

Hypomethylated poplars show higher tolerance to water deficit and highlight a dual role for DNA methylation in shoot meristem: regulation of stress response and genome integrity

M.D. D Sow, A-L Le Gac, R. Fichot, S. Lanciano, A. Delaunay, I. Le Jan, M-C Lesage-Descauses, S. Citerne, J. Caius, V. Brunaud, et al.

▶ To cite this version:

M.D. D Sow, A-L Le Gac, R. Fichot, S. Lanciano, A. Delaunay, et al.. Hypomethylated poplars show higher tolerance to water deficit and highlight a dual role for DNA methylation in shoot meristem: regulation of stress response and genome integrity. 2021. hal-03239719

HAL Id: hal-03239719 https://hal.science/hal-03239719

Preprint submitted on 27 May 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Title:

1

5

8 9

28

32

- 2 Hypomethylated poplars show higher tolerance to water deficit and highlight
- a dual role for DNA methylation in shoot meristem: regulation of stress
- 4 response and genome integrity
- 6 Short title:
- 7 DDM1-dependant DNA methylation in meristem
- 10 M.D. Sow*¹, A-L. Le Gac*^{1¥}, R. Fichot¹, S. Lanciano^{2,3}, A. Delaunay¹, I. Le Jan¹, M-C. Lesage-
- 11 Descauses⁴, S. Citerne⁵, J. Caius⁶, V. Brunaud⁶, L. Soubigou-Taconnat⁶, H. Cochard⁷, V.
- 12 Segura^{4†}, C. Chaparro⁸, C. Grunau⁸, C. Daviaud⁹, J. Tost⁹, F. Brignolas¹, S.H. Strauss¹⁰, M.
- 13 Mirouze^{2,3} and S. Maury^{\$1}
- ¹ LBLGC, INRAE, Université d'Orléans, EA 1207 USC 1328, 45067 Orléans, France. ² IRD, UMR 232
- 15 DIADE, University of Montpellier, France. ³ Université de Perpignan, Laboratory of Plant Genome and
- Development, France. ⁴ BioForA, INRAE, ONF, UMR 0588, 45075 Orléans, France. ⁵ Institut Jean-Pierre
- 17 Bourgin, INRAE, AgroParisTech, Université Paris-Saclay, 78000, Versailles, France. ⁶ Université Paris-
- Saclay, CNRS, INRAE, Université Evry, Institute of Plant Sciences Paris-Saclay (IPS2), 91405, Orsay,
- 19 France. Université de Paris, CNRS, INRAE, Institute of Plant Sciences Paris-Saclay (IPS2), 91405, Orsay,
- 20 France. ⁷ Université Clermont Auvergne, INRAE, PIAF, 63000 Clermont-Ferrand, France. ⁸ IHPE,
- Université de Perpignan, UMR 5244, 66100, Perpignan, France. ⁹ Laboratoire Epigénétique et
- 22 Environnement, LEE, CNRGH CEA, Evry, France. ¹⁰ Department of Forest Ecosystems and Society,
- Oregon State University, Corvallis, OR 97331-5752, USA. * Present address: Institute for Biology III,
- 24 University of Freiburg, 79104 Freiburg, Germany. † Present address: AGAP, Université Montpellier,
- 25 CIRAD, INRA, Montpellier SupAgro, UMR 1334, 34060 Montpellier, France.
- *: First co-authors with equal contribution.
- 27 \$: Corresponding author, stephane.maury@univ-orleans.fr
- 29 The author responsible for distribution of materials integral to the findings presented in this article in
- 30 accordance with the policy described in the Instructions for Authors (www.plantcell.org) is: Stéphane
- 31 Maury (<u>stephane.maury@univ-orleans.fr</u>).

Abstract

As fixed and long living organisms subjected to repeated environmental stresses, trees have developed mechanisms such as phenotypic plasticity that help them to cope with fluctuating environmental conditions. Here, we tested the role DNA methylation as a hub of integration, linking plasticity and physiological response to water deficit in the shoot apical meristem of the model tree poplar (*Populus*). Using a reverse genetic approach, we compared hypomethylated RNAi-*ddm1* lines to wild-type trees for drought tolerance. An integrative analysis was realized with phytohormone balance, methylomes, transcriptomes and mobilomes.

Hypomethylated lines were more tolerant when subjected to moderate water deficit and were intrinsically more tolerant to drought-induced cavitation. The alteration of the *DDM1* machinery induced variation in DNA methylation in a cytosine context dependent manner, both in genes and transposable elements. Hypomethylated lines subjected to water deficit showed altered expression of genes involved in phytohormone pathways, such as salicylic acid and modified hormonal balance. Several transposable elements showed stress- and/or line-specific patterns of reactivation, and we could detect copy number variations for two of them in stressed *ddm1* lines.

Overall, our data highlight two major roles for DNA methylation in the shoot apical meristem: control of stress response and plasticity through transduction of hormone signaling and maintenance of genome integrity through the control of transposable elements.

Keywords: Epigenetics; meristem; drought; transposable element; DNA methylation; phytohormone

INTRODUCTION

59

60

61

62

63

64

65

66

67

68

69

70

71

72

73

74

75

76

77

78

79

80

81

82

83

84

85

86

87

88

89

As long living organisms, trees are subjected to repeated environmental challenges over their lifetime. In recent decades, forest stresses have grown; forest decline has been reported around the world due to heat and drought stress episodes (Allen et al., 2010; Anderegg et al., 2016). In order to survive, they can adjust rapidly using epigenetic as well as physiological levels of regulation (Nicotra et al., 2015). Epigenetics is defined as the study of heritable changes that affect gene expression without changing the DNA sequence (Russo et al., 1996). Efforts have been made, primarily in annuals, to unravel the role of epigenetic mechanisms (in particular DNA methylation) in plant developmental processes, stress response, plasticity, and adaptation (Slotkin and Martienssen, 2007; Colomé-Tatché et al., 2012; Cortijo et al., 2014; Kooke et al., 2015; Raju et al., 2018; Schmid et al., 2018).

Although epigenetic processes are commonly regarded as a source of flexibility in perennials like trees (Bräutigam et al., 2013; Zhu et al., 2013; Yakovlev et al., 2012, 2016; Carneros et al., 2017; Plomion et al., 2016; Lafon-Placette et al., 2018; Sow et al., 2018b), the functional role of DNA methylation in forest trees under environmental changes is still unclear. As a model tree with important genomic resources (Tuskan et al., 2006; Jansson and Douglas, 2007), poplar (*Populus* spp.) has been a prime system for the study of the ecophysiological and molecular basis of drought response (Monclus et al., 2006; Street et al., 2006; Bogeat Triboulot et al., 2007; Cohen et al., 2010; Hamanishi et al., 2012; Fichot et al., 2015). For example, differences in global DNA methylation levels among poplar hybrid genotypes have been shown to correlate with biomass production under water deficit (Gourcilleau et al., 2010; Raj et al., 2011; Le Gac et al., 2019). Recently, DNA methylation-based models have been proposed as a strategy to validate the identity, provenance or quality of agro-forestry products (Champigny et al., 2019). Lafon-Placette et al. (2018) established that drought preferentially induced changes in the DNA methylation of phytohormone-related genes, apparently elevating phenotypic plasticity (Lafon-Placette et al., 2018). This has raised the question of a possible link between epigenetics and phytohormone signaling / synthesis in order to explain plasticity in plants, in particular in meristematic tissues where development takes place (Maury et al., 2019). Phytohormones are key regulatory

elements in plant development and stress response, and their action is often fast and transient. Epigenetic regulations could play a role by modifying the expression of genes in the phytohormone pathways, notably by maintaining them after a hormonal peak, or priming their expression through time to remember the stress episode (i.e., epigenetic memory). In line with this, it has been shown that winter-dormant shoot apical meristems of poplar genotypes grown in field conditions can keep an epigenetic memory of a summer drought episode experienced during the growing season through modifications in DNA methylation (Le Gac et al., 2018; Sow et al., 2018a). The role of epigenetic memory in trees besides poplar, in response to biotic and abiotic stresses, is becoming increasingly documented (Yakovlev et al., 2014; Carneros et al., 2017; Gömöry et al., 2017; Yakovlev and Fosdal, 2017).

In plants, DNA methylation occurs in three different contexts (CHH, CHG and CpG, with H=A, C or T), and the methylation or demethylation of cytosines (*de novo* or maintenance during replication) is ensured by different DNA methyltransferases or DNA glycosylases/lyases, respectively (Zemach et al., 2010; Zhang et al., 2018). DNA methylation affects gene expression (Niederhuth and Schmitz, 2017; Bewick and Schmitz, 2017). While methylation in promoters is usually associated with gene silencing, gene-body methylation is more complex, and is often linked to tissue-specific expression or alternative splicing (Vining et al., 2012; Lafon-Placette et al., 2013; Maor et al., 2015; Zhu et al., 2016; Zhu et al., 2018).

So far, most of the studies conducted on trees and focusing on DNA methylation and gene expression have used a correlative approach. In poplar, extensive gene-body methylation is found in the open chromatin state, and is linked to structural gene characteristics, and correlated with tissue-specific gene expression or stress (Vining et al., 2012; Bräutigam et al., 2013; Lafon-Placette et al., 2013; Liang et al., 2014; Lafon-Placette et al., 2018). In addition to controlling gene expression, it is clear that methylation also helps to maintain genome integrity by silencing the relics of viral genomes (i.e., transposable elements, TEs), stopping them from spreading within the host genome (Ikeda and Nishimura, 2015; Fultz et al., 2015). For a long time considered as 'junk DNA,' the evolutionary impact of TEs is now well established, and TEs

121

122

123

124

125

126

127

128

129

130

131

132

133

134

135

136

137

138

139

140

141

142

143

144

145

146

147

148

149

contribute strongly to genome plasticity in eukaryotes (Lisch, 2012; Ayarpadikannan and Kim, 2014; Hirsch and Springer, 2017). In plants, most TEs can be activated, and their contribution to genome size is not negligible, especially for trees with large genomes (Kejnovsky et al., 2012; Lee and Kim, 2014). DNA methylation is required to silence these TEs located in the heterochromatin, and a decrease in DNA methylation level could result in their reactivation (Lippman et al., 2004; Mirouze et al., 2009; Mirouze and Paszkowski, 2011). The overall functional role of DNA methylation, both for control of gene expression and TE dynamics in a developmental and ecological context, is poorly understood.

DDM1 belongs to the SWI/SNF chromatin remodeling complex, and encodes a chromatin remodeling factor required for the maintenance of DNA methylation. Its depletion affects the distribution of methylation in all sequence contexts (Vongs et al., 1993; Jeddeloh et al., 1998; Gendrel et al., 2002; Zhu et al., 2013; Zemach et al., 2013). DDM1 was first identified in Arabidopsis through EMS (ethyl methane sulfonate) treatment, which caused a "decrease in DNA methylation" (Vongs et al., 1993). Vongs et al., showed that *Arabidopsis ddm1* mutants displayed a 70 to 75% reduction in cytosine methylation compared to the wild-type (WT). Nonetheless phenotypic variations only appeared several generations after the initial loss of *DDM1* activity, notably through reactivation of TEs (Miura et al., 2001). Several studies further characterized ddm1 mutants in Arabidopsis (Saze and Kakutani, 2007; Yao et al., 2012; Zemach et al., 2013; Cortijo et al., 2014; Ito et al., 2015; Kawanabe et al., 2016), turnip (Fujimoto et al., 2008; Sassaki et al., 2011), maize (Li et al., 2014), and rice (Higo et al., 2012; Tan et al., 2016). In poplar, RNAi ddm1 lines have been obtained by targeting the transcripts of the two orthologous *DDM1* paralogs in *Populus tremula × Populus alba* cv. INRA 717-1B4 (Zhu et al., 2013). Under standard greenhouse conditions, the regenerated lines did not show developmental defects, but newly formed leaves displayed a mottled phenotype after a cycle of dormancy (Zhu et al., 2013). These RNAi ddm1 lines have never been studied under stressed conditions.

To investigate whether variation in DNA methylation has the potential to facilitate tree plasticity under stress, we studied these *ddm1* RNAi lines during a water stress

experiment. Here, plasticity is defined as modifications in phenotype (growth, morphology, anatomy, or gene expression) under a drought - re-watering regime for a given genotype (Bradshaw, 2006; Nicotra et al., 2010, 2015). To address this question in a developmental context, we focused our analysis on the shoot apical meristem (SAM, center of plant morphogenesis) one week after re-watering in order to focus on 'stable' post-stress epigenetic events (Lafon-Placette et al., 2018). Previous studies have shown that SAM is a critical organ where epigenetic modifications can affect plant development (Gourcilleau et al., 2010; Lafon-Placette et al., 2013; Conde et al., 2017; Lafon-Placette et al., 2018; Le Gac et al., 2018, Sow et al., 2018; Maury et al., 2019). To examine whether plasticity was associated with epigenetic variation within wild type or RNAi lines, we combined a fine scale ecophysiological characterization of growth dynamics and water relations with genomics (identification of differentially methylated regions (DMR) using whole genome bisulfite sequencing, differentially expressed genes (DEG) using RNA-seq, and active transposable elements using mobilome-seq). We report a comprehensive analysis of the functional role of DNA methylation in the poplar SAM in terms of gene expression, reactivation of TEs, and hormonal balance in response to variations in water availability.

RESULTS

150

151

152

153

154

155

156

157

158

159

160

161

162

163

164

165

166

167

168

169

170

171

172

173

174

175

176

177

178

Phenotypic and physiological differences among lines under well-watered

conditions

Plants from the WW treatment remained close to field capacity during the whole experiment, with relative extractable water (REW) never dropping below 70% (Fig. 1) and Ψ_{pd} values remaining above -0.5 MPa (Sup. Fig. 2A). There was no significant difference in either REW or Ψ_{pd} among lines (Fig. 1 and Sup. Fig. 2A). The WT and ddm1 lines all showed linear growth, and exhibited a similar height growth rate during the experiment (1.27 ± 0.07 cm.day⁻¹, P = 0.67; Fig. 2A). However, the WT had a slightly higher diameter growth rate than the ddm1 lines (0.11 ± 0.02 vs. 0.08 ± 0.01 mm.day⁻¹, P = 0.036; Fig. 2A). Differences among lines were much stronger for total leaf area, with

ddm1 lines exhibiting significantly lower values (28 % reduction on average, P = 0.021) compared to the WT (Sup. Fig. 3). This was explained by a particular vertical profile of individual leaf area in the middle canopy (Sup. Fig. 3).

All lines showed comparable leaf Ψ_{min} , leaf $\delta^{13}\text{C}$ and stomatal density (Sup. Fig. 2B), but significant differences were observed for xylem vulnerability to cavitation (P < 0.001, Fig. 2B). The WT was the most vulnerable ($P_{50} = -2.16 \pm 0.05$ MPa), while ddm1-23 was the most resistant ($P_{50} = -2.45 \pm 0.04$ MPa), and ddm1-15 was intermediate ($P_{50} = -2.28 \pm 0.04$ MPa) (Table 1). Differences among lines were not found in other xylem structural or biochemical traits (Table 1).

The proportion of "mottled leaves" reached 40% for *ddm1-23*, and more than 60% for *ddm1-15* at the end of the experiment, while it remained close to zero for the WT (Sup. Fig. 4). Symptom occurrence was not linear but tended to increase at a specific physiological stage (Sup. Fig. 4). In addition, the line *ddm1-23* exhibited several leaves that tended to fold around the midvein, a physical defect that was not found in the WT, and only rarely in *ddm1-15* (Sup. Fig. 4).

Table 1: Xylem structural, functional and biochemical traits measured for the wild type and the two RNAi-ddm1 (ddm1-15, ddm1-23) poplar lines in control (well-watered, WW) and stress (moderate water deficit followed by rewatering, WD-RW) treatments. Values are genotypic means \pm SE (n = 6 per line per treatment). The P50 is the xylem tension inducing 50% loss of hydraulic conductance estimated from vulnerability curves (see Materials and Methods for additional information). S/G corresponds to the ratio between syringyl-like (S) and guaiacyl-like lignin monomeric units (G). Treatment effects were evaluated within each line by using a t-test. Different letters indicate significant differences between genotypes within treatments following Tukey's post hoc test. Levels of significance are *, 0.01 < P < 0.05; **, 0.001 < P < 0.01; ***, P < 0.001; ns, non-significant; na, not available.

Phenotypic traits	WT	ddm1_15	ddm1_23
Wood density (g.cm-3) - WW	0.31 ± 0.01	0.31 ± 0.004	0.32 ± 0.007
Wood density (g.cm-3) - WD-RW	0.40 ± 0.02***	0.42 ± 0.01***	0.43 ± 0.02***
Xylem vessel diameter (μm) - WW	44.28 ± 1.37	44.01 ± 0.97	41.08 ± 2.39
Xylem vessel diameter (μm) - WD-RW	42.00 ± 1,48	43.18 ± 0.56	40.36 ± 0.89
Xylem vessel density (nb.mm²) - WW	100.61 ± 10.85	100.09 ± 5.10	112.13 ± 16.67
Xylem vessel density (nb.mm²) - WD-RW	111.24 ± 9.61	105.23 ± 5.06	123.66 ± 4.37
Theoretical specific hydraulic conductivity (kg.m.s-1.Mp-1) - WW	11.81 ± 0.90	11.31 ± 0.67	9.82 ± 1.08
Theoretical specific hydraulic conductivity (kg.m.s-1.Mp-1) - WD-RW	10.15 ± 0.67	11.24 ± 0.52	10.69 ± 0.86
P50 values (Mpa) - WW	2.12 ± 0.06a	2.25 ± 0.05ab	2.39 ± 0.05b
Lignin klason prediction by MIRS (%) -WW	21.24 ± 0.42	20.90 ± 0.34	20.26 ± 0.44
Lignin klason prediction by MIRS (%) - WD-RW	20.56 ± 0.26	20.73 ± 0.46	19.99 ± 0.27
Tension wood prediction by MIRS (%) - WW	11.05 ± 3.22	13.58 ± 2.89	14.59 ± 3.68
Tension wood prediction by MIRS (%) - WD-RW	18.24 ± 1.87*	16.39 ± 2.20ns	22.39 ± 2.42ns
S/G prediction by MIRS (%) - WW	1.15 ± 0.03	1.18 ± 0.03	1.22 ± 0.30
S/G prediction by MIRS (%) - WD-RW	1.20 ± 0.02	1.20 ± 0.03	1.16 ± 0.01

Differences in drought response

Soil water content of plants in drought conditions started to be significantly lower four days after the initiation of water deficit. Values of REW were maintained around 35% until t₁; re-watering at t₁ increased REW back to control values (Fig. 1). Predawn leaf

water potential (Ψ_{pd}) at t_1 was significantly lower than in well-watered plants (P < 0.001), and reached approximately -0.8 MPa, with no difference among lines (Sup. Fig. 2A); in contrast, Ψ_{min} values were not significantly affected by drought (Sup. Fig. 2A). Height and diameter growth rates during drought were significantly lower in the WT only (Fig. 2A, P < 0.001 and P = 0.026, respectively). The effect persisted after re-watering until t_2 for diameter (P < 0.001) while height growth recovered to control values.

In response to water deficit, g_s started to decrease significantly 10 days after drought initiation, *i.e.* once REW had dropped below 40% (P = 0.027 for WT, P = 0.171 for ddm1_15 and P = 0.021 for ddm1_23 Fig. 1, 2C). The WT and ddm1-23 showed relatively comparable dynamics, and reached almost an 80% decrease relative to controls, while stomatal closure was less pronounced in ddm1-15 (Fig. 2C). A_{net} was less impacted than g_s , especially in ddm1-15, in agreement with the moderate intensity of water deficit (Fig. 2C). Therefore, the increase in intrinsic water-use efficiency (*i.e.* the ratio A_{net}/g_s) was more pronounced in the WT and ddm1-23 (Fig. 2C), which was confirmed by a greater δ^{13} C increase in these same lines (Sup. Fig. 2B). Total stomatal density was not impacted by water deficit in ddm1 lines, while it was significantly increased in the WT (P = 0.030, Sup. Fig. 2C). Xylem traits were only seldom affected by water deficit (Table 1). Xylem density was significantly increased in all lines (P < 0.001), while the proportion of tension wood increased in the WT only (Table 1). Water deficit had no significant effect on the occurrence of mottled or folded leaves (Sup. Fig. 4).

Phytohormone concentration in SAMs

There was no significant change among lines in terms of salicylic acid (SA) or the different types of cytokinin in the WW treatment (Fig. 3). In response to water deficit-rewatering, SA increased while zeatin riboside and zeatin -O- glucoside riboside decreased in RNAi lines compared to the WT (Fig. 3). The other type of cytokinin, the isopentenyladenosine, showed a more complex pattern in RNAi lines. In addition, the ddm1-23 line showed a significant response for SA and for two cytokinins, with a similar trend to WT (Fig. 3). The *ddm1-15* line showed a significant response for one cytokinin only (Fig. 3). ABA and free auxin remained unaffected in all treatments.

Methylome analysis and identification of line- and stress-specific DMRs

Global DNA methylation content (HPLC analysis) ranged from 17.5 to 21.3 % between lines and treatments (Sup. Fig. 5A). There was no significant line x treatment interaction effect. Global DNA methylation was significantly lower in RNAi lines than in the WT under water deficit only, although there was no significant effect of water deficit (Sup. Fig. 5A). Cytosine methylation percentages (WGBS analysis) for the three contexts ranged from 18.6 to 19.6% in CpG, 4.4 to 6.0 in CHG and 1.6 to 2.0 in CHH contexts, with the *ddm1-15* lines displaying the lowest values in all contexts (Sup. Table 1, Sup. Fig. 1D).

Only a few stress-specific DMRs were identified. In contrast, thousands of line-specific DMRs were identified, especially for *ddm1-15* (Sup. Fig. 5B). The two RNAi lines displayed a different number of DMRs (29785 *vs.* 30925 for *ddm1-15* in WW and WD-RW treatments, respectively, and 11409 *vs.* 11104 for *ddm1-23* in WW and WD-RW treatments, respectively). Most of these DMRs were hypomethylated and context-dependent with higher values found in CHG context, especially in *ddm1-15* (20310 *vs.* 20847 DMRs in WW and WD-RW treatments, respectively) (Sup. Fig. 5C & 5D). Line-specific DMRs were unequally distributed in the three different contexts. In the CpG context, DMRs presented a bimodal distribution with both hypo and hypermethylated DMRs (Sup. Fig. 5E). In the CHG context, most DMRs were hypomethylated, while in the CHH context DMRs were mostly slightly hypomethylated (Sup. Fig. 5E). The number of stress-specific DMRs was similar between the WT and *ddm1* lines, and between the hypo and hypermethylated states (Fig. 4A). These DMRs were mainly found in CG and CHG contexts (Fig. 4A).

