

Instituto de Biología Molecular y Celular de Plantas (IBMCP), CSIC-Universidad Politécnica de Valencia, 46011 Valencia, Spain

Corresponding author: Javier Gallego-Bartolomé (jagalbar@ibmcp.upv.es)

DNA methylation is an epigenetic mark that regulates multiple processes, such as gene expression and genome stability. Mutants and pharmacological treatments have been instrumental in the study of this mark in plants, although their genome-wide effect complicates the direct association between changes in methylation and a particular phenotype. A variety of tools that allow locus-specific manipulation of DNA methylation can be used to assess its direct role in specific processes, as well as to create novel epialleles. Recently, we have developed new tools that recruit the methylation machinery directly to target loci through programmable DNA-binding proteins. These tools allowed us to add or remove DNA methylation in a locus-specific manner and study different features associated with targeted DNA methylation such as heritability, genomic preference and impact on gene expression.

PLANT GENOME DYNAMICS IN A CHANGING CLIMATE: STRESS ADAPTATION AND CROP BREEDING

David Roquis1, Marta Robertson1, Nai-Chiang Dai2, Ming-Hsin Lai3, Mahnaz Katouzi1, Yue-Ie C. Hsing2 and Etienne Bucher1

1 Plant Breeding and Genetic Resources, Agroscope, 1260 Nyon, Switzerland
2 Institute of Plant and Microbial Biology, Academic Sinica, Nankang, Taipei 115, Taiwan
3 Crop Science Division, Taiwan Agricultural Research Institute, Council of Agriculture (COA), Taiwan, ROC

Climate change is accelerating and may soon cause abrupt and irreversible climatic alterations. This will result in amplified biotic and abiotic stresses to which wild plants and cultivated crops will have to adapt to. It is crucial that we understand how plants can evolve to adapt to these climatic changes in order to accelerate crop breeding. In recent years, it has been proposed that transposable elements (TEs, 'jumping genes') may play a key role in these adaptive processes. Indeed, TEs have the ability to create a direct link between the environment and a plant's genome. Here, we will present how novel heat-stress responsive TE insertions can modulate transcription at numerous levels in Arabidopsis. Building on this knowledge we are currently in the process of testing if similar results can be obtained in cultivated crops. We will provide a general overview of our work on crops and will present first results obtained in field trials with rice.

RESPONSE OF THE TOMATO DDM1 MUTANT TO HEAT STRESS

Prashant Kumar Singh1, Golan Miller2, and Michal Lieberman-Lazarovich2

1 Department of Biotechnology, Mizoram University, Pachhunga University College Campus, Mizoram, India.
2 Institute of plant sciences, Agricultural Research Organization – Volcani Institute, Rishon LeZion, Israel.

DECREASE IN DNA METHYLATION1 (DDM1), a chromatin remodeling protein that belongs to the SWI2/SNF2 family, is involved in heterochromatin configuration. Specifically, it allows access to condensed heterochromatin for enzymes maintaining epigenetic marks on DNA or histones. In Arabidopsis thaliana, DDM1 is essential to sustain global levels of DNA methylation and ddm1 mutants are extensively hypomethylated in all cytosine contexts. In tomato, DDM1 is encoded by two genes: SlDDM1A and SlDDM1B. Loss-of-function alleles of these genes do not show an obvious phenotype under normal conditions. We aimed at testing the ddm1 single mutant lines under heat stress conditions. Our phenotypic results suggest that the mutant lines, ddm1a and ddm1b, respond differently to moderate chronic heat stress (MCHS) conditions. Moreover, ddm1b seems to be more tolerant than the respective background line, M82. As a first attempt to understand these observations, we have carried out a transcriptomic analysis of leaf tissue from mutant and M82 lines, grown under stress and non-stress conditions. Preliminary data will be presented and discussed.

CONTRIBUTION OF TRANSPOSABLE ELEMENTS TO STRUCTURAL VARIATION AND PHENOTYPIC ADAPTATION IN TOMATO

Matthias Benoit1, Michael Alonge2, Xingang Wang3, Florian Maumus4, Hajk-Georg Drost5, Marco Catoni6, Quentin Gouil7, Sara Lopez-Gomollon8, David Baulcombe8, Jerzy Paszkowski9, Michael C. Schatz2,10, Zachary B. Lippman1