In order to focus on DMRs systematically associated with *DDM1* defects, we identified DMRs commonly shared between *ddm1-23* and *ddm1-15* RNAi lines in either WW or WD-RW treatments (Fig. 4B). Regardless of the treatment, common DMRs were systematically over-represented in the CHG context (3463 *vs.* 3378 DMRs in WW and WD-RW treatments, respectively) and were mostly hypomethylated (Fig. 4B). Among common DMRs, 19 and 21% were localized in genes, 7 and 8% in promoters (+/-2kb from the TSS) and 1% in transposable elements (TEs), for WW and WD-RW treatments,

respectively (Sup. Fig. 6A). The majority of DMRs (73 and 71% in WW and WD-RW treatments, respectively) were therefore localized in intergenic regions (Sup. Fig. 6A). In the WW treatment, 879 genes were found to be strictly included within the common DMRs (hereafter called DMGs for Differentially Methylated Genes), while 910 DMGs were found in the WD-RW treatment. These numbers increased considerably (up to more than 13,000 genes) when enlarging the windows for DMR identification from 2 kb to 25 kb (Sup. Fig. 6B). In both treatments, a similar number of hypo and hypermethylated DMGs was found in the CG context, while in the CHG and CHH contexts, DMGs were mostly hypomethylated (Fig. 4C). In the CHH context, DMGs were slightly methylated (between 25 to 50% of difference), compared to the CG and CHG contexts (Fig. 4C). Gene Ontology annotation of DMGs revealed significant enrichment in biological functions such as multicellular organism development (including shoot system development), negative regulation of biological processes, and response to abiotic stress (including response to hormones) (Sup. Fig. 6C).

Transcriptome analysis for the water deficit – rewatering condition

The identification of DEGs focused on the WD-RW treatment, but revealed clear differences between the WT and the *ddm1*-23 lines. An average of 96 % mapping efficiency was found for the *P. tremula* × *alba* reference genome (v1). A total of 32 048 genes were analyzed, but only 136 genes were significantly differentially expressed (*P* < 0.05). Gene ontology annotation revealed significant enrichment in functions such as defense response, including immune response, response to hormones (SA, Ethylene), response to chitin, and regulation of RNA metabolism (Fig. 5A). The 136 DEGs (76 upregulated and 60 down-regulated) were grouped according to *Arabidopsis thaliana* gene annotation homology into seven main classes: cell death, defense response and cell wall, immune response, metabolism, signalization, transcription factors, and unknown function (Fig. 5B). Genes related to immune response were systematically up-regulated (*RBOHD*, *CYP94B1*, *RLP1*, *RLP56*, *RPM1*, *PLDGAMMA1*, *PDF1*). Most genes related to transcription factors (15/17) were also up-regulated (*WRKY*, *MYB106*, *ERF*, *SZF2*, *PDF2*, *SVP/AGL22*), with only two genes down-regulated (*MYB48* and *DTA2*). Defense and cell wall related genes were both up- (18, including *CHITIV*, *KT11*, *PR4*, etc.

involved in plant pathogen-interaction) and down-regulated (13). Phytohormone pathways were also over-represented in distinct classes with 13 DEGs (8 up- and 5 down-regulated) directly involved in defense responsive hormone biosynthetic pathways, such as SA pathways (*SAMTs*), the jasmonic acid (JA) pathway (*OPR2*, *CYP94B1*), the ethylene (ET) pathway (*ERF1*, *ERF12*), or auxin responsive genes (*SAUR29*, *GH3.1*, *IBR3*, *BG1*, *ABCG36*), gibberellic acid (GA) synthesis (*GA3OX1*) and cytokines (CK) pathways (*AHP1*) (Fig. 5B).

In order to test the link between gene expression and DNA methylation, DEGs were co-localized with common DMRs among ddm1 lines. Although only seven DEGs (Potri.001G048700, Potri.001G065300, Potri.002G192400, Potri.009G051300, Potri.016G130900, Potri.T041700, Potri.T085000) overlapped with the DMR genomic locations, 53 were located in the direct vicinity of a DMR (+/- 10 kb) and 98 at +/- 25 kb (Sup. Fig. 7A). A significant and negative rank correlation (Spearman's rho = -0.32, P < 0.001) was observed between methylation in the three contexts and expression values when considering at least a +/- 10 kb window for DMRs to reach statistical significance (Sup. Fig. 7B).

Mobilome analysis and identification of line- and/or stress-specific active TEs

We identified between 44 (ddm1-23 in WW) and 169 (ddm1-15 in WD-RW) TE families producing extrachromosomal circular DNAs (eccDNAs), depending on lines and treatments (Sup. Fig. 8A). In each line, the number of identified TE families was always higher in the WD-RW treatment (Sup. Fig. 8A). Overall, the two different classes of TEs (DNA transposons and retrotransposons) were detected in our mobilome-seq data (Fig. 6A). Most of the eccDNAs identified belonged to the annotated Gypsy, Copia, ENSPM, L1, Ogre, POPGY and SAT superfamilies of TEs and repeats. TEs Depth depth oOf cCoverage (DOC) ranged from 4X to 51000X for the most active TEs, whereas Split Reads (SRs) coverage ranged from 3X to 4600X (Fig. 6A). Reads spanning the two TE extremities constitute an evidence of a circular TE and were detected using a split reads (SRs) mapping strategy. We detected a high number of SRs with a coverage ranged from 3X to 4600X confirming the presence of eccDNAs from TEs (Fig. 6A). The detection of SRs suggested the presence of reads spanning the junction of eccDNAs.

333

334

335

336

337

338

339

340

341342

343

344

345

346

347

348

349

350

351

352

353

354

355

356

357

358

359

360

Given the range of variation of the DOC coverage, we assigned TE families to four groups following Lanciano et al., (2017). TEs identified in the WT and RNAi lines belonged to the four groups in both WW and WD-RW treatments (Fig. 6A). The "TE***"group was exclusively represented by the *Gypsy* superfamily, while the "TE***"group was represented by DNA transposons. In contrast, "TE*" and "TE" groups were represented by different superfamilies (Fig. 6A).

The most active TE (Gypsy23, with a DOC ranging from 36000X to 52000X) was present in all lines, but only in the WD-RW treatment (Fig. 6A). The second most active TE also belonged to the Gypsy superfamily (Gypsy27, DOC ranging from 14000X to 25000X), and was detected in the three lines in the WW treatment but only in the WT line in the WD-RW treatment. We also identified eccDNAs that were line- and/or stressspecific, such as those originating from the satellite SAT-1 specifically activated in ddm1-15, in both WW and WD-RW treatments (9000X and 5200X, respectively), and in the WT line only in the WD-RW condition. Two DNA-3-3 TEs with the same name, but different in terms of sequence were also detected in the WW treatment only. The first one (named DNA-3-3 1) was activated in the two RNAi lines (6000X in ddm1-15 and 1500X in ddm1-23), while the second one (named DNA-3-3_2) was specific to ddm1-15 (5200X) (Fig. 6A). We were also able to detect TEs that belonged to the "TE+" group that were line- or stress-specific (Fig. 6A). GO annotation of the genes co-localizing with TEs (+/- 10 kb of genes) revealed enrichment in functions such as response to stress. including hormone response, multicellular organism development, and negative regulation of cellular processes (Sup. Fig. 8B). The number of genes identified in the vicinity of TEs varied between 45 (TEs inside genes) and 1788 (when considering TEs at +/-25kb of genes) (Sup. Fig. 8C). However, only a few of these genes showed changes in their expression level (seven DEGs when considering the vicinity of +/- 25kb; Potri.005G223200, Potri.006G062100, Potri.013G100800, Potri.013G101000, Potri.013G103000, Potri.013G120800, Potri.016G070100).

Methylation of active TEs and estimation of copy number variations for highly active TEs

About 21% of the mobilome-seq TE families strictly co-localized within common DMRs. This percentage raised to more than 50% when considering the presence of +/- 25 kb of a DMR in the vicinity (Sup. Fig. 8C). These methylated active TE families were in majority hypomethylated (*ca.* 92% of the TE families) in *ddm1* lines (Fig. 6B). In the WW treatment, active TEs were hypomethylated mostly in CG and CHG contexts, while in the WD-RW treatment, active TEs were hypomethylated in CG and CHG contexts but mostly hypermethylated in the CHH context (Fig. 6B). The most active TEs were methylated in CHG context.

To investigate whether TE activity (as detected by eccDNA presence) had led to new integrations in the genome, copy number variation was assessed for three active TEs (*DNA-3-3_1*, *Gypsy23* and *SAT-1*) localized in or near DMRs by qPCR analysis (Fig. 6C). For *DNA-3-3_1*, there was no significant variation in the copy number regardless of the lines and treatments (Fig. 6C). In contrast, an increase in copy number was detected in the WD-RW treatment for *Gypsy23* in *ddm1-23* (15 copies), and for *SAT-1* in *ddm1-15* (18 copies) (Fig. 6C). *Gypsy23* was hypomethylated in the CHG context, while *SAT-1* was found in +/- 2kb of DMRs that were CG and CHG hypomethylated.

DISCUSSION

DDM1-dependent DNA methylation plays a role in tree phenotypic plasticity in response to water deficit

Hypomethylated poplar RNAi-ddm1 lines are more tolerant to water deficit

Tolerance to water deficit is a complex trait encompassing multiple physiological determinants that can relate to processes as diverse as growth maintenance, survival, or recovery, depending on the context {intensity × duration} considered (McDowell et al., 2008; Volaire et al., 2018). Poplars are among the most sensitive temperate trees to water deficit although significant variation naturally occurs between and within species (Monclus et al., 2006; Street et al., 2006; Fichot et al., 2015). The water deficit imposed in our experiment was deliberately controlled and moderate, as attested by the relatively

391

392

393

394

395

396

397

398

399

400

401

402

403

404

405

406

407

408

409

410

411

412

413

414

415

416

417

418

419

420

high Ψ_{pd} (ca. -0.8 MPa) and the small effects on net CO₂ assimilation rates. This avoided rapid growth cessation and instead promoted steady-state acclimation. However, this was sufficient to reveal clear differences in drought responses between the wild type and hypomethylated RNA_i-ddm1 lines. While growth was progressively slowed down in the wild type as REW dropped below 40% (Bogeat-Triboulot et al., 2007), both RNAi-ddm1 lines remained unaffected, suggesting improved tolerance to moderate water deficit. RNA-ddm1 lines showed a limited increase in time-integrated WUE in response to water deficit as compared to the wild type, which was partly attributable to a less important stomatal closure, at least in ddm1-15. The slightly more negative leaf Ψ_{min} observed in RNA;-ddm1 lines tended to confirm the idea that improved tolerance might have been linked partly to a better ability for leaf gas exchange maintenance. In addition, while stomatal density was comparable between the wild type and RNA_i-ddm1 lines under standard conditions, stomatal density increased in response to water deficit in the wild type only. ddm1 mutants in Arabidopsis were reported to have more stomata with modified organization (grouped clusters of two or more stomata) (Vassileva et al., 2016), suggesting that *DDM1* modifications have the potential to modify stomatal patterning and therefore leaf physiology. Our findings go further and suggest that these effects may also depend on the environmental context. Interestingly, stomatal density seems to be tightly linked to the dynamics of VPD- and irradiance-induced stomatal closure/opening under water deficit in poplar, with higher densities being correlated with faster stomatal dynamics (Durand et al., 2019). It is therefore possible that the increased stomatal density observed in the wild type under water deficit contributed to a higher stomatal sensitivity, providing one possible explanation for constrained leaf gas exchange and growth reduction as compared to RNA_i-ddm1 lines.

Besides differences in dynamic drought responses, our results also suggest that RNA_i-ddm1 lines were intrinsically more tolerant to severe water deficit because of higher xylem resistance to drought-induced cavitation. Xylem resistance to drought-induced cavitation is a key trait for plant water relations in a context of survival, as it partly sets operational limits for water transport under tension (Brodribb & Cochard, 2009; Barigah et al., 2013). How modifications of the DDM1 machinery can affect xylem resistance to cavitation remains unknown at this stage. Interestingly, basic xylem

422

423

424

425

426

427

428

429

430

431

432

433

434

435

436

437

438

439

440

441

442

443

444

445

446

447

448

449

properties such as vessel diameter and density, xylem density, or even xylem biochemical composition were not significantly different from the wild type. However, given the mechanistic understanding of drought-induced cavitation in angiosperms (Choat et al., 2018), it is likely that the increased resistance observed in the RNA_i-ddm1 lines was primarily linked to modifications of the ultrastructure of vessel-vessel bordered pits (Plavcová Hacke, 2011; Awad et al., 2012; Dusotoit-Coucaud et al., 2014; Herbette et al., 2014). Whether the slight gain in intrinsic cavitation resistance (*i.e.* a few tenth of an MPa) does promote increased survival rates under severe water deficit, and whether epigenetics might be exploited as such for increasing drought tolerance, remains to be purposely tested.

Several DEGs identified in the SAM of RNAi-ddm1 lines could explain at least in part the improved tolerance to moderate water deficit. Indeed, genes involved in the cuticle and waxes (CER8, FLA12) that provide protection from abiotic and biotic stresses were upregulated in RNAi-ddm1 lines. Increased levels of cuticular waxes have been associated with enhanced drought tolerance by preventing uncontrolled water loss (Chen et al., 2011; Wettstein-Knowles, 2016). Similarly, the MYB106 TF, a major regulator of cuticle formation was upregulated in the ddm1 line (Oshima and Misuda, 2013, 2016). Other transcription factors (TFs) (SVP, MYB48, MYB106, WRKY36, WRKY33, WRKY53) associated with drought tolerance in plants were also upregulated in the ddm1 lines (Bechtold et al., 2016; Sun & Yu, 2015; He et al., 2016; Guo et al., 2019). Finally, previous studies in Arabidopsis ddm1 mutants and derived epiRILs subjected to drought, or more broadly to increased nutrients or salt stress, have provided evidence that variation in DDM1-derived DNA methylation can cause substantial heritable variation in ecologically important plant traits and their plasticity (Reinders et al., 2009; Johannes et al., 2009; Latzel et al., 2013; Cortijo et al., 2014; Zhang et al., 2013, Kooke et al., 2015; Cho et al., 2016; Zhang et al., 2018; Furci et al., 2019).

Hypomethylated poplar RNAi-ddm1 lines show leaf symptoms commonly observed in response to pathogen infection

First characterized by Zhu et al., 2013, poplar RNAi-ddm1 lines did not show any growth or developmental defects when grown under standard greenhouse conditions, but some newly formed leaves displayed a mottled phenotype after a dormancy cycle. This is similar to other reports in *Arabidopsis* and other species, where developmental abnormalities usually appear in later generations (Kakutani, 1997; Tan et al., 2016; Corem et al., 2018; Long et al., 2019). In our RNAi-ddm1 lines we found two distinct leaf phenotypes: "mottled leaves" and "folded leaves." However, the two RNAi lines differed in terms of the quantities of symptomatic leaves, with higher values in *ddm1-15* for mottled leaves. This was observed even though our stress treatments had no effect on leaf symptom numbers for either line. The alteration of leaf phenotype has already been attributed to *DDM1* mutation in *Arabidopsis*, where mutants showed altered leaf shape (Kakutani et al., 1995; Qüesta et al., 2013; Kooke et al., 2015), and curled or folded leaves were also observed in hypomethylated *ddc* (*drm1 drm2 cmt3*) mutants (Forgione et al., 2019). However, here we report that stressed conditions do not have an effect on this phenotype.

The presence of mottled leaves could be suggestive of a hypersensitive response (HR) which could result in the hyperactivation of disease resistance genes (Zhu et al., 2013) due to the constitutive hypomethylation in RNAi-ddm1 lines. This is in agreement with the recent report of Furci et al., (2019) showing that hypomethylation in Arabidopsis ddm1-epiRILs at selected pericentromeric regions controls quantitative disease resistance against Hyaloperonospora arabidopsidis, which is associated with genomewide priming of defense-related genes. Lesion mimic mutants, characterized by the formation of necrotic leaves (hereafter called mottled leaves) in the absence of pathogens have been identified, and most importantly, these mutants show enhanced resistance to pathogen infection. This is probably due to mis-regulation of defense responsive genes (Lorrain et al., 2003; Wu et al., 2008). In poplar RNAi-ddm1 lines, we found an important set of genes involved in defense and immune response that were significantly and differentially expressed in RNAi lines compared to the WT. Immune responsive genes were upregulated in RNAi-ddm1 lines, while defense related genes were in majority downregulated. Consequently, genes involved in cell death and leaf senescence (MLO12 and NHL10) were upregulated. The activation of immune response

genes in RNAi-ddm1 lines suggests that trees react as if they were attacked by pathogens. This could be particularly important as it could prime ddm1 lines against future pathogen infections (Lopez Sanchez et al., 2016; Furci et al., 2019). Indeed, different TFs (WRKY18, WRKY33, WRKY70, WRKY53 and ERF1) known to be activated during pathogen attack were overexpressed in ddm1 lines. The WRKY TFs are known to play important roles in plant defense responses that are related to attacks by several pathogens. Accordingly, overexpression of one of these WRKY TFs in A. thaliana, Brassica napus or Oryza sativa resulted in enhanced disease resistance (Li et al., 2004; Wang et al., 2014; Wang et al., 2017; Chujo et al., 2007; Marcel et al., 2010; Chen and Chen, 2002; Abeysinghe et al., 2018). In poplar, overexpression of WRKY18 (with WRKY35) also activates pathogenesis-related genes, and increases resistance to the biotrophic pathogen Melampsora (Jiang et al., 2017).

The RNAi-ddm1 lines also had altered expression of a cluster of disease resistance genes, as was already reported in *A. thaliana* (Saze and Kakutani, 2007; Stokes et al., 2002; Lopez Sanchez et al., 2016; Furci et al., 2019). There are multiple mechanisms by which DNA hypomethylation could regulate defense gene induction in *cis* (promoter or nearby TEs) or *trans* contexts. A few *cis*-regulated genes can control the induction of several groups of defense genes by DNA (de)methylation, and hypomethylation can influence chromatin structure at distant genome loci such as TEs activating the RdDM pathway (Grandbastien, 1998; Makarevitch et al., 2015; Quadrana et al., 2019). This recent data in Arabidopsis have shown that methylation controls global defense gene responsiveness *via* trans-acting mechanisms (Lopez Sanchez et al., 2016; Cambiagno et al., 2018; Furci et al., 2019). Accordingly, we found, by overlapping DMRs and DEGs, that only seven DEGs co-localized with DMRs. Expression and methylation values (DEGs at +/-10 kb of DMRs) showed a significant correlation. This suggests that these genes may not be the primary target of *DDM1*.

Active extrachromosomal forms of TEs from several families were identified in water deficit conditions or in *DDM1* lines (mostly hypomethylated). Some of these endogenous TE insertions are located in the vicinity of stress responsive genes (45) and of DEGs (3, at +/-10 kb of TEs). Furci et al., (2019) reported that DNA hypomethylation at TE-rich epiQTLs in *Arabidopsis thaliana* could mediate the induction of defense-

513

514

515

516

517

518

519

520

521

522

523

524

525

526

527

528

529

530

531

532

533

534

535

536

537

538

539

540

541

542

related genes across the genome via a *trans*-acting mechanism. Quadrana et al., (2019) further showed that in *Arabidopsis* epiRILs, the insertion of *Copia* elements preferentially targets environmentally responsive genes such as cell death, defense response and immune response, potentially facilitating rapid adaptation. Here, we could detect increased copy numbers for two TE families in the hypomethylated *ddm1* stressed lines. The potential impact of these new insertions on adaptation is unclear. Finally the fact that only two TE families showed increased copy number suggests that additional mechanisms prevent genomic insertions of reactivated TEs.

Hypomethylated poplar lines exhibit an altered phytohormonal balance in the shoot apical meristem

Phytohormones are key regulators of plant development and response to stress (Gaillochet & Lohmann, 2015), and have been linked to epigenetic control (Latzel et al., 2012; Yamamuro et al., 2016; Ojolo et al., 2018; Raju et al., 2018), where this interplay could have a major role in meristems for developmental plasticity (Maury et al., 2019). Here, we report that ddm1 lines exhibited modified shoot apex hormonal balance immediately post-rewatering. Although abscisic acid (ABA) (Zhang et al., 2006; Fernando & Schroeder, 2015) and free auxins (Shi et al., 2014; Basu et al., 2016) are known to mediate physiological responses to water deficit, we found no treatmentinduced difference in the SAMs of ddm1-lines. In contrast, salicylic acid (SA) and cytokinins (CK) showed significant variations among our ddm1 lines compared to the WT after drought treatment. Increased SA level was accompanied by a decrease in CK content (especially for zeatine riboside and zeatine-O-glucoside riboside) in post-stress ddm1 lines. This is in agreement with several reports, which found that drought-stressed plants tend to increase the endogenous level of SA promoting tolerance to several stresses including drought (Munne-Bosch and Penuelas, 2003; Bandurska & Stroi ski, 2005; Azooz & Youssef 2010; Pandey & Chakraborty, 2015; Sedaghat et al., 2017), and decreasing CK levels (Havlovà et al., 2008; Nishiyama et al., 2011; Ha et al., 2012). Altogether our data show that the shoot apex of hypomethylated, stressed lines displayed specific hormonal changes for SA and CK. Shoot apices were collected after three weeks of stress (the day of rewatering) to measure the hormonal balance at the

544

545

546

547

548

549

550

551

552

553

554

555

556

557

558

559

560

561

562

563

564

565

566

567

568

569

570

571

572

end of the treatment. This timing of sampling could explain why drought-related modifications in ABA or auxin contents were not observed. Correia et al., (2014) have shown in *Eucalyptus globulus* that while drought causes an increase in ABA levels in leaves, rewatering was accompanied by a gradual decrease and stressed and non-stressed plants reached the same amount of ABA seven days post-drought. This also in agreement with Cotrozzi et al., (2017) who showed a very transient peak of ABA following drought conditions in *Quercus ilex*. However, this timing of sampling for hormonal content enabled us to compare it with the presumably (meta)stable epigenetic condition (memory) one week post-rewatering.

DMGs and DEGs nearby active TEs identified in the SAM of ddm1 stressed lines were mainly involved in development, stress response and phytohormone pathways (such as JA, SA and ethylene). When comparing the genome-wide distribution of DMRs to DEGs in poplar, Lafon-Placette et al., (2018) showed that variations in soil water availability induced changes in DNA methylation preferentially in genes involved in phytohormone metabolism and signaling, potentially promoting phenotypic plasticity. Accordingly, poplar SAMs may also retain an environmental epigenetic memory by targeting hormone-responsive genes (Le Gac et al., 2019). SAMT1, a salicylic acid methyltransferase gene was still up-regulated one week post-stress in RNAi-ddm1 lines compared to the WT, supporting the increase in SA content at the end of the stress. When screening for candidate genes for drought tolerance in *Coffea arabica* cultivars, Mofatto et al., (2016) found that SAMT1 was upregulated under drought conditions. Zhang et al., (2016) have also shown that *DDM1* affects early seedling growth heterosis in Col/C24 hybrids. Indeed, ddm1 mutants showed impaired heterosis (Kawanabe et al., 2016) and increased expression of non-additively expressed genes related to salicylic acid metabolism. They proposed that *DDM1* acts as an epigenetic link between salicylic acid metabolism and heterosis, also protecting plants from pathogens and abiotic stress. SA accumulation has also been widely used as a reliable marker of elevated defense responses under pathogen infection, and has been associated with HR cell death or systemic acquired resistance, as well as with *DDM1* mutation (Dong, 2004; Song et al., 2004; Liu et al., 2010; Zhang et al., 2016; Badmi et al., 2019).