1. Howard Hughes Medical Institute, Cold Spring Harbor Laboratory, Cold Spring Harbor, NY
2. Department of Computer Science, Johns Hopkins University, Baltimore, MD
3. Cold Spring Harbor Laboratory, Cold Spring Harbor, NY
4. URGI, INRAE, Université Paris-Saclay, Versailles, France
5. Max Planck Institute for Developmental Biology, Tübingen, Germany
6. School of Biosciences, University of Birmingham, Birmingham, United Kingdom
7. Walter and Eliza Hall Institute of Medical Research, Parkville, Australia
8. Department of Plant Sciences, University of Cambridge, Cambridge, United Kingdom
9. Radachowka, Kolbiel, Poland
10. Department of Biology, Johns Hopkins University, Baltimore, MD

Structural variation has fueled phenotypic diversification and underlies important domestication and quantitative traits in crops plants. Nevertheless, the genetic drivers of plant structural variation at the population level remain poorly understood. We recently reported long-read sequencing of 100 diverse tomato genomes, which captured the extent and genomic features of structural variants. Most of this structural variation can be traced to transposable element (TE) activity. Annotation of TEs in 14 diverse accessions revealed their prevalence in tomato genomes, with a large fraction retaining transpositional potency, likely facilitating new structural variation. The Copia-like Rider family is over-represented within the TEs involved in structural variation and has generated structural variants underlying several traits of agricultural interest in tomato. Nevertheless, mechanisms regulating Rider activity remain unexplored. Through experimentally-controlled activation of the Rider family, we identified DNA methylation, phytohormones, and drought stress as molecular regulators of Rider activity in tomato. We further show differences in Rider distribution between Solanaceae species, suggesting contrasted evolutionary success of Rider and variable contribution to structural variation between species. Artificially promoting TE activity could generate agriculturally-relevant structural and epigenetic variation in tomato and related crops.

PACK-TYPE TRANSPOSABLE ELEMENTS AND GENOME PLASTICITY IN PLANTS

Marco Catoni

School of Biosciences, University of Birmingham, Birmingham, B15 2TT, United Kingdom

Pack-TYPE transposable elements (TEs) are a group of non-autonomous DNA transposons found in plants. These elements can efficiently capture and shuffle coding DNA across the host genome, accelerating the evolution of genes. Despite their relevance for plant genome plasticity, the detection and study of Pack-TYPE TEs are challenging due to the high similarity these elements have with genes. We produced an automated annotation pipeline designed to study Pack-TYPE elements and used it to successfully annotate and analyse more than 4000 new Pack-TYPE TEs in the rice and maize genomes. Our analysis indicates that Pack-TYPE TEs are an abundant and heterogeneous group of elements. We found that these elements are associated with all main superfamilies of Class II DNA transposons in plants and likely share a similar mechanism to capture new chromosomal DNA sequences. Furthermore, we report examples of the direct contribution of these TEs to coding genes, suggesting a generalised and extensive role of Pack-TYPE TEs in plant genome evolution.

MOLECULAR RESPONSES TO HEAT STRESS DURING POLLEN MICROGAMETOGENESIS

Kevin Begcy

University of Florida, Environmental Horticulture Department, Gainesville, Florida 32611-0670

Email: kbegcy.padilla@ufl.edu

Historically, pollen development studies under heat stress are performed across several developmental stages and occasionally through the entire pollen formation. However, high temperature spikes have become more extreme and with increasing frequency, and in many cases with greater intensity. Thus, although most pollen developmental stages appear to be sensitive to abiotic stresses, the molecular, physiological and biochemical bases that contribute to male sterility in response to heat stress during each pollen developmental stage are not well understood. To test the long-term effects of heat stress on individual stages of pollen development (tetrad, unicellular, bicellular and tricellular) at maturity, we allowed non-stressed and heat stressed plants to continue their development under normal conditions until pollen maturation. We heat stressed each pollen development stage individually and analyzed pollen germination and viability. After pollen reached maturity, we germinated released pollen on media and observed that non-stressed plants produced pollen that germinated (~80%) and grew normally. In contrast, a large portion of pollen originating from heat stressed plants at the tetrad stage showed a greatly reduced germination rate (~20%). While plants that were heat stressed during the unicellular stage showed a less dramatic reduction in germination (69%) compared to the tetrad stage, heat stress at the unicellular stage was able to impair pollen germination. Surprisingly, plants heat stressed at the bicellular stage did not show significant differences in germination (76%) compared to non-stressed pollen. The reduction observed in the pollen germination rate of heat stressed maize plants indicates that even though heat stress impairs pollen germination, it affects differentially each development stage. At the tetrad stage, transient heat stress resulted in reduced starch content, decreased enzymatic activity, and reduced pollen germination, resulting in sterility. A transcriptomic comparison pointed toward misregulation of starch, lipid, and energy biosynthesis-related genes. Metabolomic studies showed an increase of Suc and its monosaccharide components, as well as a reduction in pyruvate. Lipidomic analysis showed increased levels of unsaturated fatty acids and decreased levels of saturated fatty acids.

DNA METHYLATION AND DROUGHT STRESS IN POPLAR

Stéphane Maury1, Mamadou Dia Sow1, Julien Vigneaud1, Régis Fichot1, Alain Delaunay1, Isabelle Le Jan1, Marie Mirouze2, Steven H Strauss3, Vincent Segura4, Jérôme Salse5, Christophe Ambroise6, Jörg Tost7 & Christophe Plomion8

1 LBLGC – University Orléans INRA, Orléans, France
2 LPGD – IRD, Perpignan, France
3 Department of Forest Ecosystems and Society – Orgeon University, Corvallis, USA
4 BioFoRa - INRA, Orléans, France
5 GDEC - INRA, Clermont-Ferrand, France
6 LaMME – University Evry, Evry, France
7 LEE - CNRGH CEA, Evry, France
8 Biogeco – INRA University Bordeaux, Cestas, France

Forest die-off is reported all around the world due to heat and drought stress episodes. As fixed and long living organisms subjected to repeated environmental stresses, trees have developed mechanisms enabling them to cope with fluctuating environmental conditions. Recently, epigenetics has been proposed as a hub of integration linking physiological response and environmental constraints that needs evaluation in trees. Our objective is to evaluate the potential of epigenetics and more specifically DNA methylation to significantly participate to phenotypic plasticity in trees in response to stress and the potential use for trees breeders and forest managers.

Using a transgenomic approach, we have shown in shoot apical meristem of poplar trees that DNA methylation controls genes involved in the developmental plasticity such as phytohormone genes in response to environmental constraints (temperature, drought). We have also start to investigate how these epigenetic variations could be transmitted to primed organs, participate to stress memory and trees priming facing recurrent water stress.

Using reverse genetic approach (RNAi lines), we found that poplar trees with altered methylation profiles are affected for their tolerance to drought and display spontaneous lesion mimic responses suggesting a “priming system to pathogen attack”. We have identified genes and transposable elements targeted during this process and highlight a trade-off situation between plasticity and genome integrity in meristematic cells.

Finally, using a population epigenomic approach, we are evaluating the adaptive potential of DNA methylation variations in natural trees populations. Altogether, our data highlights functional and evolutionary roles of DNA methylation in natural population of trees in a context of climate change giving promising perspectives for tree breeding.

RESISTANCE PRIMING OF FOREST TREE SPECIES

Hans Hoenicka

Thünen Institute of Forest Genetics
Sieker Landstr. 2, 22927 Grosshandorf, Germany

Long drought periods and pandemics are becoming increasing stress factors for trees worldwide. Although resistance breeding could address these problems, the use of this approach in trees is difficult. Crossing breeding is hampered in this case by the long generation times and the unavailability of resistant trees. Furthermore, many promising biotechnological approaches have remained banned from applied research for decades. Therefore, the development of alternative methods for faster resistance induction in tree species is of paramount importance.
The role of the epigenome on the adaptation of plants to the environment was unknown until recently. The targeted promotion of epigenetic changes is a very promising approach for faster resistance induction in tree species. However, methods for "epigenetic modification" still have to be defined.
Some studies have found connections between priming and epigenetic changes. Priming is a physiological state that enables plants to respond to very low levels of a stimulus in a more rapid and robust manner than non-primed plants. Priming has been used for many years in many plant species with different methods. This approach can become the basis for a targeted resistance induction strategy through the induction of epigenetic changes in trees.

EPIMUTATIONS MEDIATE PHENOTYPIC EVOLUTION IN NATURAL POPULATIONS

Zaigham Shahzad1, Jonathan D. Moore1, Jaemyung Choi1, Daniel Zilberman1,2

1Department of Cell & Developmental Biology, John Innes Centre, Norwich, NR4 7UH, UK
2Institute of Science and Technology, 3400 Klosterneuburg, Austria

Genetic variation is regarded as a prerequisite for biological evolution. Theoretical models suggest epigenetic information inherited independently of DNA sequence can also enable evolution. However, whether epigenetic inheritance mediates phenotypic evolution in natural populations is unknown. We show that natural epigenetic DNA methylation variation in gene bodies regulates genes expression, and thereby influences the diversity of complex traits in Arabidopsis thaliana natural populations. We find that the phenotypic effects of epiallelic and genetic variation are largely independent. Notably, the effects of methylation and DNA sequence polymorphism in shaping phenotypic variation are comparable particularly for adaptive traits such as transition to flowering. We also identify methylation epialleles in numerous genes associated with environmental conditions in native habitats, suggesting that intragenic methylation facilitates adaptation to fluctuating environments. Our study demonstrates that natural methylation variation fundamentally shapes phenotypic diversity in plant populations and provides an epigenetic basis for adaptive evolution independent of genetic polymorphism.