574

575

576

577

578

579

580

581

582

583

584

585

586

587

588

589

590

591

592

593

594

595

596

597

598

599

600

601

602

The elevated amount of SA levels in RNAi-ddm1 lines could be suggestive of acquired disease resistance in ddm1 mutants. Similarly, two genes (CYP94B1 and OPR2) involved in JA metabolism were upregulated in the RNAi-ddm1 lines. CYP94B1 and OPR2 have been shown to contribute to the attenuation of the JA-dependent wound responses in response to pathogen attack (Koo et al., 2014; Pandey et al., 2017; Wasternack & Hausse, 2018). Moreover, Latzel et al., (2012) have established a positive correlation between DNA methylation variations (epiRILs) and JA and SA responses, and proposed that part of the variation of plant defenses observed in natural populations may be due to underlying epigenetic, rather than entirely genetic, variation. Several TFs involved in abiotic (drought) or biotic stress, and acting in phytohormone pathways, were upregulated in stressed ddm1 lines in comparison to WT; this includes genes such as SVP (SHORT VEGETATIVE PHASE) that can confer drought resistance by regulating ABA catabolism (Wang et al., 2018), MYB48 that can improve tolerance to drought when overexpressed (Wang et al., 2017) and ERF1, which can activate a subset of ethyleneinducible genes as the immune responsive gene PDF1 (Solano et al., 1998; Fujimoto et al., 2000; Heyman et al., 2018).

Altogether our data suggest a direct connection between epigenetic regulation and phytohormones in the meristem for the control of plasticity as previously proposed (Maury et al., 2019). This interplay could control the expression of cell identity genes, the stable activation of hormone-responsive genes post-stress, or act as an integrative hub for the sensing of hormonal balance to ensure plasticity, and potentially environmental memory (Maury et al., 2019).

DDM1-dependent DNA methylation in poplar shoot apical meristem is context dependent and affects both genes and TE activity

DDM1-dependent DNA methylation is cytosine context dependent

Poplar *ddm1* RNAi knock down lines were hypomethylated in SAMs according to global DNA methylation levels (7 to 17% reduction compared to WT). This is in agreement with both the WGBS analysis, which showed DMRs mostly hypomethylated, and with the report of Zhu et al., (2013), who found comparable reductions in leaves. While poplar *DDM1*-dependent DNA methylation was affected in the three contexts (CpG, CHG &

CHH), strong differences were observed among the contexts. The methylation level in CHG was drastically reduced compared to CpG or CHH contexts, suggesting that in poplar, *DDM1* preferentially targets methylation in the CHG context. This is in accordance with rice (Tan et al., 2016), and maize (Li et al., 2014; Long et al., 2019), but contrasts with Arabidopsis and tomato, where the disruption of *DDM1* led to a drastic hypomethylation of the genome, mainly in CpG and CHG contexts (Vongs et al., 1993; Kakutani et al., 1995, 1997; Lippman et al., 2004; Zemach et al., 2013; Corem et al., 2018). These observations suggest that *DDM1* has differential effect on DNA methylation patterns in diverse species (Tan et al., 2016; Long et al., 2019).

We also found that *DDM1* reduction caused extensive CpG, and to a lower extent CHG, hypermethylation of intergenic regions and genes, and that CHH hypermethylation of TEs only occurred in stressed conditions. The loss of *DDM1* has already been associated with hypermethylation in CHG contexts in genes of Arabidopsis and rice, as well as more limited hypermethylation in both CpG and CHG contexts for euchromatic regions in tomato and maize (Lippman et al., 2004; Mathieu et al., 2006; Saze & Kakutani, 2007; Zemach et al., 2013; Tan et al., 2016; Corem et al., 2018; Long et al., 2019). CHH hypermethylation has also been reported for heterochromatic TEs in rice and tomato (Tan et al., 2016; Corem et al., 2018). Here, we found that extensive CpG hypermethylation, notably in genes, was not associated with differential expression level, and overlapped with only a few active TEs, while hypermethylated CHH TEs showed reduced activity in comparison to hypomethylated CG and CHG TEs. It has been proposed that these hypermethylation events are likely to be mediated by different, potentially overlapping mechanisms that act as an internal balancing mechanism to compensate for the extensive loss of methylation in other contexts (Zemach et al., 2013; Tan et al., 2016; Corem et al., 2018).

Altogether, we propose that hypermethylation events, being species-dependent, may participate in pleiotropic effects. This could be related to variations in the functional role of *DDM1* in the different species, and/or in relation to their epigenetic machinery and genome complexity. We provide evidence that this phenomenon is also stress-

dependent, and occurs in the shoot apical meristem with possible implications for mitotic and meiotic transmission.

DDM1 impairment of gene methylation has limited effects on gene expression

632

633

634

635

636

637

638

639

640

641

642

643

644

645

646

647

648

649

650

651

652

653

654

655

656

657

658

659

660

661

DDM1 decrease in poplar affected the methylation of 879 and 910 genes in WW and WD-RW treatments, respectively. In poplar, gene methylation typically occurs in CpG and CHG contexts, and to a lower extent in the CHH context (Feng et al., 2010; Vining et al., 2012; Lafon-Placette et al., 2013). Despite a strong reduction in genome-wide CHG methylation, the numbers of DMGs found in CpG and CHG were of similar order. However, in CHG and CHH contexts genes found were in majority hypomethylated (>90%), whereas in the CpG context an equal number of genes were hypo- or hypermethylated.

Transcriptomic analysis in SAMs only revealed a limited number of DEGs (136) between the WT and ddm1-23 in response to water deficit, with 76 upregulated and 60 downregulated genes. Previous data on Arabidopsis and tomato ddm1 mutants were of similar magnitude (Zemach et al., 2013; Corem et al., 2018), while more DEGs were reported in rice (Tan et al., 2016) or in infected Arabidopsis EpiRILs (Furci et al., 2019). Among DEGs, only seven strictly overlapped with DMRs (up to 39% for genes at ~ +/-10 kb of DMRs); in agreement with tomato ddm1 mutants (Corem et al., 2018). This suggests that not all of these DEGs are primary targets of DDM1. A significant negative rank correlation was detected, however, between gene expression and methylation for the 53 DEGs located at less than +/-10 kb of DMRs. Although changes in 5' DNA methylation may influence gene expression (Seymour & Becker, 2017), the role of genebody methylation still remains disputed (Bewick & Schmitz, 2017), and to date it has been difficult to differentiate between direct changes mediated by DNA methylation and secondary effects (Meyer, 2015). In most available studies, no correlation could be detected between DNA methylation and expression changes at the genomic level. However, in agreement with other studies, our data show that the transcriptional activity of a subset of genes might be regulated by DNA methylation in response to abiotic stress (Karan et al., 2012; Garg et al., 2015; Chwialkowska et al., 2016, Lafon-Placette et al., 2018). These genes, including TFs and hormones-related pathways, are likely to explain, at least in part, the developmental plasticity of poplar *ddm1* lines (Maury et al., 2019).

662

663

664

665

666

667

668

669

670

671

672

673

674

675

676

677

678

679

680

681

682

683

684

685

686

687

688

689

690

691

DDM1-dependent DNA methylation favors TEs reactivation and insertion during stress

The role of DNA methylation and DDM1 on TE proliferation is well-established in plants (Miura et al., 2001; Mirouze et al., 2009; Tsukahara et al., 2009). TE proliferation has also been investigated in DDM1-epiRILs in Arabidopsis and tomato (Reinders et al., 2009; Johannes et al., 2009; Corem et al., 2018; Quadrana et al., 2019). Here, we reported TE activity in the SAM of WT and RNAi-ddm1 lines using the mobilome-seq workflow (Lanciano et al., 2017). TEs, which represent ~42 % of the genome of poplar (Kejnovski et al., 2012), were evaluated both under control and post water deficit conditions. The pattern of TE methylation varied widely between the different contexts. While most TEs were hypomethylated in CG and CHG contexts, we could not detect any TEs overlapping with the common DMRs, suggesting a limited effect in the CHH context (Corem et al., 2018). This could be related also to the threshold that we applied during DMR identification, which considered only DMRs with at least 10% of difference and 10X of coverage. This is very stringent since CHH methylation level in poplar is very low compared to CG and CHH contexts (~3,25%; Feng et al., 2010). This result also supports a redundant function of CG and non-CG methylation in the transcriptional silencing of the TEs (Ikeda & Nishimura, 2015). The burst of TEs in ddm1 lines were recorded for the two different classes (DNA transposons and retrotransposons), with a notable enrichment for the retrotransposons of the Gypsy family. Interestingly, when assessing the copy number variation of the most active TEs, we could detect only increased copy number for Gypsy retrotransposons (Gypsy-23 and SAT-1/Gypsy-78_Ptr-I-int) during the post stress episode, suggesting specific control of Gypsy activity by DDM1 during the stress. Gypsy elements are long terminal repeat (LTR)-flanked retrotransposons that are concentrated in pericentromeric heterochromatin, comparison to other repeats that are more dispersed e.g.m (Copia, LINE, SINE). Wang et al., (2018) recently reported a constant conflict between Gypsy retrotransposons and CHH methylation within a stress-adapted mangrove genome, and found differential

accumulation among classes of LTR TEs mainly due to siRNA-mediated CHH methylation preferentially targeting Gypsy elements. This is consistent with our data as we observed extensive CHH methylation of TEs (such as Gypsy elements) during drought in the ddm1 lines associated with enrichment in non-coding RNA (ncRNA) GO labels. This may suggest that ddm1 lines tend to methylate TEs in CHH contexts in order to repress their activity. Wang et al., (2018) subsequently proposed that the apparent conflict between TEs activity and repression of integration may enable the maintenance of genetic diversity and thus evolutionary potential during stress adaptation. This is particularly interesting as genes found with nearby active TEs in ddm1 lines are mainly involved in stress response and development. Quadrana et al., (2019) recently proposed that TEs are potent and episodic (epi)mutagens that increase the potential for rapid adaptation. They proposed that this is in large part due to epigenetic mechanisms of suppression that limit their activity which might result in purifying selection against them, and also limits their mutation rate due to their presence in highly compact chromatin. Here our data suggest that DDM1 could play a role in these repressive but diversity maintaining mechanisms during drought stress in poplar.

Shoot apical meristem is a central place for epigenetic control of developmental plasticity

Our study focused on meristems, previously described as "organs with specific epigenetic machinery" (Baubec et al., 2014; Lafon-Placette et al., 2018; Le Gac et al., 2018, 2019) and as controlling centers of development and acclimation. They are also the loci of mitotic and meiotic transmission. Here, we report the detailed characterization from physiological to omics levels of two independent *ddm1* poplar RNAi lines. Both lines exhibited higher tolerance to drought, mottled leaves, and modification of hormonal balance. Our study shows that *DDM1*-dependent DNA methylation in the shoot apical meristem of poplar trees plays two roles: controlling developmental plasticity and enabling stress response through a direct interplay with hormonal pathways (Maury et al., 2019). *DDM1*-dependent DNA methylation also controls the activation, and probably the integration, of TEs whose movements can induce heritable mutations and affect the

potential for rapid adaptation (Kawakatsu & Ecker, 2019; Quadrana et al., 2019). These results are in agreement with previous studies in poplars (Gourcilleau et al., 2010; Zhu et al., 2013; Conde et al., 2017; Lafon-Placette et al., 2018; Le Gac et al., 2018, 2019; Sow et al., 2018) and recent findings in annuals (Raju et al., 2018; Schmid et al., 2018; Zhang et al., 2018; Furci et al., 2019; Quadrana et al., 2019), both showing that epigenetic variation and TEs have the potential to create phenotypic variation that is substantial, persistent, and stable, thus of adaptive and evolutionary significance.

Our data are consistent with recent models about role of epigenetic variation in plants (Yona et al., 2015; Richards et al., 2017; Kawakatsu & Ecker, 2019; Maury et al., 2019) that view meristems as an interface between physiological response and genetic adaptation. Further studies are needed to examine the role of stress-induced epigenetic variation and associated mutation that examine a far greater range of stresses, species, and genotypes. This will enable its importance relative to more traditional sources of adaptive and evolutionary variation to be interpreted. Such studies are of particular interest for long-lived organisms in the age of rapid, anthropogenic climate change.

METHODS

Plant material, experimental design, and control of water deficit

Experiments were conducted on two *PtDDM1* RNAi lines (*ddm1-*15 and *ddm1-*23), and a wild type (WT) line of *Populus tremula x Populus alba* (clone INRA 717-1B4). These two RNAi lines were chosen among those previously described by Zhu et al., (2013) for consistently lower levels of both cytosine methylation (17.0 and 16.7% reduction compared to WT, respectively) and *PtDDM1* residual expression (*ca.* 62% reduction). Six week-old *in vitro* propagated plantlets were first transferred into small sealed chambers for progressive acclimation. Acclimated plantlets were then transferred to 4L pots filled with a potting substrate (Klasmann RHP 25-564, pH = 5.8) complemented with Osmocote PG Mix (1 kg/m³ of N-P-K 80/35/60). The experiment was conducted in a greenhouse located at the research station of INRAE Orléans Centre Val-de-Loire (47°46'N, 1°52'E), with a photoperiod of 16:8, an average temperature of 21°C, and a

relative humidity of 32%. Right before the water deficit experiment started (2 month-old plants), three plants per line were randomly sampled (t_0). The remaining 81 plants were then randomly distributed into nine blocks (n = 3 trees per line per block) and assigned to either a well-watered control treatment (WW, n = 1 per line per block) or a water deficit treatment followed by re-watering (WD-RW, n = 2 per line per block).

Water deficit was initiated at t₀ and lasted three weeks until t₁. Watering was performed every two days and was adjusted for each plant based on volumetric soil water content (SWC) estimated via pot weighing. Values of SWC at time i (SWC_i) were converted to soil relative extractable water (REW_i, %) using the following equation: $REW_i = (SWC_i - SWC_{wp}) / (SWC_{fc} - SWC_{wp}) \times 100$ where SWC_{fc} and SWC_{wp} correspond to the SWC at field capacity and at the wilting point, respectively. Plants from the WW treatment were always watered to field capacity, while plants from the WD-RW treatment were re-watered to a target value of approx. 40% of REW. At t₁, plants from the WD-RW treatment were re-watered to field capacity, three blocks were sampled, and the remaining six blocks were maintained watered for one week until t₂, after which all remaining plants were sampled. The water deficit intensity was evaluated at t_1 by measuring the predawn leaf water potential (Ψ_{pd} , MPa) during the night preceding the re-watering. Measurements were performed on a subset of five randomly selected blocks using a pressure chamber (PMS instruments, Albany, OR, USA). Minimum leaf water potential (Ψ_{min}) was estimated for the same plants at midday on the day preceding re-watering.

Physiological and phenotypic characterization

Growth and leaf symptoms

751

752

753

754

755

756

757

758

759

760

761

762

763

764

765

766

767

768

769

770

771

772

773

774

775

776

777

778

Stem height was measured every two days using a telescopic ruler, while stem diameter was measured every four days using a digital caliper. Due to Zhu et al. (2013) reporting the occurrence of spontaneous necrotic spots on the leaves of *ddm1* RNAi lines (mottled phenotype), we repeatedly measured the number of leaves showing necrotic symptoms (mottled leaves) during the whole duration of the experiment. We also counted the

number of leaves showing a 'folded' morphology (see results section). These measurements were performed on three randomly selected blocks.

Leaf gas exchange, bulk leaf carbon isotope composition (δ^{13} C), and stomatal density

Leaf gas exchange were measured using a LI-6400 open path photosynthesis system (Li-Cor, Lincoln, NE, USA) equipped with an LED light source (LI-6400-02B). Measurements were systematically performed on fully mature leaves in the top third of the plant in the same five blocks as those used for Ψ_{pd} and Ψ_{min} . From the time of drought initiation onwards, net CO_2 assimilation rate (A_{net} , μ mol m⁻² s⁻¹), and stomatal conductance to water vapor (g_s , mol m⁻² s⁻¹) were measured every day between 9 am and 3 pm in order to characterize the dynamic response of the genotypes to water deficit. Measurements were performed at a saturating photosynthetic photon flux density (PPFD) of 2000 μ mol m⁻² s⁻¹, an ambient CO_2 concentration of 400 ppm, a constant block temperature of 25°C, and a reference vapor pressure deficit (VPD) maintained close to 1kPa.

Bulk leaf carbon isotope composition (δ^{13} C) was used as a time-integrated surrogate of leaf intrinsic water-use efficiency (Farquhar et al., 1982). Six calibrated discs (3.14 cm²) of leaf lamina were punched from a mature leaf at t₂ on all plants. Leaf disks were oven-dried at 60°C for 48hrs before being ground to a fine powder. One milligram subsamples were then enclosed in tin capsules and combusted at 1200°C. The CO₂ produced by combustion was purified, and its 13 CO₂/ 12 CO₂ ratio was analyzed using isotope ratio mass spectrometry (IRMS, Finnigan MAT Delta S, Bremen, Germany). The δ^{13} C (‰) was expressed relative to the Vienna Pee Dee Belemnite standard and calculated as δ^{13} C = (R_{sa} - R_{sd})/ R_{sd} × 1000 where R_{sa} and R_{sd} are the 13 CO₂/ 12 CO₂ ratios of the sample and the standard, respectively (Farquhar et al., 1989). The accuracy of the δ^{13} C measurements done by IRMS during the time samples was assessed using referenced standards of ± 0.05 ‰ (SE). All measurements were performed at the INRAE-Nancy technical platform of functional ecology in France.

Stomatal counts were measured on a subset of three blocks, following the method described by Xu & Zhou (2008). Stomatal imprints were taken between the central leaf vein and the leaf edge on both adaxial and abaxial sides, and then fixed on microscopic slides using scotch tape. Slides were observed under a light microscope coupled to a Moticam 580 5.0MP digital camera, and three pictures were taken on each filmstrip side.

Xylem structure, function and biochemical composition

Xylem vulnerability to drought-induced cavitation was assessed at t_2 on the well-watered plants of all blocks (INRAE Phenobois Platform, Clermont-Ferrand, France). Vulnerability to cavitation sets the operational limit of xylem under drought, and is a key trait involved in drought tolerance (Brodribb & Cochard, 2009). We used the Cavitron technique which is well suited to poplars (Cochard et al., 2005, Fichot et al., 2015). In short, the technique uses the centrifugal force to increase xylem tension (Ψ_x , MPa) in stem segments, while at the same time measuring the percent loss of hydraulic conductance (PLC, %). The dependence of PLC upon Ψ_x was used to generate vulnerability curves for each stem segment. The following sigmoid function was fitted to data (Cochard et al., 2007): PLC = $100 / (1 + \exp((s/25)x(P-P_{50})))$, where P_{50} is the xylem tension causing 50% loss of hydraulic conductance (MPa) and s is the slope of the curve at the inflexion point (%. MPa⁻¹). Values of P_{50} were used as proxies for vulnerability to xylem drought-induced cavitation.

Xylem histology was performed on stem segments of all plants at t₂. Stem cross-sections 30 μm-thick were obtained using a hand microtome (RM 2155, Leica Microsystems, Vienna, Austria), and stained with safranin (1% in 50% ethanol), and followed by Astra blue (1% in 100% ethanol), before being permanently mounted in Canada Balsam. Stained sections were examined under a light microscope coupled to a Moticam 580 5.0MP digital camera. Pictures covering pith to cambium were taken at a 10x magnification on three opposite radial sectors in order to estimate vessel diameter (μm), vessel density (mm⁻²), vessel lumen fraction (%), and theoretical xylem specific hydraulic conductivity (Fichot et al., 2010). Image analyses were all performed using the ImageJ software (Schneider et al., 2012). Xylem density was assessed on the same

stem segments using 4 cm-long samples. Measurements were realized using the Archimedes principle. Bark-free stems were split longitudinally in order to remove wood pith, submerged to estimate the volume of displaced water, and weighed after being oven-dried at 105°C. Xylem density (g.cm⁻³) was computed as the ratio between dry mass and the volume of displaced water (Fichot et al., 2010).

Xylem biochemical composition was evaluated indirectly on stem powders of all plants by using Fourier-Transform mid-Infrared Spectroscopy (FTIR, Spectrum 400, Perkin Elmer, Massachusetts, USA), and home-made calibration models previously developed at the INRAE Genobois phenotyping platform for Klason lignin content, S/G ratio and tension wood content (*unpublished data*). For each sample, a few milligrams were placed three times on the attenuated total reflectance (ATR) diamond for the scan. Spectra ranged from 650 to 4000 cm⁻¹ wave numbers with a step of 2 cm⁻¹. Spectrum analyses were realized using the R software (R Core Team, 2015). Spectra were first cut and smoothed by using the 'prospectr' package before applying normalization and first derivative processing (Bertrand & Dufour, 2006).

Phytohormone quantification

Shoot apices were immediately frozen in liquid nitrogen upon sampling, and later ground to a fine powder in an automatic ball mill (MM 200 Retsch, Germany). Phytohormone assays for abscisic acid (ABA), free auxin, salicylic acid (SA), jasmonic acid (JA) and cytokinins were performed on the SAMs collected at t1, using LC-MS according to a published procedure (OVCM platform, IJPB, INRAE Versailles, France; Li-Marchetti et al., 2015; Trapet et al., 2016). For each sample, 10 mg of dry powder was extracted with 0.8 mL of acetone/water/acetic acid (80/19/1 v:v:v). Phytohormone stable labelled isotopes used as internal standards were prepared as described in Roux et al., (2014). Two ng of each and 0,5 ng of cytokinines standard was added to the sample. The extract was vigorously shaken for 1 min, sonicated for 1 min at 25 Hz, shaken for 10 minutes at 10°C in a Thermomixer (Eppendorf®), and then centrifuged (8000 g, 10 °C, 10 min.). The supernatants were collected, and the pellets were re-extracted twice with 0.4 mL of the same extraction solution, then vigorously shaken (1 min), and sonicated (1 min; 25 Hz). After the centrifugations, the three supernatants were pooled and dried

(Final Volume 1.6 mL). Each dry extract was dissolved in 100 μL of acetonitrile/water (50/50 v/v), filtered, and analyzed using a Waters Acquity ultra performance liquid chromatograph coupled to a Waters Xevo Triple quadrupole mass spectrometer TQS (UPLC-ESI-MS/MS). The compounds were separated on a reverse-phase column (Uptisphere C18 UP3HDO, 100*2.1 mm*3μm particle size; Interchim, France) using a flow rate of 0.4 ml min⁻¹, and a binary gradient: (A) acetic acid 0.1% in water (v/v) and (B) acetonitrile with 0.1% acetic acid, and a column temperature of 40°C. Mass spectrometry was conducted using electrospray, and Multiple Reaction Monitoring scanning mode (MRM mode), in either positive ion mode (for the indole-3-acetic acid and cytokinins) or negative ion mode (for the other hormones). Relevant instrumental parameters were set as follows: capillary 1.5 kV (negative mode), with source block and desolvation gas temperatures at 130 °C and 500 °C, respectively. Nitrogen was used to assist the cone and desolvation (150 L.h⁻¹ and 800 L.h⁻¹, respectively), argon was used as the collision gas at a flow of 0.18 ml.min⁻¹.