ENHANCEMENT OF HEAVY METAL TOLERANCE IN PLANTS BY SEED PRIMING

Erna Karalijaa, Arnela Demira, Alisa Selovićb

a Laboratory for plant physiology, Department for Biology, Faculty of Science, University of Sarajevo, Zmaja od Bosne 33-35; 71000 Sarajevo, Bosnia and Herzegovina
b Department for Chemistry, Faculty of Science, University of Sarajevo, Zmaja od Bosne 33-35; 71000 Sarajevo, Bosnia and Herzegovina

Soil contamination by heavy metals has been one of the most pressing concerns in food security and safety across Europeas well as globally, due to their ubiquity, toxicity at low levels, as well as persistence and bioaccumulation. It is considered that more than >50% of EU's land is contaminated by heavy metals and their influx into groundwater impacts drinking water quality adding to risks to human health. Mechanisms of hyperaccumulation of heavy metals in tolerant species has been studied, but there are almost no data on mechanisms of further improvement of the accumulation capacity of such plants. Improvements of hyperaccumulation of heavy metals can be achieved by genetic engineering or use of chelating agents. The use of chelating agents can affect the soil microorganisms, contaminate ground water and due to their slow decomposition, they are not a favourable solution. Seed priming is a controlled rehydration (imbibition) of seeds for induction of metabolic activity without radicle emergence, followed by seed drying and re-imbibition prior to sowing. It is a technique widely used for improvement of seed vigour, enhancement of germination and achieving germination uniformity especially under stress conditions. Due to commence of re-hydration so called "pre-germinative metabolism" is triggered which includes cellular processes of de-novo nucleic acid and protein synthesis, accumulation of phospholipids and sterols, DNA repair and activation of antioxidant mechanism. The basic mechanism of priming influence on plant stress tolerance is based on assumption that the pre-treatment initiates a mild stress cue resulting in acclimation-similar response of the plant. Potential of plant priming in abiotic stress tolerance has been extensively investigating using different types of molecules added exogenously to plant organs (roots, leaves etc.) with a result of enhanced tolerance of abiotic stress. There is only few papers concerning how seed priming affects tolerance levels, and what is the mechanism of plants memory of "primed" state in seeds.

TAKING SHORTCUTS: INVESTIGATING THE ROLE OF SMALL NON-CODING RNAS DURING IN VITRO TISSUE CULTURE OF THE OIL PALM

Justine Martineau 2, Marilyne Summo 2, Júlia Arraiza Ribera 1, Thierry Beulé 1, Florence Jacob 3, Julie Leclercq 2, Romain Guyot 1, David Lopez 2 & Estelle Jaligot 2*

1 UMR DIADE (IRD, CIRAD, Univ Montpellier), Montpellier, France
2 UMR AGAP Institut (CIRAD, INRAE, Univ Montpellier, Institut Agro), Montpellier, France
3 PalmElit SAS, Montferrier-sur-Lez, France

* Contact: estelle.jaligot@cirad.fr

The implementation of in vitro tissue culture propagation methods, such as somatic embryogenesis (SE), rely on the amenability of plant cells to undergoing induced reprogrammation (de-differentiation followed by re-differentiation) after treatment by growth regulators. It has been well documented in various species that these processes involve epigenetic regulation pathways that are similar to those associated with responses to abiotic stresses, which makes in vitro-derived material a great system for studying them within (theoretically) genetically homogeneous populations.

Originally, our work on SE-derived oil palms stems from the practical necessity of understanding and preventing the emergence of a pervasive somaclonal variation (the mantled floral phenotype) with negative impact on oil production. In doing so, we also aim to leverage the knowledge acquired from this case study to address broader scientific questions related to stress memory and acclimation in perennial species. With this dual objective in mind, we are currently assessing the expression of small non-coding RNAs (sncRNAs) in embryogenic suspensions and their possible roles in the regulation of genome expression and structure. We are using high-throughput transcriptome, small RNAome and degradome datasets to identify both source and target sequences of sncRNA-mediated regulations, and annotate the biological pathways that are affected by these regulations. As our analyses are still under way, we will present a global outline of our project and report on both our progress and a few lessons learned.