DNA extraction and determination of global DNA methylation levels by HPLC

Genomic DNA was extracted from all SAMs with a CTAB protocol (Doyle & Doyle, 1987), and stored at -80°C. Quantity and quality were approximated using a NanoDrop spectrometer (NanoDrop Instrument, France).

For the determination of global DNA methylation, genomic DNA was enzymatically hydrolyzed into nucleosides, and analyzed by high-performance liquid chromatography (HPLC), as described by Zhu et al., (2013). Controls for this procedure included co-migration with commercial standards (Sigma-Aldrich), confirmation by enzyme restriction analysis, and tests for RNA contamination based on the HPLC detection of ribonucleosides. Global DNA methyl cytosine percentages (% mC) were estimated as follows: %mC = (mC/(C + mC)) × 100, where 'C' is 2'-déoxycytidine content, and 'mC' is 5-methyl-2'-déoxycytidine content. For each line in each treatment, three biological replicates were randomly chosen out of the six for analyses, with two independent genomic DNA extractions per replicate, three hydrolysis replicates and two HPLC runs.

Whole Genome Bisulfite Sequencing (WGBS) and bioinformatic pipeline for methylome characterization

896

897

898

899

900

901

902

903

904

905

906

907

908

909

910

911

912

913

914

915

916

917

918

919

920

921

922

923

924

925

An equimolar pool of 2 µg DNA at approximately 100 ng/µl, and extracted from four SAMs was made for each line in each treatment. Whole-genome bisulfite sequencing was performed by the CNRGH laboratory (J. Tost, Evry, France) in accordance with the published procedure (http://www.nugen.com/products/ovation-ultralow-methyl-seglibrary-systems) adapted from Daviaud et al., (2018). The workflow of the library preparation protocol follows the classical library preparation protocol in which methylated adaptors are ligated to the fragmented DNA prior to bisulfite conversion. A total of 200 ng of genomic DNA was fragmented to a size of approximately 200 base pairs (bp), and then purified and methylated adaptors compatible with sequencing on an Illumina HiSeq instrument were ligated. The resulting DNA library was purified and bisulfite converted. A qPCR assay was used to determine the optimal number of PCR amplification cycles (between 10 and 15 cycles) required to obtain a high diversity library with minimal duplicated reads prior to final library amplification. The sequencing was performed with paired ends (2x150bp) on an Illumina HiSeq4000 platform. Raw data were stored in FASTQ files with a minimal theoretical coverage of 30X (SRA record is under the reference PRJNA611484; https://www.ncbi.nlm.nih.gov/sra/PRJNA611484).

The bioinformatics pipeline used in this study is adapted from the ENCODE pipeline (https://www.encodeproject.org/wgbs/) and installed on the Galaxy instance, accessible of IHPE (http://galaxy.univ-perp.fr/, Perpignan, France). First, quality control and cleaning of the raw data were carried out by only considering nucleotides with a quality score over 26, and reads which had more than 95% of their nucleotides over this quality threshold. The second step was the alignment of the WGBS reads on the reference genome *Populus tremula x alba* (http://aspendb.uga.edu/index.php/databases/spta-717-genome), by using BISMARK (version 0.16.3, Krueger & Andrews, 2011) and bowtie 2 tools (version 2.1.0; Langmead et al., 2009) or a bisulfite sequence mapping program (BSMAP version 2.74) (Xi & Li, 2009). The parameters were modified for 'paired-end' alignment, read lengths were between 70 and 500 bp, and others were kept by default (See sup. Figure 1A, B and C). The methylkit R package allowed the identification of

DMRs among lines and treatments. A DMR was defined as a 500 bp region with a minimum coverage of 10X, which highlighted the differential methylation between two samples of at least 10% for CHH, and 25% for CHG and CG (q-value=0.01). Different types of DMRs were identified and are referred to as follows: stress-specific DMRs refer to DMRs between WW and WD-RW treatments, line-specific DMRs refer to DMRs between ddm1 lines and the WT, and common DMRs refer to line-specific DMRs common to both lines ddm1-15 and ddm1-23.

DMR annotation was realized by using reference data available for the *Populus tremula x alba* genome from the aspendb database. Gene Ontology (GO) term enrichment was assessed for the methylated genes with Revigo (http://revigo.irb.hr/http://revigo.irb.hr/) software, using default parameters. 'TreeMap' view was performed with rectangle size adjusted to reflect the absolute log10 *P*-value of the GO term, through use of the corresponding poplar model genes from the best v3.0 blast hits with *Arabidopsis* TAIR10 annotations.

Transcriptomics and bioinformatic pipeline

Total RNA (three biological replicates) was extracted from the wild type and one RNAi line in WD-RW condition by using a modified protocol of Chang et al., 1993). *Ddm1-23* was chosen as the most representative of the two lines as it exhibited a lower decrease in methylation compared to *ddm15-7*, but nonetheless most of its DMRs were in common among the two lines. In brief, SAMs were ground into fine powder in liquid nitrogen and total RNAs were extracted using a CTAB buffer (Changet al., 1993). RNA was precipitated using lithium chloride (10M) and purified using the Macherey Nagel Nucleospin RNA kit (740955). Sequencing was done using the Illumina NexSeq500 (IPS2 POPS platform, Saclay, France). RNA-seq libraries were performed by following the TruSeq_Stranded_mRNA_SamplePrep_Guide_15031047_D protocol (Illumina®, California, USA). The RNA-seq samples have been sequenced in paired-end (PE) with a sizing of 260 bp and a read length of 75 bases. 6 samples by lane of NextSeq500 using individual bar-coded adapters and giving approximately 15 millions of PE reads by sample are generated. To facilitate comparisons, each sample followed the same steps from trimming to counts. RNA-Seq preprocessing included trimming library adapters and

performing quality controls. The raw data (fastq) were trimmed with the Trimmomatic (Bolger et al., 2014) tool for Phred Quality Score Qscore >20, read length >30 bases, and ribosome sequences were removed with the sortMeRNA tool (Kopylova et al., 2012). The genomic mapper STAR (version 2.6, Dobin A. et al 2013) was used to align reads against the *Populus tremula x alba* hybrid genome (genotype INRA 717-1B4), with the options outSAMprimaryFlag AllBestScore--outFilterMultimapScoreRange 0, to keep only the best results. The abundance of each gene was calculated with STAR, with paired-end reads only being counted where the reads unambiguously mapped one gene, and multi-hits were removed. Following this pipeline, around 92% of PE reads were associated to a gene, 3 to 4% PE reads were unmapped and 3 to 4% of PE reads with multi-hits were removed.

Differential analyses followed the procedure described in Rigaill et al., (2016). In brief, genes with less than one read, after a count per million normalization in at least one half of the samples, were discarded. Library size was normalized using the trimmed mean of M-value (TMM) method, and count distribution was modeled with a negative binomial generalized linear model. Dispersion was estimated by the edgeR method (Version 1.12.0, McCarthy et al., 2012) in the statistical software 'R' (Version 3.2.5 R Development Core Team (2005)). Expression differences compared two samples using the likelihood ratio test, and p-values were adjusted by the Benjamini-Hochberg procedure to control False Discovery Rate (FDR). A gene was declared differentially expressed if its adjusted p-value was lower than to 0.05.

All steps of the experiment, from growth conditions to bioinformatic analyses, were managed in CATdb database (Gagnot et al., 2008; http://tools.ips2.u-psud.fr/CATdb/) with ProjectID NGS2017-01-DDM1 This project is submitted from CATdb into the international repository GEO (Gene Expression Omnibus, Edgard R. et al. 2002, http://www.ncbi.nlm.nih.gov/geo) with ProjetID GSE135313.

Mobilome-seq and copy number variation of TEs

According to their mode of transposition, TEs generate extrachromosomal circular DNAs (eccDNAs) when active. The sequencing of these eccDNAs by the mobilome sequencing was a successfully method to identify active TEs (Lanciano et al., 2017). In

987

988

989

990

991

992

993

994

995

996

997

998

999

1000

1001

1002

1003

1004

1005

1006

1007

1008

1009

1010

1011

1012

1013

1014

1015

1016

order to identify the effect of DDM1 knock down and a hydric stress on the release of TE activity we used approximately 6 µg of genomic DNA to perform mobilome-seq libraries. eccDNAs were isolated and libraries were prepared and sequenced following Lanciano et al., (2017). Bioinformatics was carried out on the *Populus tremula × alba* genome (SPta717 v1.1) by using the same pipelines as described in Lanciano et al., (2017). In order to obtain TE database for Populus tremula x alba genome, we used the TE database based on *Populus trichocarpa* genome (version 3.0). In brief, the sequencing reads were first filtered against the mitochondria and chloroplast genomes before being i) mapped against the P. tremula x alba reference genome using Bowtie2, ii) mapped for split reads (SR) using segement software (Hoffmann et al., 2014) and iii) de novo assembled using a5-miseq (Coil et al., 2015). Given the range of variation of the DOC coverage, we assigned TE families to four groups following Lanciano et al., (2017): The first group was named "moderate or not active TEs (group "TE")", and comprised TEs with a DOC ranging from 4 to 199X. The second group was named "active TEs" (group "TE+") and comprised TEs with a DOC ranging from 200-1999X. The third group was named "very active TEs" ("TE⁺⁺") and comprised TEs with a DOC ranging from 2000 to 9999X. The fourth group was named "highly active group" ("TE"++"), and comprised TEs with a DOC ranging from 10000 to 51000X. Raw and processed data are available with the **GEO** accession number GSE147934 (https://www.ncbi.nlm.nih.gov/geo/query/acc.cgi?acc=GSE147934).

Copy number variation of TEs was assessed for all studied lines in both treatments by qPCR using genomic DNA extracted from SAMs. In summary, primers of TEs were first designed using corresponding FASTA sequences with Eprimer3 and Netprimer for quality control checking (http://www.bioinformatics.nl/cgibin/emboss/eprimer3, http://www.premierbiosoft.com/NetPrimer). Primers that passed quality control (Gypsy: F=AAC-AAG-CTG-AAG-CCC-AAG-AA, R=TCG-ACC-TCG-AGT-TAG-GTT-CC; DNA-3-3: F=TAG-TGT-GCA-GTG-GAG-CAT-GG, R=AAA-AGC-AGG-GTG-TTT-TGC-TG; SAT-1: F=TCA-CCG-GAA-CCC-ACT-TCT-AC, R=GCA-ACG-ACT-GAG-TTT-CGT-CA) were used with 10 ng/µl of genomic DNA for gPCR analyses (Platinum™ SYBR™ Green gPCR SuperMix-UDG, Invitrogen™ kit). A standard cycling program was applied (50 °C for 2 min, 95 °C for 2 min, and 40 cycles of 95 °C for 15 sec and 60 °C for 30 sec). Melting curves were obtained using recommended qPCR instrument settings. Copy number variation was assessed by using absolute quantification of cycle threshold values (Schmittgen & Livak, 2008).

Statistical analyses

- Statistical analyses were performed with R statistical software under R Studio integrated development environment (R Core Team, 2015, RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/). Means are expressed with their standard errors (SE). Differences between lines and treatments for phenotypic traits were evaluated by analysis of variance (ANOVA) on individual values adjusted for block effects. Tukey's post-hoc test was used to identify differences between groups when
- ANOVAs indicated significant effects. Statistical tests were considered significant at P <
- 1028 0.05.

1029

1041

1042

1017

1018

1019

1020

Author contributions

- 1030 S.M designed and coordinated the research. The plant experimental design was established by S.M, S.S,
- 1031 R.F, and F.B. Ecophysiological measurements were performed by A.L.L.G, R.F, A.D, I.L.J and H.C;
- analysis was realized by A.L.L.G and R.F. NIRS measurements and analysis were performed by A.L.L.G
- and V.S. Phytohormones analysis was performed by S.C. DNA, RNA extractions were done by A.D and
- 1034 A.L.L.G and M.D.S. HPLC analysis was done by A.D and S.M. RNA-seq was realized and analyzed by
- 1035 J.C, V.B, L.S.T with M.D.S. J.T, C.D realized WGBS analysis. WGBS data analysis was done by S.M,
- 1036 A.L.L.G and M.D.S. Bioinformatics for WGBS was done with the help of C.C and C.G. Mobilome analysis
- 1037 was done under the supervision of M.M with S.L and A.L.L.G. QPCR analysis were done by M.C.L.D with
- A.D and M.D.S. Data analysis was done by S.M, A.L.L.G and M.D.S. Statistical analyses were done by
- 1039 R.F, A.L.L.G and M.D.S. S.M, R.F, A.L.L.G and M.D.S conceived and wrote the first draft of the
- manuscript. All authors approved the final version of the manuscript.

Acknowledgments

- 1043 M.D.S and A.L.L.G received Phd grants from the Ministère de la Recherche et Enseignement Supérieur.
- 1044 This work was supported by INRAE (grant PI EFPA-2014 to S.M.), the RTP3E CNRS grants for mobility
- 1045 (http://rtp-3e.wixsite.com/rt3e; A.L.L.G, S.M, C.G and M.M) and access to the IHPE platform
- 1046 (http://galaxy.univ-perp.fr/, Perpignan, France). The LBLGC also benefits from support of the ANR
- 1047 EPITREE (ANR-17-CE32-0009-01) to SM. English editing was done by Infinity English (N° SIRET

1048	829507°	10200012). The IJPB bene	fits from the suppo	ort of Saclay	Plant Science	es-SPS (ANR-17-EUR-
1049	0007). 7	This work	has benefited from	n the support of IJF	PB's Plant Obs	ervatory tech	nological platforms. SL
1050	and MM were supported by the French National Agency for Research (ANR-13-JSV6-0002 "ExtraChrom")						
1051	and	the	Laboratoire	d'Excellence	LABEX	TULIP	(ANR-10-LABX-41).

REFERENCES

- Abeysinghe, J. K., Lam, K.-M., & Ng, D. W.-K. (2019). Differential regulation and interaction of homoeologous WRKY18 and WRKY40 in Arabidopsis allotetraploids and biotic stress responses.

 The Plant Journal, 97(2), 352- 367. https://doi.org/10.1111/tpj.14124
- Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci, A., & Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for Forest **Ecology** and Management, 259(4), https://doi.org/10.1016/j.foreco.2009.09.001
 - Anderegg, W. R. L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A. F. A., Choat, B., & Jansen, S. (2016). Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the National Academy of Sciences*, 113(18), 5024-5029. https://doi.org/10.1073/pnas.1525678113
 - Awad, H., Herbette, S., Brunel, N., Tixier, A., Pilate, G., Cochard, H., & Badel, E. (2012). No trade-off between hydraulic and mechanical properties in several transgenic poplars modified for lignins metabolism. *Environmental and Experimental Botany*, 77, 185-195. https://doi.org/10.1016/j.envexpbot.2011.11.023
 - Ayarpadikkannan, S., & Kim, H.-S. (2014). The Impact of Transposable Elements in Genome Evolution and Genetic Instability and Their Implications in Various Diseases. *Genomics & informatics*, 12, 98- 104. https://doi.org/10.5808/GI.2014.12.3.98
 - Azooz, M. M., & Youssef, M. M. (2010). Evaluation of Heat Shock and Salicylic Acid Treatments as Inducers of Drought Stress Tolerance in Hassawi Wheat. *American Journal of Plant Physiology*, 5(2), 56-70. https://doi.org/10.3923/ajpp.2010.56.70
 - Badmi, R., Zhang, Y., Tengs, T., Brurberg, M. B., Krokene, P., Fossdal, C. G., Hytönen, T., & Thorstensen, T. (2019). Induced and primed defence responses of Fragaria vesca to Botrytis cinerea infection. *BioRxiv*, 692491. https://doi.org/10.1101/692491
 - Bandurska, H., & Stroi ski, A. (2005). The effect of salicylic acid on barley response to water deficit. *Acta Physiologiae Plantarum*, *27*(3), 379- 386. https://doi.org/10.1007/s11738-005-0015-5
 - Barigah, T. S., Charrier, O., Douris, M., Bonhomme, M., Herbette, S., Améglio, T., Fichot, R., Brignolas, F., & Cochard, H. (2013). Water stress-induced xylem hydraulic failure is a causal factor of tree mortality in beech and poplar. *Annals of Botany*, 112(7), 1431- 1437. https://doi.org/10.1093/aob/mct204
 - Basu, S., Ramegowda, V., Kumar, A., & Pereira, A. (2016). Plant adaptation to drought stress. F1000Research, 5. https://doi.org/10.12688/f1000research.7678.1
 - Baubec, T., Finke, A., Mittelsten Scheid, O., & Pecinka, A. (2014). Meristem-specific expression of epigenetic regulators safeguards transposon silencing in Arabidopsis. *EMBO Reports*, *15*(4), 446-452. https://doi.org/10.1002/embr.201337915
 - Bechtold, U., Penfold, C. A., Jenkins, D. J., Legaie, R., Moore, J. D., Lawson, T., Matthews, J. S. A., Vialet-Chabrand, S. R. M., Baxter, L., Subramaniam, S., Hickman, R., Florance, H., Sambles, C., Salmon, D. L., Feil, R., Bowden, L., Hill, C., Baker, N. R., Lunn, J. E., ... Mullineaux, P. M. (2016). Time-Series Transcriptomics Reveals That AGAMOUS-LIKE22 Affects Primary Metabolism and Developmental Processes in Drought-Stressed Arabidopsis. *The Plant Cell*, *28*(2), 345-366. https://doi.org/10.1105/tpc.15.00910
 - Bertrand, D., & Dufour, É. (2006). La Spectroscopie Infrarouge et ses Applications Analytiques. Tec & Doc / Lavoisier. http://www.lavoisier.fr/notice/fr2743008090.html
 - Bewick, A. J., & Schmitz, R. J. (2017). Gene body DNA methylation in plants. *Current Opinion in Plant Biology*, 36, 103- 110. https://doi.org/10.1016/j.pbi.2016.12.007
- Bogeat-Triboulot, M.-B., Brosché, M., Renaut, J., Jouve, L., Thiec, D. L., Fayyaz, P., Vinocur, B., Witters, E., Laukens, K., Teichmann, T., Altman, A., Hausman, J.-F., Polle, A., Kangasjärvi, J., & Dreyer, E. (2007). Gradual Soil Water Depletion Results in Reversible Changes of Gene Expression, Protein Profiles, Ecophysiology, and Growth Performance in Populus euphratica, a Poplar

- 1104 Growing in Arid Regions. *Plant Physiology*, *143*(2), 876-892. 1105 https://doi.org/10.1104/pp.106.088708
- Bolger, A. M., Lohse, M., & Usadel, B. (2014). Trimmomatic: A flexible trimmer for Illumina sequence data. *Bioinformatics (Oxford, England)*, 30(15), 2114-2120. https://doi.org/10.1093/bioinformatics/btu170
- 1109 Bradshaw, A. D. (2006). Unravelling phenotypic plasticity why should we bother? *New Phytologist*, 1110 170(4), 644- 648. https://doi.org/10.1111/j.1469-8137.2006.01761.x
 - Bräutigam, K., Vining, K. J., Lafon-Placette, C., Fossdal, C. G., Mirouze, M., Marcos, J. G., Fluch, S., Fraga, M. F., Guevara, M. Á., Abarca, D., Johnsen, Ø., Maury, S., Strauss, S. H., Campbell, M. M., Rohde, A., Díaz-Sala, C., & Cervera, M.-T. (2013). Epigenetic regulation of adaptive responses of forest tree species to the environment. *Ecology and Evolution*, *3*(2), 399-415. https://doi.org/10.1002/ece3.461
- 1116 Brodribb, T. J., & Cochard, H. (2009). Hydraulic Failure Defines the Recovery and Point of Death in 1117 Water-Stressed Conifers. *Plant Physiology*, 149(1), 575-584. https://doi.org/10.1104/pp.108.129783
 - Cambiagno, D. A., Nota, F., Zavallo, D., Rius, S., Casati, P., Asurmendi, S., & Alvarez, M. E. (2018). Immune receptor genes and pericentromeric transposons as targets of common epigenetic regulatory elements. *The Plant Journal*, *96*(6), 1178- 1190. https://doi.org/10.1111/tpj.14098
 - Carneros, E., Yakovlev, I., Viejo, M., Olsen, J. E., & Fossdal, C. G. (2017). The epigenetic memory of temperature during embryogenesis modifies the expression of bud burst-related genes in Norway spruce epitypes. *Planta*, *246*(3), 553-566. https://doi.org/10.1007/s00425-017-2713-9
 - Champigny, M. J., Unda, F., Skyba, O., Soolanayakanahally, R. Y., Mansfield, S. D., & Campbell, M. M. (s. d.). Learning from methylomes: Epigenomic correlates of Populus balsamifera traits based on deep learning models of natural DNA methylation. *Plant Biotechnology Journal*, *n/a*(n/a). https://doi.org/10.1111/pbi.13299
 - Chang, S., Puryear, J., & Cairney, J. (1993). A simple and efficient method for isolating RNA from pine trees. *Plant Molecular Biology Reporter*, *11*(2), 113- 116. https://doi.org/10.1007/BF02670468
 - Chen, C., & Chen, Z. (2002). Potentiation of Developmentally Regulated Plant Defense Response by AtWRKY18, a Pathogen-Induced Arabidopsis Transcription Factor. *Plant Physiology*, 129(2), 706-716. https://doi.org/10.1104/pp.001057
 - Chen, G., Komatsuda, T., Ma, J. F., Li, C., Yamaji, N., & Nevo, E. (2011). A functional cutin matrix is required for plant protection against water loss. *Plant Signaling & Behavior*, *6*(9), 1297-1299. https://doi.org/10.4161/psb.6.9.17507
 - Cho, E. J., Choi, S. H., Kim, J. H., Kim, J. E., Lee, M. H., Chung, B. Y., Woo, H. R., & Kim, J.-H. (2016). A Mutation in Plant-Specific SWI2/SNF2-Like Chromatin-Remodeling Proteins, DRD1 and DDM1, Delays Leaf Senescence in Arabidopsis thaliana. *PLoS ONE*, 11(1). https://doi.org/10.1371/journal.pone.0146826
 - Choat, B., Brodribb, T. J., Brodersen, C. R., Duursma, R. A., López, R., & Medlyn, B. E. (2018). Triggers of tree mortality under drought. *Nature*, *558*(7711), 531- 539. https://doi.org/10.1038/s41586-018-0240-x
 - Chujo, T., Takai, R., Akimoto-Tomiyama, C., Ando, S., Minami, E., Nagamura, Y., Kaku, H., Shibuya, N., Yasuda, M., Nakashita, H., Umemura, K., Okada, A., Okada, K., Nojiri, H., & Yamane, H. (2007). Involvement of the elicitor-induced gene OsWRKY53 in the expression of defense-related genes in rice. *Biochimica et Biophysica Acta (BBA) Gene Structure and Expression*, 1769(7), 497-505. https://doi.org/10.1016/j.bbaexp.2007.04.006
 - Chwialkowska, K., Nowakowska, U., Mroziewicz, A., Szarejko, I., & Kwasniewski, M. (2016). Water-deficiency conditions differently modulate the methylome of roots and leaves in barley (*Hordeum vulgare* L.). *Journal of Experimental Botany*, 67(4), 1109-1121. https://doi.org/10.1093/jxb/erv552
- 1153 Cochard, H., Casella, E., & Mencuccini, M. (2007). Xylem vulnerability to cavitation varies among poplar 1154 and willow clones and correlates with yield. *Tree Physiology*, 27(12), 1761- 1767. 1155 https://doi.org/10.1093/treephys/27.12.1761
- 1156 Cochard, H., Damour, G., Bodet, C., Tharwat, I., Poirier, M., & Glio, T. (2005). Evaluation of a new centrifuge technique for rapid generation of xylem vulnerability curves. *Physiologia Plantarum PHYSIOL PLANT*, *124*. https://doi.org/10.1111/j.1399-3054.2005.00526.x

- Cohen, D., Bogeat-Triboulot, M.-B., Tisserant, E., Balzergue, S., Martin-Magniette, M.-L., Lelandais, G., Ningre, N., Renou, J.-P., Tamby, J.-P., Le Thiec, D., & Hummel, I. (2010). Comparative transcriptomics of drought responses in Populus: A meta-analysis of genome-wide expression profiling in mature leaves and root apices across two genotypes. *BMC Genomics*, *11*(1), 630. https://doi.org/10.1186/1471-2164-11-630
- 1164 Coil, D., Jospin, G., & Darling, A. E. (2015). A5-miseq: An updated pipeline to assemble microbial genomes from Illumina MiSeq data. *Bioinformatics (Oxford, England)*, 31(4), 587- 589. https://doi.org/10.1093/bioinformatics/btu661
 - Colomé-Tatché, M., Cortijo, S., Wardenaar, R., Morgado, L., Lahouze, B., Sarazin, A., Etcheverry, M., Martin, A., Feng, S., Duvernois-Berthet, E., Labadie, K., Wincker, P., Jacobsen, S. E., Jansen, R. C., Colot, V., & Johannes, F. (2012). Features of the Arabidopsis recombination landscape resulting from the combined loss of sequence variation and DNA methylation. *Proceedings of the National Academy of Sciences*, 109(40), 16240-16245. https://doi.org/10.1073/pnas.1212955109
 - Conde, D., Le Gac, A.-L., Perales, M., Dervinis, C., Kirst, M., Maury, S., González-Melendi, P., & Allona, I. (2017). Chilling-responsive DEMETER-LIKE DNA demethylase mediates in poplar bud break: Role of active DNA demethylase in trees' bud break. *Plant, Cell & Environment*, *40*(10), 2236-2249. https://doi.org/10.1111/pce.13019
 - Corem, S., Doron-Faigenboim, A., Jouffroy, O., Maumus, F., Arazi, T., & Bouché, N. (2018). Redistribution of CHH Methylation and Small Interfering RNAs across the Genome of Tomato ddm1 Mutants. *The Plant Cell*, *30*(7), 1628- 1644. https://doi.org/10.1105/tpc.18.00167
 - Correia, B., Pintó-Marijuan, M., Castro, B. B., Brossa, R., López-Carbonell, M., & Pinto, G. (2014). Hormonal dynamics during recovery from drought in two Eucalyptus globulus genotypes: From root to leaf. *Plant Physiology and Biochemistry*, 82, 151- 160. https://doi.org/10.1016/j.plaphy.2014.05.016
 - Cortijo, S., Wardenaar, R., Colome-Tatche, M., Gilly, A., Etcheverry, M., Labadie, K., Caillieux, E., Hospital, F., Aury, J.-M., Wincker, P., Roudier, F., Jansen, R. C., Colot, V., & Johannes, F. (2014). Mapping the Epigenetic Basis of Complex Traits. *Science*, 343(6175), 1145-1148. https://doi.org/10.1126/science.1248127
 - Cotrozzi, L., Pellegrini, E., Guidi, L., Landi, M., Lorenzini, G., Massai, R., Remorini, D., Tonelli, M., Trivellini, A., Vernieri, P., & Nali, C. (2017). Losing the Warning Signal: Drought Compromises the Cross-Talk of Signaling Molecules in Quercus ilex Exposed to Ozone. *Frontiers in Plant Science*, 8. https://doi.org/10.3389/fpls.2017.01020
 - Daviaud, C., Renault, V., Mauger, F., Deleuze, J.-F., & Tost, J. (2018). Whole-Genome Bisulfite Sequencing Using the Ovation® Ultralow Methyl-Seq Protocol. *Methods in Molecular Biology* (*Clifton, N.J.*), 1708, 83- 104. https://doi.org/10.1007/978-1-4939-7481-8_5
 - Dong, X. (2004). NPR1, all things considered. *Current Opinion in Plant Biology*, *7*(5), 547- 552. https://doi.org/10.1016/j.pbi.2004.07.005
 - Durand, M., Brendel, O., Buré, C., & Le Thiec, D. (2019). Altered stomatal dynamics induced by changes in irradiance and vapour-pressure deficit under drought: Impacts on the whole plant transpiration efficiency of poplar genotypes. *New Phytologist*, 222. https://doi.org/10.1111/nph.15710
 - Dusotoit-Coucaud, A., Brunel, N., Tixier, A., Cochard, H., & Herbette, S. (2014). Hydrolase treatments help unravel the function of intervessel pits in xylem hydraulics. *Physiologia Plantarum*, *150*(3), 388- 396. https://doi.org/10.1111/ppl.12092
 - Farquhar, G. D., Ehleringer, J. R., & Hubick, K. T. (1989). Carbon Isotope Discrimination and Photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*, *40*(1), 503-537. https://doi.org/10.1146/annurev.pp.40.060189.002443
 - Farquhar, G., O'Leary, M. H., & Berry, J. (1982). On the Relationship Between Carbon Isotope Discrimination and the Intercellular Carbon Dioxide Concentration in Leaves. *Australian Journal of Plant Physiology*, *13*, 281- 292. https://doi.org/10.1071/PP9820121
- Feng, S., Jacobsen, S. E., & Reik, W. (2010). Epigenetic Reprogramming in Plant and Animal Development. *Science*, 330(6004), 622- 627. https://doi.org/10.1126/science.1190614
- Fernando, V. C. D., & Schroeder, D. F. (2016). Role of ABA in Arabidopsis Salt, Drought, and Desiccation
 Tolerance. Abiotic and Biotic Stress in Plants Recent Advances and Future Perspectives.
 https://doi.org/10.5772/61957

- Fichot, R., Barigah, T. S., Chamaillard, S., Thiec, D. L., Laurans, F., Cochard, H., & Brignolas, F. (2010).

 Common trade-offs between xylem resistance to cavitation and other physiological traits do not hold among unrelated Populus deltoides xPopulus nigra hybrids. *Plant, Cell & Environment*, 33(9), 1553- 1568. https://doi.org/10.1111/j.1365-3040.2010.02164.x
- Fichot, R., Brignolas, F., Cochard, H., & Ceulemans, R. (2015). Vulnerability to drought-induced cavitation in poplars: Synthesis and future opportunities. *Plant, Cell & Environment*, *38*(7), 1233-1251. https://doi.org/10.1111/pce.12491
 - Forgione, I., Woloszynska, M., Pacenza, M., Chiappetta, A., Greco, M., Araniti, F., Abenavoli, M. R., Van Lijsebettens, M., Bitonti, M. B., & Bruno, L. (2019). Hypomethylated drm1 drm2 cmt3 mutant phenotype of Arabidopsis thaliana is related to auxin pathway impairment. *PLANT SCIENCE*, 280, 383-396. http://dx.doi.org/10.1016/j.plantsci.2018.12.029
 - Fujimoto, R., Sasaki, T., Inoue, H., & Nishio, T. (2008). Hypomethylation and transcriptional reactivation of retrotransposon-like sequences in ddm1 transgenic plants of Brassica rapa. *Plant Molecular Biology*, *66*(5), 463-473. https://doi.org/10.1007/s11103-007-9285-1
 - Fujimoto, S. Y., Ohta, M., Usui, A., Shinshi, H., & Ohme-Takagi, M. (2000). Arabidopsis Ethylene-Responsive Element Binding Factors Act as Transcriptional Activators or Repressors of GCC Box–Mediated Gene Expression. *The Plant Cell*, *12*(3), 393-405.
 - Fultz, D., Choudury, S. G., & Slotkin, R. K. (2015). Silencing of active transposable elements in plants. *Current opinion in plant biology*, 27, 67- 76. https://doi.org/10.1016/j.pbi.2015.05.027
 - Furci, L., Jain, R., Stassen, J., Berkowitz, O., Whelan, J., Roquis, D., Baillet, V., Colot, V., Johannes, F., & Ton, J. (2019). Identification and characterisation of hypomethylated DNA loci controlling quantitative resistance in Arabidopsis. *ELife*, 8, e40655. https://doi.org/10.7554/eLife.40655
 - Gagnot, S., Tamby, J.-P., Martin-Magniette, M.-L., Bitton, F., Taconnat, L., Balzergue, S., Aubourg, S., Renou, J.-P., Lecharny, A., & Brunaud, V. (2008). CATdb: A public access to Arabidopsis transcriptome data from the URGV-CATMA platform. *Nucleic Acids Research*, *36*(Database issue), D986-990. https://doi.org/10.1093/nar/gkm757
 - Gaillochet, C., & Lohmann, J. U. (2015). The never-ending story: From pluripotency to plant developmental plasticity. *Development (Cambridge, England)*, 142(13), 2237- 2249. https://doi.org/10.1242/dev.117614
 - Garg, R., Narayana Chevala, V., Shankar, R., & Jain, M. (2015). Divergent DNA methylation patterns associated with gene expression in rice cultivars with contrasting drought and salinity stress response. *Scientific Reports*, *5*. https://doi.org/10.1038/srep14922
 - Gebreselassie, M. N., Ader, K., Boizot, N., Millier, F., Charpentier, J.-P., Alves, A., Simões, R., Rodrigues, J. C., Bodineau, G., Fabbrini, F., Sabatti, M., Bastien, C., & Segura, V. (2017). Near-infrared spectroscopy enables the genetic analysis of chemical properties in a large set of wood samples from Populus nigra (L.) natural populations. *Industrial Crops and Products*, 107, 159-171. https://doi.org/10.1016/j.indcrop.2017.05.013
 - Gendrel, A.-V., Lippman, Z., Yordan, C., Colot, V., & Martienssen, R. A. (2002). Dependence of Heterochromatic Histone H3 Methylation Patterns on the Arabidopsis Gene DDM1. *Science*, 297(5588), 1871- 1873. https://doi.org/10.1126/science.1074950
 - Gömöry, D., Hrivnák, M., Krajmerova, D., & Longauer, R. (2017). Epigenetic memory effects in forest trees: A victory of "Michurinian biology? *Central European Forestry Journal*, 63. https://doi.org/10.1515/forj-2017-0024
 - Gourcilleau, D., Bogeat-Triboulot, M.-B., Le Thiec, D., Lafon-Placette, C., Delaunay, A., El-Soud, W. A., Brignolas, F., & Maury, S. (2010). DNA methylation and histone acetylation: Genotypic variations in hybrid poplars, impact of water deficit and relationships with productivity. *Annals of Forest Science*, 67(2), 208.
- Grandbastien, M.-A. (1998). Activation of plant retrotransposons under stress conditions. *Trends in Plant Science*, *3*(5), 181- 187. https://doi.org/10.1016/S1360-1385(98)01232-1
 - Guo, Y., Ping, W., Chen, J., Zhu, L., Zhao, Y., Guo, J., & Huang, Y. (2019). Meta-analysis of the effects of overexpression of WRKY transcription factors on plant responses to drought stress. *BMC Genetics*, 20(1), 63. https://doi.org/10.1186/s12863-019-0766-4
- Ha, S., Vankova, R., Yamaguchi-Shinozaki, K., Shinozaki, K., & Tran, L.-S. P. (2012). Cytokinins:

 Metabolism and function in plant adaptation to environmental stresses. *Trends in Plant Science*,

 17(3), 172- 179. https://doi.org/10.1016/j.tplants.2011.12.005

- Hamanishi, E. T., Thomas, B. R., & Campbell, M. M. (2012). Drought induces alterations in the stomatal development program in Populus. *Journal of Experimental Botany*, *63*(13), 4959-4971. https://doi.org/10.1093/jxb/ers177
- Havlová, M., Dobrev, P. I., Motyka, V., Štorchová, H., Libus, J., Dobrá, J., Malbeck, J., Gaudinová, A., & Vanková, R. (2008). The role of cytokinins in responses to water deficit in tobacco plants over-expressing trans-zeatin O-glucosyltransferase gene under 35S or SAG12 promoters. *Plant, Cell & Environment*, 31(3), 341- 353. https://doi.org/10.1111/j.1365-3040.2007.01766.x
 - He, G.-H., Xu, J.-Y., Wang, Y.-X., Liu, J.-M., Li, P.-S., Chen, M., Ma, Y.-Z., & Xu, Z.-S. (2016). Drought-responsive WRKY transcription factor genes TaWRKY1 and TaWRKY33 from wheat confer drought and/or heat resistance in Arabidopsis. *BMC Plant Biology*, 16. https://doi.org/10.1186/s12870-016-0806-4
 - Herbette, S., Bouchet, B., Brunel, N., Bonnin, E., Cochard, H., & Guillon, F. (2015). Immunolabelling of intervessel pits for polysaccharides and lignin helps in understanding their hydraulic properties in Populus tremula x alba. *Annals of Botany*, 115(2), 187- 199. https://doi.org/10.1093/aob/mcu232
 - Heyman, J., Canher, B., Bisht, A., Christiaens, F., & De Veylder, L. (2018). Emerging role of the plant ERF transcription factors in coordinating wound defense responses and repair. *Journal of Cell Science*, 131(2). https://doi.org/10.1242/jcs.208215
 - Higo, H., Tahir, M., Takashima, K., Miura, A., Watanabe, K., Tagiri, A., Ugaki, M., Ishikawa, R., Eiguchi, M., Kurata, N., Sasaki, T., Richards, E., Takano, M., Kishimoto, N., Kakutani, T., & Habu, Y. (2012). DDM1 (Decrease in DNA Methylation) genes in rice (Oryza sativa). *Molecular Genetics and Genomics*, 287(10), 785-792. https://doi.org/10.1007/s00438-012-0717-5
 - Hirsch, C. D., & Springer, N. M. (2017). Transposable element influences on gene expression in plants. *Biochimica et Biophysica Acta - Gene Regulatory Mechanisms*, 1860(1), 157-165. https://doi.org/10.1016/j.bbagrm.2016.05.010
 - Hoffmann, S., Otto, C., Doose, G., Tanzer, A., Langenberger, D., Christ, S., Kunz, M., Holdt, L. M., Teupser, D., Hackermüller, J., & Stadler, P. F. (2014). A multi-split mapping algorithm for circular RNA, splicing, trans-splicing and fusion detection. *Genome Biology*, *15*(2), R34. https://doi.org/10.1186/gb-2014-15-2-r34
 - Ikeda, Y., & Nishimura, T. (2015). The role of DNA methylation in transposable element silencing and genomic imprinting. *Nuclear Functions in Plant Transcription, Signaling and Development*, 13-29. https://doi.org/10.1007/978-1-4939-2386-1_2
 - Ito, T., Tarutani, Y., To, T. K., Kassam, M., Duvernois-Berthet, E., Cortijo, S., Takashima, K., Saze, H., Toyoda, A., Fujiyama, A., & others. (2015). Genome-wide negative feedback drives transgenerational DNA methylation dynamics in Arabidopsis. *PLoS Genet*, *11*(4), e1005154.
 - Jansson, S., & Douglas, C. J. (2007). *Populus*: A Model System for Plant Biology. *Annual Review of Plant Biology*, *58*(1), 435-458. https://doi.org/10.1146/annurev.arplant.58.032806.103956
 - Jeddeloh, J. A., Bender, J., & Richards, E. J. (1998). The DNA methylation locusDDM1 is required for maintenance of gene silencing in Arabidopsis. *Genes & Development*, *12*(11), 1714–1725.
 - Jiang, Y., Guo, L., Ma, X., Zhao, X., Jiao, B., Li, C., & Luo, K. (2017). The WRKY transcription factors PtrWRKY18 and PtrWRKY35 promote Melampsora resistance in Populus. *Tree Physiology*, *37*(5), 665-675. https://doi.org/10.1093/treephys/tpx008
 - Johannes, F., Porcher, E., Teixeira, F. K., Saliba-Colombani, V., Simon, M., Agier, N., Bulski, A., Albuisson, J., Heredia, F., Audigier, P., Bouchez, D., Dillmann, C., Guerche, P., Hospital, F., & Colot, V. (2009). Assessing the Impact of Transgenerational Epigenetic Variation on Complex Traits. *PLOS Genetics*, *5*(6), e1000530. https://doi.org/10.1371/journal.pgen.1000530
 - Kakutani, T. (1997). Genetic characterization of late-flowering traits induced by DNA hypomethylation mutation in Arabidopsis thaliana. *The Plant Journal*, *12*(6), 1447- 1451. https://doi.org/10.1046/j.1365-313x.1997.12061447.x
- Kakutani, T., Jeddeloh, J. A., & Richards, E. J. (1995). Characterization of an Arabidopsis thaliana DNA hypomethylation mutant. *Nucleic acids research*, *23*(1), 130–137.
- Karan, R., DeLeon, T., Biradar, H., & Subudhi, P. K. (2012). Salt Stress Induced Variation in DNA
 Methylation Pattern and Its Influence on Gene Expression in Contrasting Rice Genotypes. *PLoS ONE*, 7(6). https://doi.org/10.1371/journal.pone.0040203
- 1322 Kawakatsu, T., & Ecker, J. R. (2019). Diversity and dynamics of DNA methylation: Epigenomic resources 1323 and tools for crop breeding. *Breeding Science*, 69(2), 191-204. 1324 https://doi.org/10.1270/jsbbs.19005

- Kawakatsu, T., Huang, S. C., Jupe, F., Sasaki, E., Schmitz, R. J., Urich, M. A., Castanon, R., Nery, J. R., Barragan, C., He, Y., Chen, H., Dubin, M., Lee, C.-R., Wang, C., Bemm, F., Becker, C., O'Neil, R., O'Malley, R. C., Quarless, D. X., ... Zhou, X. (2016). Epigenomic Diversity in a Global Collection of Arabidopsis thaliana Accessions. Cell. 166(2), 505. https://doi.org/10.1016/j.cell.2016.06.044
- Kawanabe, T., Ishikura, S., Miyaji, N., Sasaki, T., Wu, L. M., Itabashi, E., Takada, S., Shimizu, M., Takasaki-Yasuda, T., Osabe, K., Peacock, W. J., Dennis, E. S., & Fujimoto, R. (2016). Role of DNA methylation in hybrid vigor in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences*, *113*(43), E6704- E6711. https://doi.org/10.1073/pnas.1613372113
- Kejnovsky, E., Hawkins, J. S., & Feschotte, C. (2012). Plant Transposable Elements: Biology and Evolution. In J. F. Wendel, J. Greilhuber, J. Dolezel, & I. J. Leitch (Éd.), *Plant Genome Diversity Volume 1* (p. 17- 34). Springer Vienna. https://doi.org/10.1007/978-3-7091-1130-7_2
- Koo, A. J., Thireault, C., Zemelis, S., Poudel, A. N., Zhang, T., Kitaoka, N., Brandizzi, F., Matsuura, H., & Howe, G. A. (2014). Endoplasmic reticulum-associated inactivation of the hormone jasmonoyl-L-isoleucine by multiple members of the cytochrome P450 94 family in Arabidopsis. *The Journal of Biological Chemistry*, 289(43), 29728- 29738. https://doi.org/10.1074/jbc.M114.603084
 - Kooke, R., Johannes, F., Wardenaar, R., Becker, F., Etcheverry, M., Colot, V., Vreugdenhil, D., & Keurentjes, J. J. B. (2015). Epigenetic Basis of Morphological Variation and Phenotypic Plasticity in *Arabidopsis thaliana*. *The Plant Cell Online*, 27(2), 337-348. https://doi.org/10.1105/tpc.114.133025
 - Kopylova, E., Noé, L., & Touzet, H. (2012). SortMeRNA: Fast and accurate filtering of ribosomal RNAs in metatranscriptomic data. *Bioinformatics (Oxford, England)*, 28(24), 3211- 3217. https://doi.org/10.1093/bioinformatics/bts611
 - Krueger, F., & Andrews, S. R. (2011). Bismark: A flexible aligner and methylation caller for Bisulfite-Seq applications. *Bioinformatics*, 27(11), 1571- 1572. https://doi.org/10.1093/bioinformatics/btr167
 - Lafon-Placette, C., Faivre-Rampant, P., Delaunay, A., Street, N., Brignolas, F., & Maury, S. (2013). Methylome of DNase I sensitive chromatin in *Populus trichocarpa* shoot apical meristematic cells: A simplified approach revealing characteristics of gene-body DNA methylation in open chromatin state. *New Phytologist*, 197(2), 416-430. https://doi.org/10.1111/nph.12026
 - Lafon-Placette, C., Le Gac, A.-L., Chauveau, D., Segura, V., Delaunay, A., Lesage-Descauses, M.-C., Hummel, I., Cohen, D., Jesson, B., Le Thiec, D., Bogeat-Triboulot, M.-B., Brignolas, F., & Maury, S. (2018). Changes in the epigenome and transcriptome of the poplar shoot apical meristem in response to water availability affect preferentially hormone pathways. *Journal of Experimental Botany*, 69(3), 537-551. https://doi.org/10.1093/jxb/erx409
 - Lanciano, S., Carpentier, M.-C., Llauro, C., Jobet, E., Robakowska-Hyzorek, D., Lasserre, E., Ghesquière, A., Panaud, O., & Mirouze, M. (2017). Sequencing the extrachromosomal circular mobilome reveals retrotransposon activity in plants. *PLoS Genetics*, *13*(2). https://doi.org/10.1371/journal.pgen.1006630
 - Langmead, B., Trapnell, C., Pop, M., & Salzberg, S. L. (2009). Ultrafast and memory-efficient alignment of short DNA sequences to the human genome. *Genome Biology*, 10(3), R25. https://doi.org/10.1186/gb-2009-10-3-r25
 - Latzel, V., Allan, E., Bortolini Silveira, A., Colot, V., Fischer, M., & Bossdorf, O. (2013). Epigenetic diversity increases the productivity and stability of plant populations. *Nature Communications*, *4*. https://doi.org/10.1038/ncomms3875
 - Latzel, V., Zhang, Y., Karlsson Moritz, K., Fischer, M., & Bossdorf, O. (2012). Epigenetic variation in plant responses to defence hormones. *Annals of Botany*, 110(7), 1423-1428. https://doi.org/10.1093/aob/mcs088
 - Le Gac, A.-L., Lafon-Placette, C., Chauveau, D., Segura, V., Delaunay, A., Fichot, R., Marron, N., Le Jan, I., Berthelot, A., Bodineau, G., Bastien, J.-C., Brignolas, F., & Maury, S. (2018). Winter-dormant shoot apical meristem in poplar trees shows environmental epigenetic memory. *Journal of Experimental Botany*, 69(20), 4821- 4837. https://doi.org/10.1093/jxb/ery271
- Le Gac, A.-L., Lafon-Placette, C., Delaunay, A., & Maury, S. (2019). Developmental, genetic and environmental variations of global DNA methylation in the first leaves emerging from the shoot apical meristem in poplar trees. *Plant Signaling & Behavior*, 14. https://doi.org/10.1080/15592324.2019.1596717

1388

1389

1390

1391 1392

1393

1394

1395

1396

1397

1398

1399

1400 1401

1402

1403

1404

1405

1406

1407

1408

1409

1410 1411

1412

1413

1414

1415

1416

1417

1418

1419

1420

1421

- Lee, S.-I., & Kim, N.-S. (2014). Transposable Elements and Genome Size Variations in Plants. *Genomics & Informatics*, 12(3), 87. https://doi.org/10.5808/GI.2014.12.3.87
- Li, J., Brader, G., & Palva, E. T. (2004). The WRKY70 Transcription Factor: A Node of Convergence for Jasmonate-Mediated and Salicylate-Mediated Signals in Plant Defense. *The Plant Cell*, 16(2), 319-331. https://doi.org/10.1105/tpc.016980
- Li, Q., Eichten, S. R., Hermanson, P. J., & Springer, N. M. (2014). Inheritance Patterns and Stability of DNA Methylation Variation in Maize Near-Isogenic Lines. *Genetics*, 196(3), 667-676. https://doi.org/10.1534/genetics.113.158980
 - Liang, D., Zhang, Z., Wu, H., Huang, C., Shuai, P., Ye, C.-Y., Tang, S., Wang, Y., Yang, L., & Wang, J. (2014). Single-base-resolution methylomes of Populus trichocarpa reveal the association between DNA methylation and drought stress. *BMC genetics*, *15*, S9.
 - Li-Marchetti, C., Le Bras, C., Relion, D., Citerne, S., Huché-Thélier, L., Sakr, S., Morel, P., & Crespel, L. (2015). Genotypic differences in architectural and physiological responses to water restriction in rose bush. *Frontiers in Plant Science*, *6*. https://doi.org/10.3389/fpls.2015.00355
 - Lippman, Z., Gendrel, A.-V., Black, M., Vaughn, M. W., Dedhia, N., Richard McCombie, W., Lavine, K., Mittal, V., May, B., Kasschau, K. D., Carrington, J. C., Doerge, R. W., Colot, V., & Martienssen, R. (2004). Role of transposable elements in heterochromatin and epigenetic control. *Nature*, 430(6998), 471-476. https://doi.org/10.1038/nature02651
 - Lisch, D. (2012). How important are transposons for plant evolution? *Nature Reviews Genetics*, *14*(1), 49-61. https://doi.org/10.1038/nrg3374
 - Liu, G., Ji, Y., Bhuiyan, N. H., Pilot, G., Selvaraj, G., Zou, J., & Wei, Y. (2010). Amino acid homeostasis modulates salicylic acid-associated redox status and defense responses in Arabidopsis. *The Plant Cell*, 22(11), 3845- 3863. https://doi.org/10.1105/tpc.110.079392
 - Long, J. C., Xia, A. A., Liu, J. H., Jing, J. L., Wang, Y. Z., Qi, C. Y., & He, Y. (2019). Decrease in DNA methylation 1 (DDM1) is required for the formation of mCHH islands in maize. *Journal of Integrative Plant Biology*, 61(6), 749-764. https://doi.org/10.1111/jipb.12733
 - López Sánchez, A., Stassen, J. H. M., Furci, L., Smith, L. M., & Ton, J. (2016). The role of DNA (de)methylation in immune responsiveness of Arabidopsis. *The Plant Journal*, *88*(3), 361- 374. https://doi.org/10.1111/tpj.13252
 - Lorrain, S., Vailleau, F., Balagué, C., & Roby, D. (2003). Lesion mimic mutants: Keys for deciphering cell death and defense pathways in plants? *Trends in Plant Science*, 8(6), 263-271. https://doi.org/10.1016/S1360-1385(03)00108-0
 - Makarevitch, I., Waters, A. J., West, P. T., Stitzer, M., Hirsch, C. N., Ross-Ibarra, J., & Springer, N. M. (2015). Transposable Elements Contribute to Activation of Maize Genes in Response to Abiotic Stress. *PLoS Genetics*, *11*(1). https://doi.org/10.1371/journal.pgen.1004915
 - Maor, G. L., Yearim, A., & Ast, G. (2015). The alternative role of DNA methylation in splicing regulation. *Trends in Genetics*, 31(5), 274- 280. https://doi.org/10.1016/j.tig.2015.03.002
 - Marcel, S., Sawers, R., Oakeley, E., Angliker, H., & Paszkowski, U. (2010). Tissue-Adapted Invasion Strategies of the Rice Blast Fungus Magnaporthe oryzae[W]. *The Plant Cell*, 22(9), 3177- 3187. https://doi.org/10.1105/tpc.110.078048
 - Mauch-Mani, B., Baccelli, I., Luna, E., & Flors, V. (2017). Defense Priming: An Adaptive Part of Induced Resistance. *Annual Review of Plant Biology*, *68*(1), 485- 512. https://doi.org/10.1146/annurev-arplant-042916-041132
- Maury, S., Sow, M. D., Le Gac, A.-L., Genitoni, J., Lafon-Placette, C., & Mozgova, I. (2019).

 Phytohormone and Chromatin Crosstalk: The Missing Link For Developmental Plasticity?

 Frontiers in Plant Science, 10. https://doi.org/10.3389/fpls.2019.00395
- McCarthy, D. J., Chen, Y., & Smyth, G. K. (2012). Differential expression analysis of multifactor RNA-Seq experiments with respect to biological variation. *Nucleic Acids Research*, *40*(10), 4288-4297. https://doi.org/10.1093/nar/gks042
- McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., & Yepez, E. A. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, 178(4), 719- 739. https://doi.org/10.1111/j.1469-8137.2008.02436.x
- Meyer, P. (2015). Epigenetic variation and environmental change: Fig. 1. *Journal of Experimental Botany*, 66(12), 3541- 3548. https://doi.org/10.1093/jxb/eru502

- Mirouze, M., & Paszkowski, J. (2011). Epigenetic contribution to stress adaptation in plants. *Current Opinion in Plant Biology*, *14*(3), 267- 274. https://doi.org/10.1016/j.pbi.2011.03.004
- Mirouze, M., Reinders, J., Bucher, E., Nishimura, T., Schneeberger, K., Ossowski, S., Cao, J., Weigel, D.,
 Paszkowski, J., & Mathieu, O. (2009). Selective epigenetic control of retrotransposition in
 Arabidopsis. *Nature*, *461*(7262), 427- 430. https://doi.org/10.1038/nature08328
 - Miura, A., Yonebayashi, S., Watanabe, K., Toyama, T., Shimada, H., & Kakutani, T. (2001). Mobilization of transposons by a mutation abolishing full DNA methylation in Arabidopsis. *Nature*, *411*(6834), 212- 214. https://doi.org/10.1038/35075612
 - Mofatto, L. S., Carneiro, F. de A., Vieira, N. G., Duarte, K. E., Vidal, R. O., Alekcevetch, J. C., Cotta, M. G., Verdeil, J.-L., Lapeyre-Montes, F., Lartaud, M., Leroy, T., De Bellis, F., Pot, D., Rodrigues, G. C., Carazzolle, M. F., Pereira, G. A. G., Andrade, A. C., & Marraccini, P. (2016). Identification of candidate genes for drought tolerance in coffee by high-throughput sequencing in the shoot apex of different Coffea arabica cultivars. BMC Plant Biology, 16. https://doi.org/10.1186/s12870-016-0777-5
 - Monclus, R., Dreyer, E., Villar, M., Delmotte, F. M., Delay, D., Petit, J.-M., Barbaroux, C., Le Thiec, D., Bréchet, C., & Brignolas, F. (2006). Impact of drought on productivity and water use efficiency in 29 genotypes of Populus deltoidesxPopulus nigra. *New Phytologist*, 169(4), 765-777. https://doi.org/10.1111/j.1469-8137.2005.01630.x
 - Munné-Bosch, S., & Peñuelas, J. (2003). Photo- and antioxidative protection, and a role for salicylic acid during drought and recovery in field-grown Phillyrea angustifolia plants. *Planta*, *217*(5), 758-766. https://doi.org/10.1007/s00425-003-1037-0
 - Nicotra, A.B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., Poot, P., Purugganan, M. D., Richards, C. L., Valladares, F., & van Kleunen, M. (2010). Plant phenotypic plasticity in a changing climate. *Trends in Plant Science*, *15*(12), 684-692. https://doi.org/10.1016/j.tplants.2010.09.008
 - Nicotra, Adrienne B., Segal, D. L., Hoyle, G. L., Schrey, A. W., Verhoeven, K. J. F., & Richards, C. L. (2015). Adaptive plasticity and epigenetic variation in response to warming in an Alpine plant. *Ecology and Evolution*, *5*(3), 634- 647. https://doi.org/10.1002/ece3.1329
 - Niederhuth, C. E., & Schmitz, R. J. (2017). Putting DNA methylation in context: From genomes to gene expression in plants. *Biochimica et Biophysica Acta (BBA) Gene Regulatory Mechanisms*, 1860(1), 149- 156. https://doi.org/10.1016/j.bbagrm.2016.08.009
 - Nishiyama, R., Watanabe, Y., Fujita, Y., Le, D. T., Kojima, M., Werner, T., Vankova, R., Yamaguchi-Shinozaki, K., Shinozaki, K., Kakimoto, T., Sakakibara, H., Schmülling, T., & Tran, L.-S. P. (2011). Analysis of cytokinin mutants and regulation of cytokinin metabolic genes reveals important regulatory roles of cytokinins in drought, salt and abscisic acid responses, and abscisic acid biosynthesis. *The Plant Cell*, 23(6), 2169- 2183. https://doi.org/10.1105/tpc.111.087395
 - Ojolo, S. P., Cao, S., Priyadarshani, S. V. G. N., Li, W., Yan, M., Aslam, M., Zhao, H., & Qin, Y. (2018). Regulation of Plant Growth and Development: A Review From a Chromatin Remodeling Perspective. *Frontiers in Plant Science*, *9*. https://doi.org/10.3389/fpls.2018.01232
 - Ong-Abdullah, M., Ordway, J. M., Jiang, N., Ooi, S.-E., Kok, S.-Y., Sarpan, N., Azimi, N., Hashim, A. T., Ishak, Z., Rosli, S. K., Malike, F. A., Bakar, N. A. A., Marjuni, M., Abdullah, N., Yaakub, Z., Amiruddin, M. D., Nookiah, R., Singh, R., Low, E.-T. L., ... Martienssen, R. A. (2015). Loss of Karma transposon methylation underlies the mantled somaclonal variant of oil palm. *Nature*, *525*(7570), 533- 537. https://doi.org/10.1038/nature15365
 - Oshima, Y., & Mitsuda, N. (2013). The MIXTA-like Transcription factor MYB16 is a major regulator of cuticle formation in vegetative organs. *Plant Signaling & Behavior*, *8*(11). https://doi.org/10.4161/psb.26826
 - Oshima, Y., & Mitsuda, N. (2016). Enhanced cuticle accumulation by employing MIXTA-like transcription factors. *Plant Biotechnology*, 33, 161- 168. https://doi.org/10.5511/plantbiotechnology.16.0627a
 - Pandey, S., & Chakraborty, D. (2015). Salicylic Acid and Drought Stress Response: Biochemical to Molecular Crosstalk. In B. N. Tripathi & M. Müller (Éd.), Stress Responses in Plants: Mechanisms of Toxicity and Tolerance (p. 247- 265). Springer International Publishing. https://doi.org/10.1007/978-3-319-13368-3 10
- Pandey, S. P., Srivastava, S., Goel, R., Lakhwani, D., Singh, P., Asif, M. H., & Sane, A. P. (2017). Simulated herbivory in chickpea causes rapid changes in defense pathways and hormonal

- transcription networks of JA/ethylene/GA/auxin within minutes of wounding. *Scientific Reports*, 7(1), 1- 14. https://doi.org/10.1038/srep44729
- Plavcová, L., & Hacke, U. G. (2011). Heterogeneous distribution of pectin epitopes and calcium in different pit types of four angiosperm species. *New Phytologist*, 192(4), 885-897. https://doi.org/10.1111/j.1469-8137.2011.03842.x
 - Plomion, C., Bastien, C., Bogeat-Triboulot, M.-B., Bouffier, L., Déjardin, A., Duplessis, S., Fady, B., Heuertz, M., Le Gac, A.-L., Le Provost, G., Legué, V., Lelu-Walter, M.-A., Leplé, J.-C., Maury, S., Morel, A., Oddou-Muratorio, S., Pilate, G., Sanchez, L., Scotti, I., ... Vacher, C. (2016). Forest tree genomics: 10 achievements from the past 10 years and future prospects. *Annals of Forest Science*, 73(1), 77- 103. https://doi.org/10.1007/s13595-015-0488-3
 - Quadrana, L., & Colot, V. (2016). Plant Transgenerational Epigenetics. *Annual Review of Genetics*, *50*, 467-491. https://doi.org/10.1146/annurev-genet-120215-035254
 - Quadrana, L., Etcheverry, M., Gilly, A., Caillieux, E., Madoui, M.-A., Guy, J., Bortolini Silveira, A., Engelen, S., Baillet, V., Wincker, P., Aury, J.-M., & Colot, V. (2019). Transposition favors the generation of large effect mutations that may facilitate rapid adaption. *Nature Communications*, *10*(1), 1- 10. https://doi.org/10.1038/s41467-019-11385-5
 - Qüesta, J. I., Fina, J. P., & Casati, P. (2013). DDM1 and ROS1 have a role in UV-B induced- and oxidative DNA damage in A. thaliana. *Frontiers in Plant Science*, *4*. https://doi.org/10.3389/fpls.2013.00420
 - Raj, S., Bräutigam, K., Hamanishi, E. T., Wilkins, O., Thomas, B. R., Schroeder, W., Mansfield, S. D., Plant, A. L., & Campbell, M. M. (2011). Clone history shapes Populus drought responses. *Proceedings of the National Academy of Sciences*, *108*(30), 12521–12526.
 - Raju, S. K. K., Shao, M.-R., Sanchez, R., Xu, Y.-Z., Sandhu, A., Graef, G., & Mackenzie, S. (2018). An epigenetic breeding system in soybean for increased yield and stability. *Plant Biotechnology Journal*, *16*(11), 1836- 1847. https://doi.org/10.1111/pbi.12919
 - Reinders, J., Wulff, B. B. H., Mirouze, M., Marí-Ordóñez, A., Dapp, M., Rozhon, W., Bucher, E., Theiler, G., & Paszkowski, J. (2009). Compromised stability of DNA methylation and transposon immobilization in mosaic Arabidopsis epigenomes. *Genes & Development*, 23(8), 939-950. https://doi.org/10.1101/gad.524609
 - Richards, C. L., Alonso, C., Becker, C., Bossdorf, O., Bucher, E., Colomé-Tatché, M., Durka, W., Engelhardt, J., Gaspar, B., Gogol-Döring, A., Grosse, I., van Gurp, T. P., Heer, K., Kronholm, I., Lampei, C., Latzel, V., Mirouze, M., Opgenoorth, L., Paun, O., ... Verhoeven, K. J. F. (2017). Ecological plant epigenetics: Evidence from model and non-model species, and the way forward. *Ecology Letters*, 20(12), 1576- 1590. https://doi.org/10.1111/ele.12858
 - Rigaill, G., Balzergue, S., Brunaud, V., Blondet, E., Rau, A., Rogier, O., Caius, J., Maugis-Rabusseau, C., Soubigou-Taconnat, L., Aubourg, S., Lurin, C., Martin-Magniette, M.-L., & Delannoy, E. (2018). Synthetic data sets for the identification of key ingredients for RNA-seq differential analysis. *Briefings in Bioinformatics*, *19*(1), 65- 76. https://doi.org/10.1093/bib/bbw092
 - Roux, B., Rodde, N., Jardinaud, M.-F., Timmers, T., Sauviac, L., Cottret, L., Carrère, S., Sallet, E., Courcelle, E., Moreau, S., Debellé, F., Capela, D., de Carvalho-Niebel, F., Gouzy, J., Bruand, C., & Gamas, P. (2014). An integrated analysis of plant and bacterial gene expression in symbiotic root nodules using laser-capture microdissection coupled to RNA sequencing. *The Plant Journal: For Cell and Molecular Biology*, 77(6), 817-837. https://doi.org/10.1111/tpj.12442
 - Roux, F., Colomé-Tatché, M., Edelist, C., Wardenaar, R., Guerche, P., Hospital, F., Colot, V., Jansen, R. C., & Johannes, F. (2011). Genome-Wide Epigenetic Perturbation Jump-Starts Patterns of Heritable Variation Found in Nature. *Genetics*, 188(4), 1015-1017. https://doi.org/10.1534/genetics.111.128744
- Russo, V. E. A., Riggs, A. D., & Martienssen, R. A. (1996). *Epigenetic mechanisms of gene regulation*.

 Cold Spring Harbour, NY: Cold Spring Harbour Laboratory Press.

 https://trove.nla.gov.au/version/27736760
- Sasaki, T., Kobayashi, A., Saze, H., & Kakutani, T. (2012). RNAi-independent de novo DNA methylation revealed in Arabidopsis mutants of chromatin remodeling gene DDM1. *The Plant Journal*, *70*(5), 750-758. https://doi.org/10.1111/j.1365-313X.2012.04911.x
- Saze, H., & Kakutani, T. (2007). Heritable epigenetic mutation of a transposon-flanked Arabidopsis gene due to lack of the chromatin-remodeling factor DDM1. *The EMBO Journal*, *26*(15), 3641–3652.

- Schmid, M. W., Giraldo-Fonseca, A., Rövekamp, M., Smetanin, D., Bowman, J. L., & Grossniklaus, U. (2018). Extensive epigenetic reprogramming during the life cycle of Marchantia polymorpha. *Genome Biology*, *19*(1). https://doi.org/10.1186/s13059-017-1383-z
 - Schmittgen, T. D., & Livak, K. J. (2008). Analyzing real-time PCR data by the comparative C(T) method. Nature Protocols, 3(6), 1101- 1108. https://doi.org/10.1038/nprot.2008.73
 - Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), 671-675. https://doi.org/10.1038/nmeth.2089
 - Sedaghat, M., Tahmasebi-Sarvestani, Z., Emam, Y., & Mokhtassi-Bidgoli, A. (2017). Physiological and antioxidant responses of winter wheat cultivars to strigolactone and salicylic acid in drought. *Plant Physiology and Biochemistry*, *119*, 59- 69. https://doi.org/10.1016/j.plaphy.2017.08.015
 - Seymour, D. K., & Becker, C. (2017). The causes and consequences of DNA methylome variation in plants. *Current Opinion in Plant Biology*, *36*, 56- 63. https://doi.org/10.1016/j.pbi.2017.01.005
 - Shi, H., Chen, L., Ye, T., Liu, X., Ding, K., & Chan, Z. (2014). Modulation of auxin content in Arabidopsis confers improved drought stress resistance. *Plant Physiology and Biochemistry*, *82*, 209-217. https://doi.org/10.1016/j.plaphy.2014.06.008
 - Slotkin, R. K., & Martienssen, R. (2007). Transposable elements and the epigenetic regulation of the genome. *Nature Reviews. Genetics*, *8*(4), 272- 285. https://doi.org/10.1038/nrg2072
 - Solano, R., Stepanova, A., Chao, Q., & Ecker, J. R. (1998). Nuclear events in ethylene signaling: A transcriptional cascade mediated by ETHYLENE-INSENSITIVE3 and ETHYLENE-RESPONSE-FACTOR1. *Genes & Development*, *12*(23), 3703-3714.
 - Song, J. T., Lu, H., McDowell, J. M., & Greenberg, J. T. (2004). A key role for ALD1 in activation of local and systemic defenses in Arabidopsis. *The Plant Journal*, 40(2), 200-212. https://doi.org/10.1111/j.1365-313X.2004.02200.x
 - Sow, M. D., Allona, I., Ambroise, C., Conde, D., Fichot, R., Gribkova, S., Jorge, V., Le-Provost, G., Pâques, L., Plomion, C., Salse, J., Sanchez-Rodriguez, L., Segura, V., Tost, J., & Maury, S. (2018). Epigenetics in Forest Trees. In *Advances in Botanical Research* (Vol. 88, p. 387-453). Elsevier. https://doi.org/10.1016/bs.abr.2018.09.003
 - Sow, M. D., Segura, V., Chamaillard, S., Jorge, V., Delaunay, A., Lafon-Placette, C., Fichot, R., Faivre-Rampant, P., Villar, M., Brignolas, F., & Maury, S. (2018). Narrow-sense heritability and PST estimates of DNA methylation in three Populus nigra L. populations under contrasting water availability. *Tree Genetics & Genomes*, *14*(5). https://doi.org/10.1007/s11295-018-1293-6
 - Springer, N. M., & Schmitz, R. J. (2017). Exploiting induced and natural epigenetic variation for crop improvement. *Nature Reviews Genetics*, *18*(9), 563- 575. https://doi.org/10.1038/nrg.2017.45
 - Stokes, T. L., Kunkel, B. N., & Richards, E. J. (2002). Epigenetic variation in Arabidopsis disease resistance. *Genes & Development*, *16*(2), 171- 182. https://doi.org/10.1101/gad.952102
 - Street, N. R., Skogström, O., Sjödin, A., Tucker, J., Rodríguez- Acosta, M., Nilsson, P., Jansson, S., & Taylor, G. (2006a). The genetics and genomics of the drought response in Populus. *The Plant Journal*, 48(3), 321- 341. https://doi.org/10.1111/j.1365-313X.2006.02864.x
 - Street, N. R., Skogström, O., Sjödin, A., Tucker, J., Rodríguez- Acosta, M., Nilsson, P., Jansson, S., & Taylor, G. (2006b). The genetics and genomics of the drought response in Populus. *The Plant Journal*, *48*(3), 321- 341. https://doi.org/10.1111/j.1365-313X.2006.02864.x
 - Sun, Y., & Yu, D. (2015). Activated expression of AtWRKY53 negatively regulates drought tolerance by mediating stomatal movement. *Plant Cell Reports*, 34(8), 1295-1306. https://doi.org/10.1007/s00299-015-1787-8
 - Tan, F., Zhou, C., Zhou, Q., Zhou, S., Yang, W., Zhao, Y., Li, G., & Zhou, D.-X. (2016). Analysis of Chromatin Regulators Reveals Specific Features of Rice DNA Methylation Pathways. *Plant Physiology*, 171(3), 2041- 2054. https://doi.org/10.1104/pp.16.00393
 - Trapet, P., Avoscan, L., Klinguer, A., Pateyron, S., Citerne, S., Chervin, C., Mazurier, S., Lemanceau, P., Wendehenne, D., & Besson-Bard, A. (2016). The Pseudomonas fluorescens Siderophore Pyoverdine Weakens Arabidopsis thaliana Defense in Favor of Growth in Iron-Deficient Conditions. *Plant Physiology*, 171(1), 675-693. https://doi.org/10.1104/pp.15.01537
- Tsukahara, S., Kobayashi, A., Kawabe, A., Mathieu, O., Miura, A., & Kakutani, T. (2009). Bursts of retrotransposition reproduced in Arabidopsis. *Nature*, *461*(7262), 423-426. https://doi.org/10.1038/nature08351
- Tuskan, G. A., DiFazio, S., Jansson, S., Bohlmann, J., Grigoriev, I., Hellsten, U., Putnam, N., Ralph, S., Rombauts, S., Salamov, A., Schein, J., Sterck, L., Aerts, A., Bhalerao, R. R., Bhalerao, R. P.,

- 1600 Blaudez, D., Boerjan, W., Brun, A., Brunner, A., ... Rokhsar, D. (2006). The Genome of Black 1601 Cottonwood, Populus trichocarpa (Torr. & Gray). *Science*, 313(5793), 1596-1604. 1602 https://doi.org/10.1126/science.1128691
- Vassileva, V., Hollwey, E., Todorov, D., & Meyer, P. (s. d.). Leaf epidermal profiling as a phenotyping tool for DNA methylation mutants. 18.
 - Vining, K. J., Pomraning, K. R., Wilhelm, L. J., Priest, H. D., Pellegrini, M., Mockler, T. C., Freitag, M., & Strauss, S. H. (2012). Dynamic DNA cytosine methylation in the Populus trichocarpa genome: Tissue-level variation and relationship to gene expression. *Bmc Genomics*, *13*(1), 27.
 - Volaire, F., Lens, F., Cochard, H., Xu, H., Chacon-Doria, L., Bristiel, P., Balachowski, J., Rowe, N., Violle, C., & Picon-Cochard, C. (2018). Embolism and mechanical resistances play a key role in dehydration tolerance of a perennial grass Dactylis glomerata L. *Annals of Botany*, 122(2), 325-336. https://doi.org/10.1093/aob/mcy073
 - Vongs, A., Kakutani, T., Martienssen, R. A., & Richards, E. J. (1993). Arabidopsis thaliana DNA methylation mutants. *Science (New York, N.Y.)*, *260*(5116), 1926-1928. https://doi.org/10.1126/science.8316832
 - Wang, J., Tao, F., An, F., Zou, Y., Tian, W., Chen, X., Xu, X., & Hu, X. (2017). Wheat transcription factor TaWRKY70 is positively involved in high-temperature seedling plant resistance to Puccinia striiformis f. Sp. Tritici. *Molecular Plant Pathology*, 18(5), 649-661. https://doi.org/10.1111/mpp.12425
 - Wang, Yan, Wang, Q., Liu, M., Bo, C., Wang, X., Ma, Q., Cheng, B., & Cai, R. (2017). Overexpression of a maize MYB48 gene confers drought tolerance in transgenic arabidopsis plants. *Journal of Plant Biology*, 60(6), 612-621. https://doi.org/10.1007/s12374-017-0273-y
 - Wang, Yushuai, Liang, W., & Tang, T. (2018). Constant conflict between Gypsy LTR retrotransposons and CHH methylation within a stress-adapted mangrove genome. *New Phytologist*, *220*(3), 922-935. https://doi.org/10.1111/nph.15209
 - Wang, Zhen, Wang, F., Hong, Y., Yao, J., Ren, Z., Shi, H., & Zhu, J.-K. (2018). The Flowering Repressor SVP Confers Drought Resistance in Arabidopsis by Regulating Abscisic Acid Catabolism. *Molecular Plant*, 11(9), 1184-1197. https://doi.org/10.1016/j.molp.2018.06.009
 - Wang, Zheng, Fang, H., Chen, Y., Chen, K., Li, G., Gu, S., & Tan, X. (2014). Overexpression of BnWRKY33 in oilseed rape enhances resistance to Sclerotinia sclerotiorum. *Molecular Plant Pathology*, *15*(7), 677- 689. https://doi.org/10.1111/mpp.12123
 - Wasternack, C., & Hause, B. (2018). A Bypass in Jasmonate Biosynthesis the OPR3-independent Formation. *Trends in Plant Science*, 23(4), 276-279. https://doi.org/10.1016/j.tplants.2018.02.011
 - Wettstein- Knowles, P. von. (2016). Plant Waxes. In *ELS* (p. 1- 13). American Cancer Society. https://doi.org/10.1002/9780470015902.a0001919.pub3
 - Wu, C., Bordeos, A., Madamba, Ma. R. S., Baraoidan, M., Ramos, M., Wang, G., Leach, J. E., & Leung, H. (2008). Rice lesion mimic mutants with enhanced resistance to diseases. *Molecular Genetics and Genomics*, 279(6), 605-619. https://doi.org/10.1007/s00438-008-0337-2
 - Xi, Y., & Li, W. (2009). BSMAP: Whole genome bisulfite sequence MAPping program. BMC Bioinformatics, 10, 232. https://doi.org/10.1186/1471-2105-10-232
 - Xu, Z., & Zhou, G. (2008). Responses of leaf stomatal density to water status and its relationship with photosynthesis in a grass. *Journal of Experimental Botany*, *59*(12), 3317- 3325. https://doi.org/10.1093/jxb/ern185
 - Yakovlev, I. A., Carneros, E., Lee, Y., Olsen, J. E., & Fossdal, C. G. (2016). Transcriptional profiling of epigenetic regulators in somatic embryos during temperature induced formation of an epigenetic memory in Norway spruce. *Planta*, *243*(5), 1237- 1249. https://doi.org/10.1007/s00425-016-2484-8
- Yakovlev, I. A., & Fossdal, C. G. (2017). In Silico Analysis of Small RNAs Suggest Roles for Novel and Conserved miRNAs in the Formation of Epigenetic Memory in Somatic Embryos of Norway Spruce. Frontiers in Physiology, 8. https://doi.org/10.3389/fphys.2017.00674
- Yakovlev, I. A., Lee, Y., Rotter, B., Olsen, J. E., Skrøppa, T., Johnsen, Ø., & Fossdal, C. G. (2014).

 Temperature-dependent differential transcriptomes during formation of an epigenetic memory in Norway spruce embryogenesis. *Tree Genetics & Genomes*, 10(2), 355-366.

 https://doi.org/10.1007/s11295-013-0691-z

- Yakovlev, I., Fossdal, C. G., Skrøppa, T., Olsen, J. E., Jahren, A. H., & Johnsen, Ø. (2012). An adaptive epigenetic memory in conifers with important implications for seed production. Seed Science Research, 22(02), 63-76. https://doi.org/10.1017/S0960258511000535
- Yamamuro, C., Zhu, J.-K., & Yang, Z. (2016). Epigenetic modifications and plant hormone action.

 Molecular plant, 9(1), 57- 70. https://doi.org/10.1016/j.molp.2015.10.008
 - Yao, Y., Bilichak, A., Golubov, A., & Kovalchuk, I. (2012). Ddm1 plants are sensitive to methyl methane sulfonate and NaCl stresses and are deficient in DNA repair. *Plant Cell Reports*, *31*(9), 1549-1561. https://doi.org/10.1007/s00299-012-1269-1
 - Yona, A. H., Frumkin, I., & Pilpel, Y. (2015). A Relay Race on the Evolutionary Adaptation Spectrum. *Cell*, *163*(3), 549-559. https://doi.org/10.1016/j.cell.2015.10.005
 - Zemach, A., Kim, M. Y., Hsieh, P.-H., Coleman-Derr, D., Eshed-Williams, L., Thao, K., Harmer, S. L., & Zilberman, D. (2013). The Arabidopsis Nucleosome Remodeler DDM1 Allows DNA Methyltransferases to Access H1-Containing Heterochromatin. *Cell*, 153(1), 193-205. https://doi.org/10.1016/j.cell.2013.02.033
 - Zemach, A., McDaniel, I. E., Silva, P., & Zilberman, D. (2010). Genome-Wide Evolutionary Analysis of Eukaryotic DNA Methylation. *Science*, *328*(5980), 916-919. https://doi.org/10.1126/science.1186366
- Zhang, J., Jia, W., Yang, J., & Ismail, A. M. (2006). Role of ABA in integrating plant responses to drought and salt stresses. *Field Crops Research*, *97*(1), 111- 119. https://doi.org/10.1016/j.fcr.2005.08.018
 - Zhang, Q., Li, Y., Xu, T., Srivastava, A. K., Wang, D., Zeng, L., Yang, L., He, L., Zhang, H., Zheng, Z., Yang, D.-L., Zhao, C., Dong, J., Gong, Z., Liu, R., & Zhu, J.-K. (2016). The chromatin remodeler DDM1 promotes hybrid vigor by regulating salicylic acid metabolism. *Cell Discovery*, 2, 16027. https://doi.org/10.1038/celldisc.2016.27
 - Zhang, Y.-Y., Fischer, M., Colot, V., & Bossdorf, O. (2013). Epigenetic variation creates potential for evolution of plant phenotypic plasticity. *New Phytologist*, 197(1), 314-322. https://doi.org/10.1111/nph.12010
 - Zhang, Y.-Y., Latzel, V., Fischer, M., & Bossdorf, O. (2018). Understanding the evolutionary potential of epigenetic variation: A comparison of heritable phenotypic variation in epiRILs, RILs, and natural ecotypes of Arabidopsis thaliana. *Heredity*, 121(3), 257- 265. https://doi.org/10.1038/s41437-018-0095-9
- Zhu, H., Wang, G., & Qian, J. (2016). Transcription factors as readers and effectors of DNA methylation.

 Nature Reviews Genetics, 17(9), 551- 565. https://doi.org/10.1038/nrg.2016.83
- Zhu, L.-Y., Zhu, Y.-R., Dai, D.-J., Wang, X., & Jin, H.-C. (2018). Epigenetic regulation of alternative splicing. *American Journal of Cancer Research*, *8*(12), 2346- 2358.
- Zhu, R., Shevchenko, O., Ma, C., Maury, S., Freitag, M., & Strauss, S. H. (2013). Poplars with a PtDDM1 RNAi transgene have reduced DNA methylation and show aberrant post-dormancy morphology.
 Planta, 237(6), 1483- 1493. https://doi.org/10.1007/s00425-013-1858-4

Figure & Table legends

- Figure 1: Time course of soil relative extractable water (REW) during the experiment for the wild type and the two RNAi-ddm1 (ddm1-15, ddm1-23) poplar lines in control (well-watered, WW) and stress (moderate water deficit followed by rewatering, WD-RW) treatments. Open symbols and dashed lines for WW treatment; closed symbols and solid lines for WD-RW treatment. Circles for the wild type; triangles for the RNAi-ddm1-15 line; squares for the RNAi-ddm1-23 line. The arrows represent the end of the water deficit and the onset of rewatering. Values are genotypic means \pm SE (n = 6 per line for WW, n = 12 per line for
- 1701 WD-RW).

- 1702 Figure 2: Phenotypic and physiological characterization of the wild type and the two RNAi-ddm1 (ddm1-
- 1703 15, ddm1-23) poplar lines in control (well-watered, WW) and stress (moderate water deficit followed by
- 1704 rewatering, WD-RW) treatments. Open symbols and open bars for WW; closed symbols and closed bars
- for WD-RW. Values are genotypic means \pm SE. **A.** Time course of stem height and diameter (n = 6 per
- line in WW, n = 12 per line in WD-RW). The arrows represent the end of the water deficit and the onset of
- 1707 rewatering. **B**. Xylem vulnerability to drought-induced cavitation measured at the end of the experiment (n
- 1708 = 6 per line). C. Time course of leaf gas exchange (A_{net} , net CO_2 assimilation rate, g_s , stomatal
- 1709 conductance to water vapour, WUE_i, intrinsic water-use efficiency computed as A_{net}/g_s). Values presented
- 1710 are those of WD-RW plants relative to WW controls (n = 5 per line per treatment). Treatment effects were
- evaluated within each line using a t-test. Levels of significance are *, 0.01 < P < 0.05; **, 0.001 < P < 0.01;
- 1712 ***, *P* < 0.001; ns, non-significant.
- 1713 Figure 3: Phytohormone contents (cytokinins, abscisic acid, salicylic acid and free auxin) measured in
- shoot apex just after rewatering (t_1). Values are genotypic means \pm SE (n = 3 per line in WW and in WD-
- 1715 RW). Treatment effects were evaluated within each line by using t-test. Levels of significance are *: p<
- 1716 0.05, **: p< 0.01, ***: p< 0.001 and ns: non-significant. The different letters indicate the differences
- between lines within a water regime following a Tukey's post hoc test (lower case letters for WW, capital
- 1718 letters for WD-RW).
- 1719 Figure 4: Variations in DNA methylation among RNAi and WT lines in shoot apical meristem one week
- 1720 after rewatering (t2). A. Common DMRs between WW and WD-RW conditions. Black bars for
- 1721 hypomethylated DMRs and grey bars for hypermethylated DMRs. B. Common DMRs between the two
- 1722 RNAi lines (ddm1 15 & ddm1 23) vs. the WT lines in all contexts (CG, CHG & CHH) and in WW and WD-
- 1723 RW conditions. Black bars for hypomethylated DMRs and grey bars for hypermethylated DMRs. C. DNA
- 1724 methylation variation of the common DMRs in the RNAi lines vs. the WT line in WW and WD-RW per
- 1725 context of methylation. Only DMRs with at least a 25 % difference were kept except for CHH where a
- threshold of 10% was applied due to the low proportion of DMRs in that context.
- 1727 Figure 5: Gene expression variations in ddm1-23 vs. the WT line in non-irrigated condition (WD-RW) in
- 1728 shoot apical meristem collected one week after rewatering (t2). A. GO annotation of the differentially

expressed genes (genes with an adjusted p-value by FDR, false discovery rate < 0.05 = 136 DEGs identified) between ddm1-23 and the WT line. GO labels were retrieved from popgenie and treemap realized with REVIGO. **B**. Annotation of DEGs with expression variation values (log2FoldChange) using GO labels retrieved from popgenie. Blue for downregulated genes and red for upregulated genes. The * indicates hormone related genes found in DEGs. The numbers (1), (31), (8), (25), (19), (17), (35) represent respectively the number of DEGs found in Cell death, Defense & Cell wall, Immune response, Metabolism, Signalization, Transcription factors and Unknown processes respectively. Log2FoldChange = log-ratio of normalized mean read counts in RNAi vs. WT lines.

Figure 6: Transposable elements activity among RNAi and WT lines in shoot apical meristem collected one week after rewatering (t2). **A**. Depth of coverage (read per million, rpm) of different TE families in the three different lines and in both WW (white) and WD-RW (black) regimes. TE, TE+, TE+++ represent different groups of TE families according to their coverage. TE ranges from 0 to 200X; TE+ = 200X – 2000X; TE++ = 2000X - 10000X; TE+++ = 10000X – 55000X. **B**. DNA methylation variations in TEs for each context of methylation in WW (white) and WD-RW (black) conditions. **C**. Copy number variations of three different TEs (DNA-3-3, Gypsy23 and SAT-1) in the three different lines in both WW and WD-RW regimes. White cicles for WW and black circles for WD-RW.

Table 1: Xylem structural, functional and biochemical traits measured for the wild type and the two RNAiddm1 (ddm1-15, ddm1-23) poplar lines in control (well-watered, WW) and stress (moderate water deficit followed by rewatering, WD-RW) treatments. Values are genotypic means \pm SE (n = 6 per line per treatment). The P₅₀ is the xylem tension inducing 50% loss of hydraulic conductance estimated from vulnerability curves (see Materials and Methods for additional information). S/G corresponds to the ratio between syringyl-like (S) and guaiacyl-like lignin monomeric units (G). Treatment effects were evaluated within each line by using a t-test. Different letters indicate significant differences between genotypes within treatments following Tukey's post hoc test. Levels of significance are *, 0.01 < P < 0.05; **, 0.001 < P < 0.01; ***, P < 0.001; ns, non-significant; na, not available.

Supplemental materials:

Supplemental Figure 1: Strategies for methylome bioinformatic analysis **A.** Impact of different types of quality controls on the percentage of mapped reads on two distinct genomes: *P. trichocarpa* and *P. tremula* × *P. alba*. Dots shapes are quality control specific. 1. Circles for quality control with trimming, 2. Triangular for sample with only trimming control and 3. Squared for sample without any quality control. Colors are distinct between the two genomes (black for *P. trichocarpa* and white for *P. tremula* × *P.alba*). On the left, the results for Well-Watered (WW) conditions and on the other side Water Deficit and ReWatering (WD-RW). **B.** Impact of two different tools for mapping reads, BISMARK and BSMAP on the percentage of mapped reads on two distinct genomes: *P. trichocarpa* and *P. tremula* × *P. alba*. Dark bars are for BISMARK and light bars for BSMAP software. On the left, the results for Well-Watered (WW)

conditions and on the other side Water Deficit and ReWatering (WD-RW). Values are 'QC' means quality control with trimming and filtering. **C**. Percentages of cytosine considered by BISMARK after quality control and 10X minimal coverage filtering on the two genomes: *P. trichocarpa* and *P. tremula* × *P. alba*. Bars are for methylation percentage and dots are for coverage values. Black color is for Well-Watered (WW) conditions and white for Water Deficit and Re-Watering one (WD-RW). **D**. Percentages of cytosine considered by BISMARK after quality control and 10X minimal coverage filtering for the three methylation contexts (CG, CHG and CHH) for *P. tremula* × *P. alba*.

- **Supplemental Figure 2**: Phenotypic and physiological characterization of the wild type and the two RNAiddm1 (ddm1-15, ddm1-23) poplar lines in control (well-watered, WW) and stress (moderate water deficit followed by rewatering, WD-RW) treatments. Open symbols and open bars for WW; closed symbols and closed bars for WD-RW. Values are genotypic means \pm SE. **A**. Predawn and minimum leaf water potential measured before rewatering (n = 5 per line per treatment). **B**. Bulk leaf carbon isotope composition (δ^{13} C) measured on leaves sampled at the end of the experiment (n = 6 per line in WW, n = 12 per line in WD-RW). **C**. Total stomatal density measured at the end of the experiment (n = 3 per line per treatment). Treatment effects were evaluated within each line using a t-test. Levels of significance are *, 0.01 < P <0.05; **, 0.001 < P < 0.01; ***, P < 0.001; ns, non-significant.
- **Supplemental Figure 3: A.** Variation among *Populus* RNAi *ddm1* lines concerning the effect of leaf position on the stem on leaf area. White dots for control line and black dots for RNAi lines. Values are line means (± SE, n=3 by lines WW). For each line the rank effect was evaluated using a T-test (IF: leaf index). **B.** Total leaf area variations among Populus RNAi ddm1 lines. White bars represent well-watered conditions. Values are line mean (± SE, n=3 by lines WW). Global line effect was evaluated using a T-test (L: line). Levels of significance are *: p< 0.05, **: p< 0.01, ***: p< 0.001 and ns: non-significant
- **Supplemental Figure 4**: Particular leaf phenotypes among *Populus* RNAi ddm1 lines. Open symbols for control (well-watered, WW) condition; closed symbols for stress (moderate water deficit followed by rewatering, WD-RW) condition. Values are genotypic means \pm SE (n = 6 per line for WW and WD-RW). Treatment effects were evaluated within each line by using a t-test. The different letters indicate the differences between lines within a water regime following a Tukey's post hoc test (small letter, well-watered condition and capital letter water deficit follow by rewatering condition). Levels of significance are *: p< 0.05, **: p< 0.01, ***: p< 0.001 and ns: non-significant.
- **Supplemental Figure 5**: Variations in DNA methylation among RNAi and WT lines in shoot apical meristem one week after rewatering (t2). **A.** Global DNA methylation percentage calculated by HPLC in WT and RNAi lines in both Well-Watered (WW, white bars) and water-deficit followed by ReWatering conditions (WD-RW, black bars). Values are genotypic mean (± SE, n=3 by lines in WW and n=3 by lines in WD-RW). Global genetic variations and the effect of water deficit re-watering were evaluated using ANOVA. Different letters indicate the differences between genotypes within WW and WD-RW conditions

following a Tukey's post hoc test. Levels of significance are *: p< 0.05, **: p< 0.01, ***: p< 0.001 and ns: non-significant. **B**. Differentially methylated regions (DMRs) between treatment and lines. Black bars for hypomethylated DMRs and white bars for hypermethylated DMRs. DMRs represented are mapped against *Populus tremula* x *alba* reference genome and have passed 10X of coverage and show a cut-off of methylation of 25 % with qvalue 0.01. **C**. DMRs count between ddm1_15 and WT line. **D**. DMRs count between ddm1_23 the WT line. **E**. Distributions of the DMRs between the RNAi and the WT lines in the different contexts of methylation.

Supplemental figure 6: Identification of differentially methylated genes. **A**. Annotation of the common DMRs between the RNAi and the WT lines in WW and WD-RW regimes. Gene annotation was retrieved from *P. tremula* x *P. alba* v1.1 annotation. Promoters correspond to +/- 2kb from TSS (transcription start site). TE (Transposable element) annotations were retrieved from *P. trichocarpa* annotation and blasted against *P. tremula* x P. reference genome. **B**. Identification of common differentially methylated genes (DMGs) between the two RNAi lines vs. the WT line in both WW and WD-RW regimes. In DMRs = Genes that overlapped with the common DMRs, 2 kb = Genes in +/- 2 kb of DMR, 5 kb = Genes in +/- 5 kb of DMR, 10 kb = Genes in +/- 10 kb of DMR and 25 kb = Genes that are found in +/- 25 kb of DMR. **C**. Genes Ontology (GO) annotation of the common DMRs in WD-RW regimes for all contexts. GO labels were retrieved from A. thaliana annotation and a treemap was realized using REVIGO software.

- **Supplemental figure 7**: Relationship between variation in DNA methylation and gene expression. **A**. Overlap between DEGs and DMRs. DEGs that are localized in DMRs or in the proximity of DMRs are represented: In DMRs = DEGs that overlapped with the DMRs, 2 kb = DEGs in +/- 2 kb of DMR, 5 kb = DEGs in +/- 5 kb of DMR, 10 kb = DEGs in +/- 10 kb of DMR and 25 kb = DEGs that are found in +/- 25 kb of DMR. **B**. Covariation between DNA methylation and gene expression. DEGs found in or near +/- 10 kb of DMRs were used for correlation (spearman t test correlation, pvalue = 0.0004).
- **Supplemental figure 8**: Transposable elements activity among RNAi and WT lines in shoot apical meristem collected one week after rewatering (t2). **A**. Counts of transposable element families found in the mobilome-seq analysis in the three different lines and in WW and WD-RW regimes. White bars for WW and black bars for WD-RW. **B**. GO annotation of biological process of genes found in or near +/- 25 kb of mobilome-seq TE families. The treemap was realized using REVIGO. **C**. Overlap between TE families vs. DMRs and Genes. In = TEs that overlapped with the DMRs, 2 kb = TEs in +/- 2 kb of DMR, 5 kb = TEs in +/- 5 kb of DMR, 10 kb = TEs in +/- 10 kb of DMR and 25 kb = TEs that are found in +/- 25 kb of DMR.
- Supplemental Table 1: Mean methylation level in ddm1 and WT lines in both WW and WD-RW conditions, Values are the average of methylation (in %) for each lines in the three different contexts (CG, CHG and CHH).

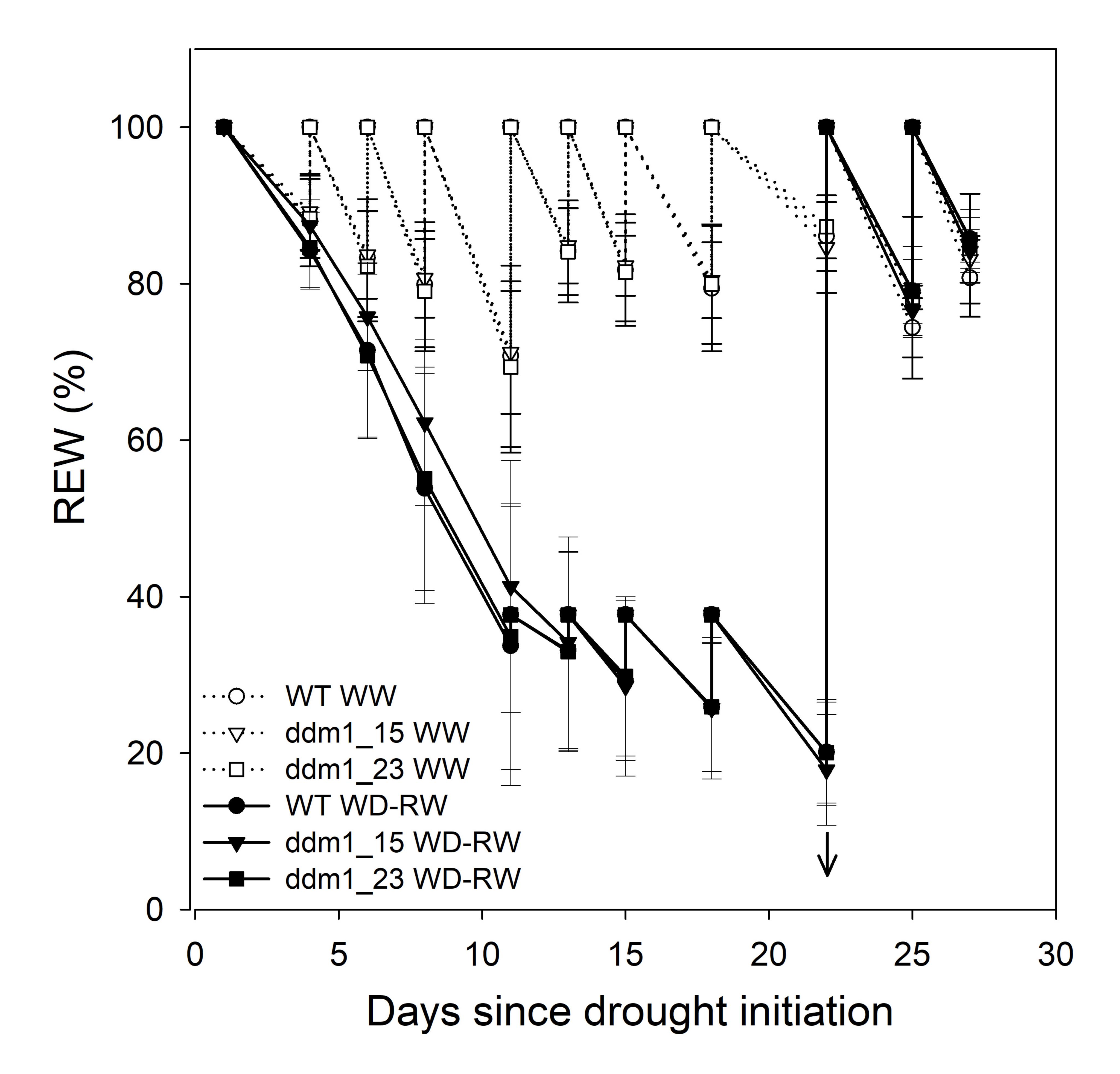
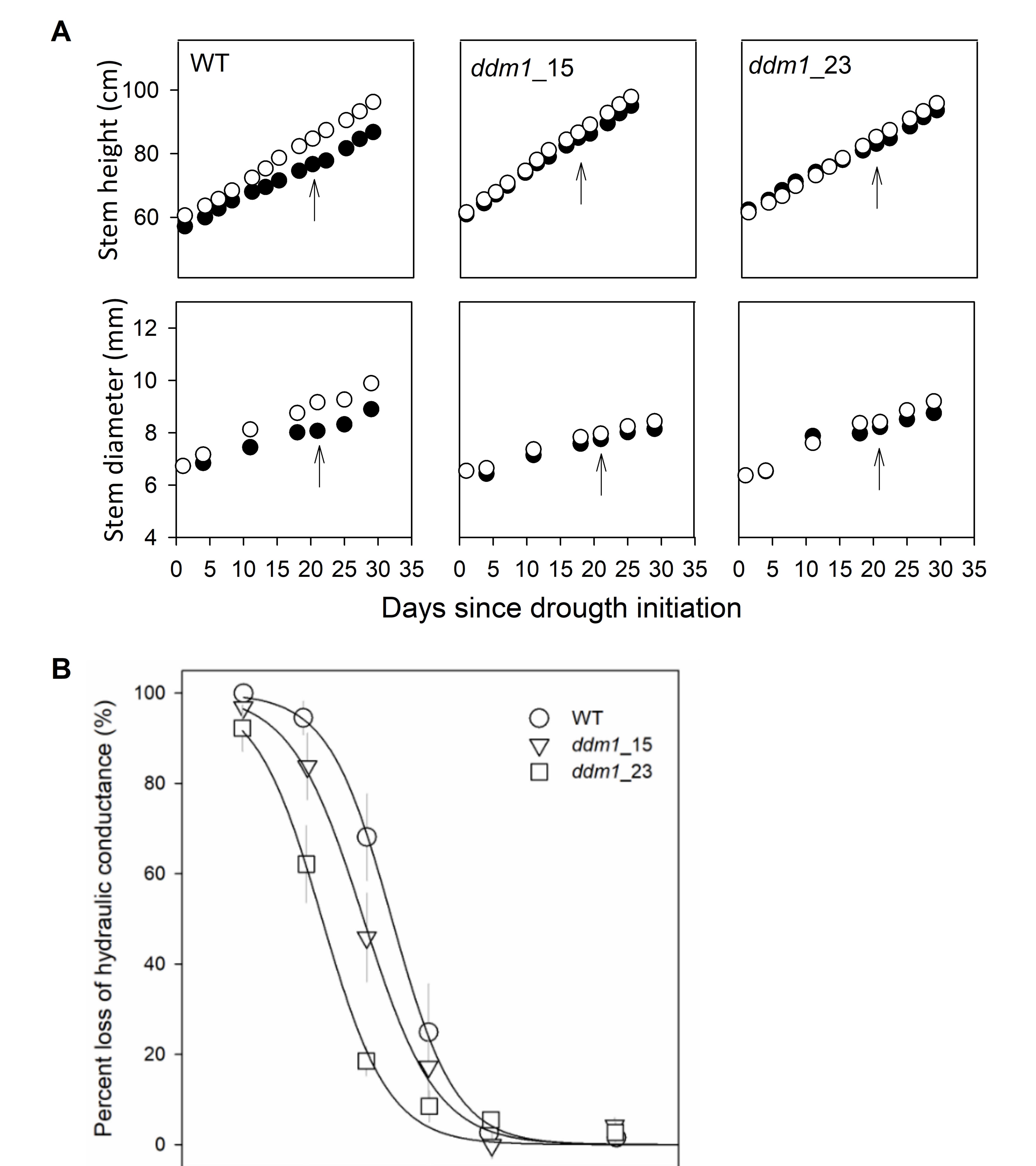
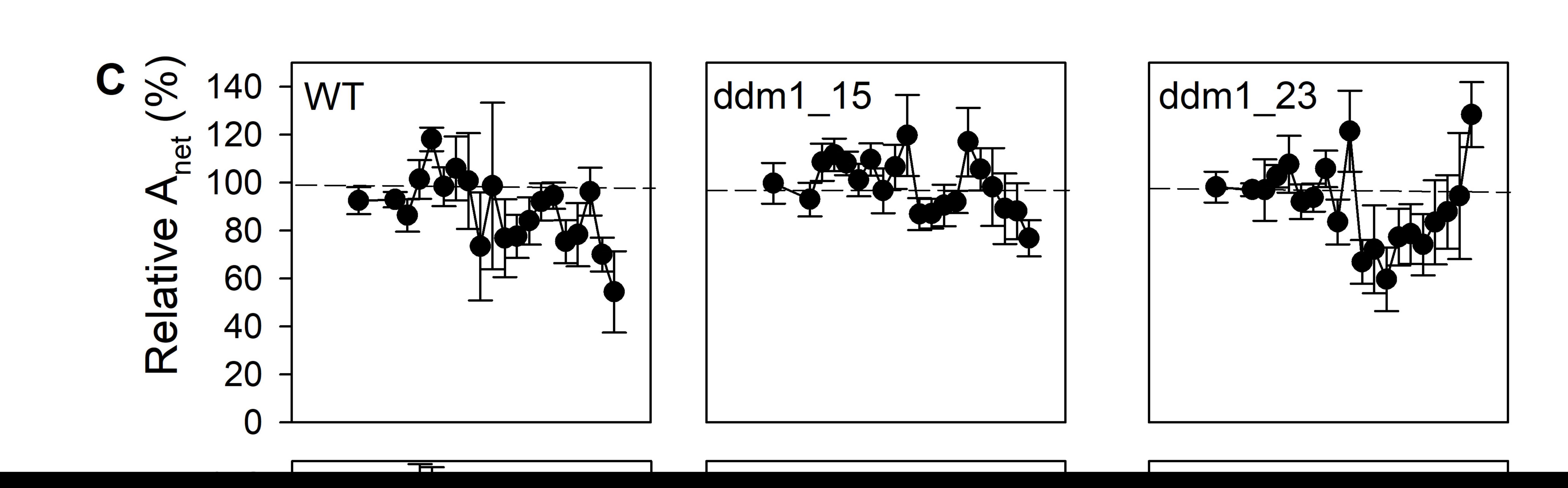


Figure 1: Time course of soil relative extractable water (REW) during the experiment for the wild type and the two RNAiddm1 (ddm1-15, ddm1-23) poplar lines in control (well-watered, WW) and stress (moderate water deficit followed by rewatering, WD-RW) treatments. Open symbols and dashed lines for WW treatment; closed symbols and solid lines for WD-RW treatment. Circles for the wild type; triangles for the RNAi-ddm1-15 line; squares for the RNAi-ddm1-23 line. The arrows represent the end of the water deficit and the onset of rewatering. Values are genotypic means \pm SE (n = 6 per line for WW, n = 12 per line for WD-RW).





Xylem tension (MPa)

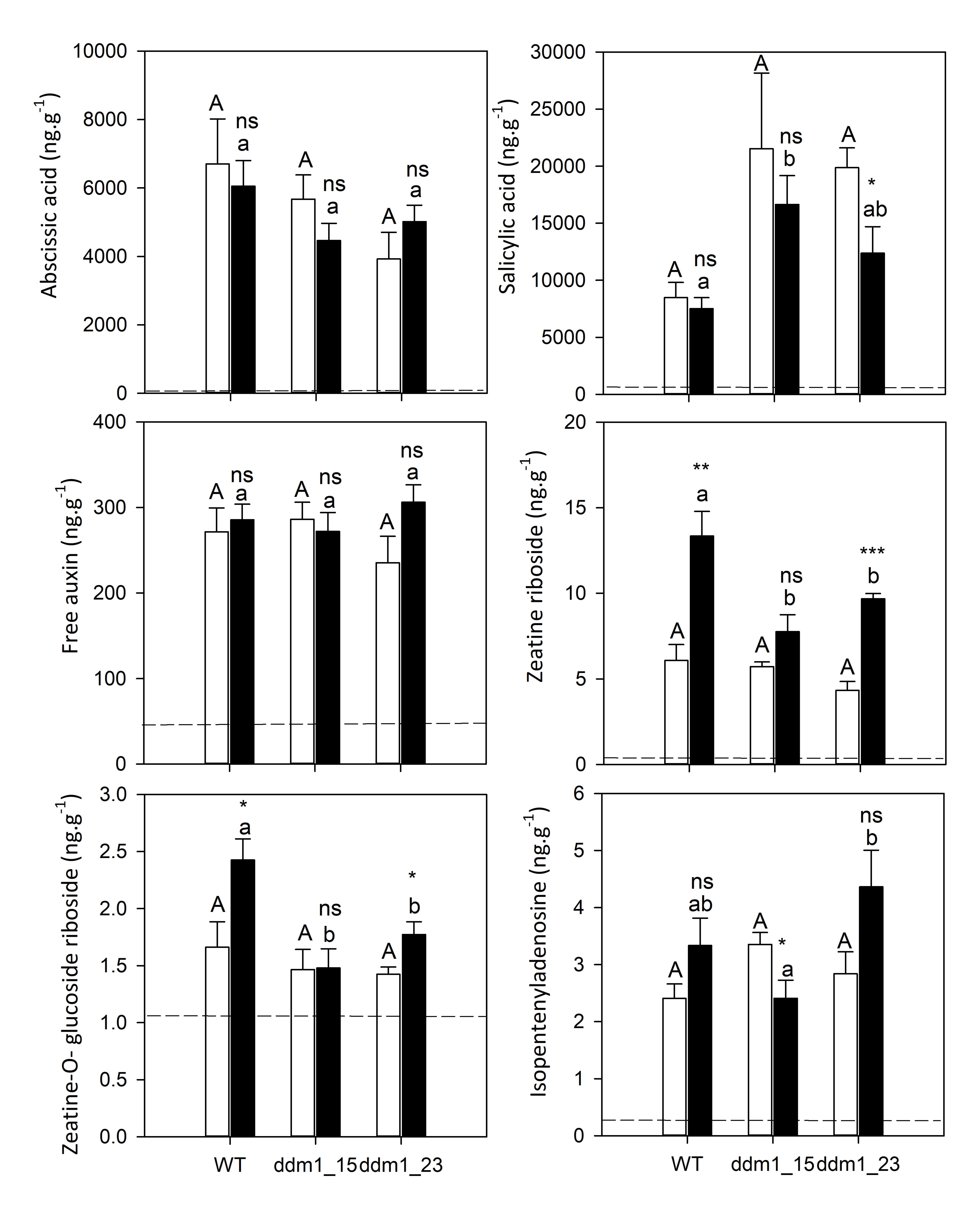


Figure 3: Phytohormone contents (cytokinins, abscisic acid, salicylic acid and free auxin) measured in shoot apex just after rewatering (t_1). Values are genotypic means \pm SE (n = 3 per line in WW and in WD-RW). Treatment effects were evaluated within each line by using t-test. Levels of significance are *: p< 0.05, **: p< 0.01, ***: p< 0.001 and ns: non-significant. The different letters indicate the differences between lines within a water regime following a Tukey's post hoc test (lower case letters for WW, capital letters for WD-RW).

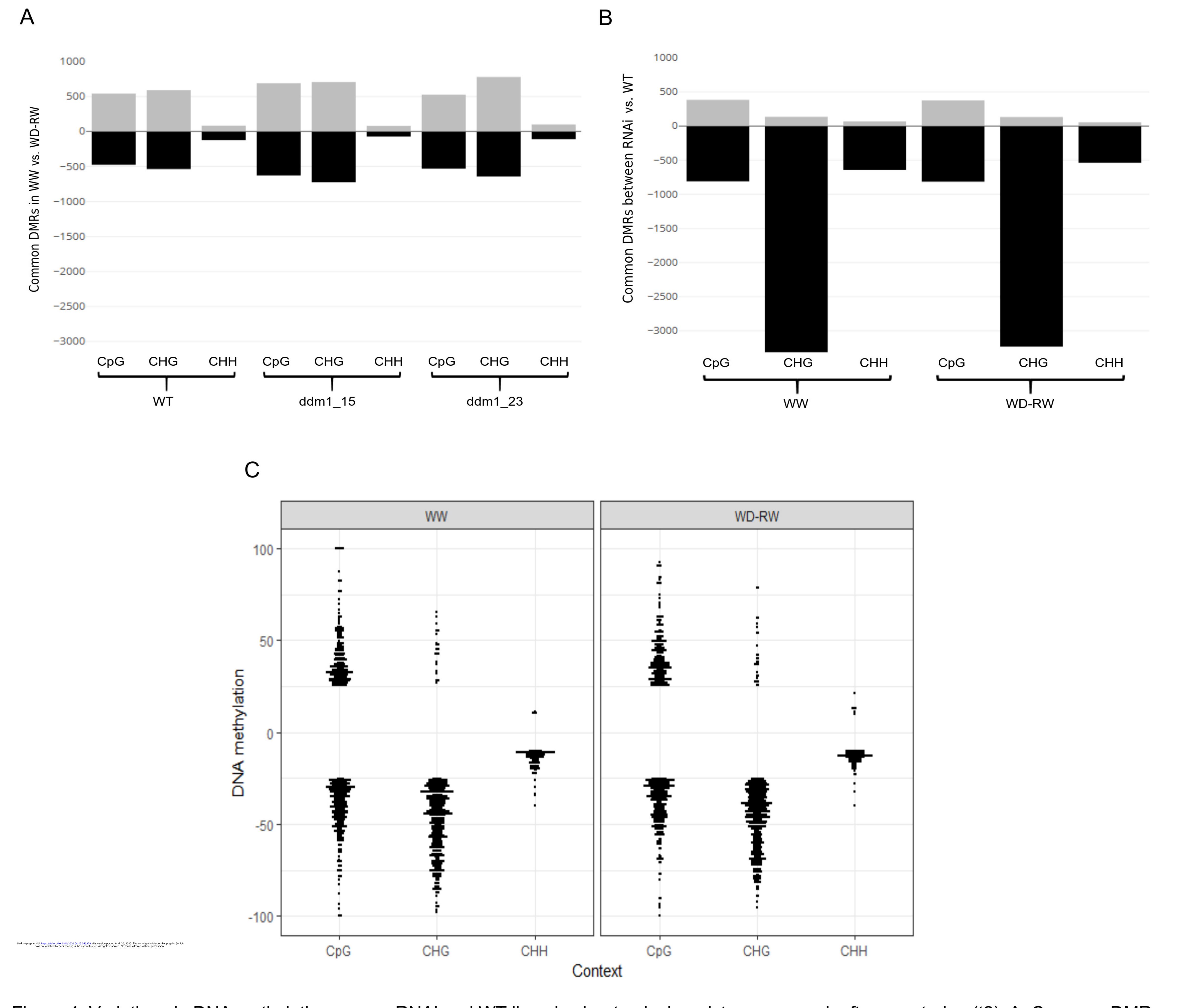


Figure 4: Variations in DNA methylation among RNAi and WT lines in shoot apical meristem one week after rewatering (t2). A. Common DMRs between WW and WD-RW conditions. Black bars for hypomethylated DMRs and grey bars for hypermethylated DMRs. B. Common DMRs between the two RNAi lines (ddm1_15 & ddm1_23) vs. the WT lines in all contexts (CG, CHG & CHH) and in WW and WD-RW conditions. Black bars for hypomethylated DMRs and grey bars for hypermethylated DMRs. C. DNA methylation variation of the common DMRs in the RNAi lines vs. the WT line in WW and WD-RW per context of methylation. Only DMRs with at least a 25 % difference were kept except for CHH where a threshold of 10% was applied due to the low proportion of DMRs in that context.

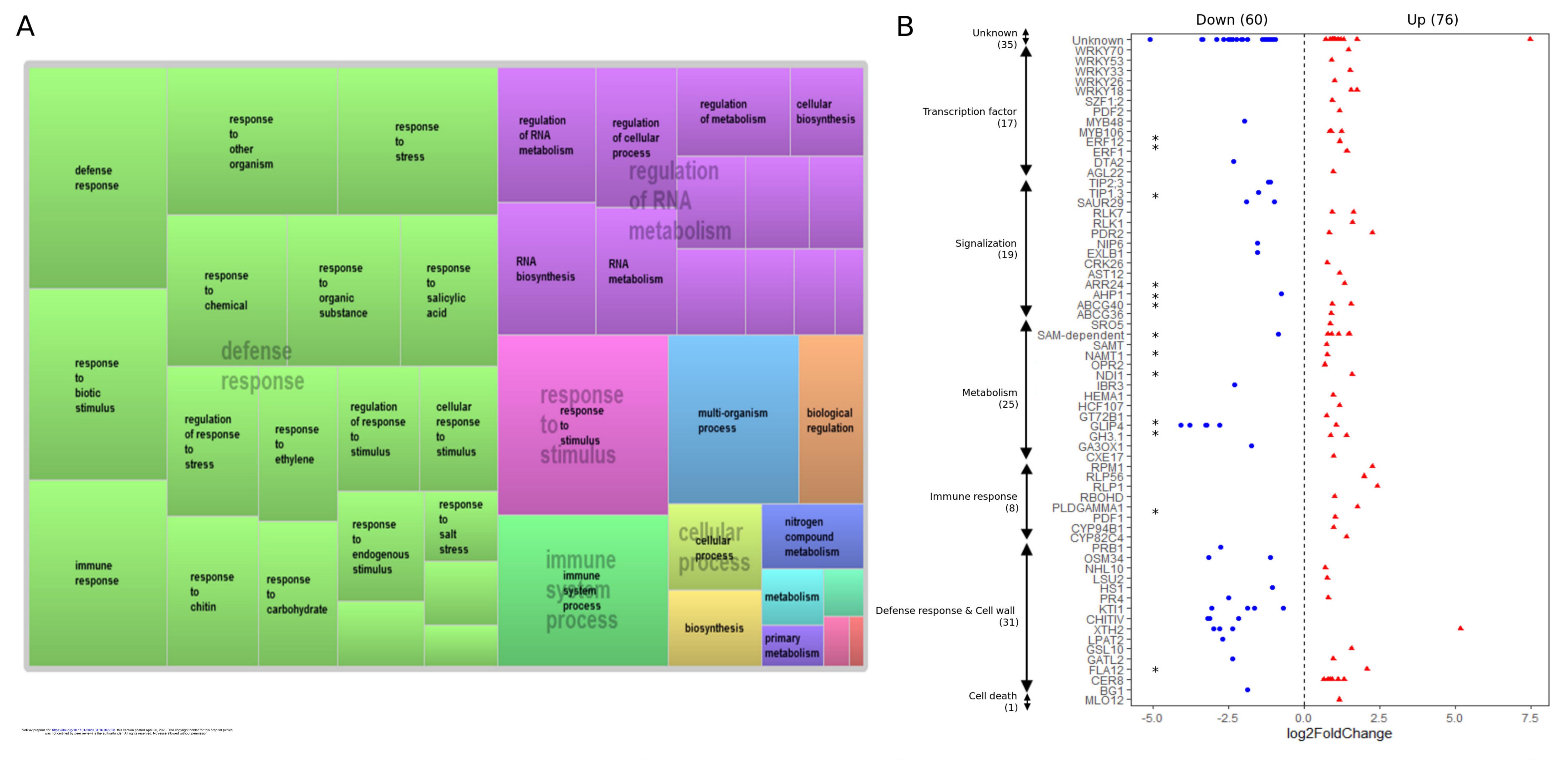


Figure 5: Gene expression variations in ddm1-23 vs. the WT line in non-irrigated condition (WD-RW) in shoot apical meristem collected one week after rewatering (t2). A. GO annotation of the differentially expressed genes (genes with an adjusted p-value by FDR, false discovery rate < 0.05 = 136 DEGs identified) between ddm1-23 and the WT line. GO labels were retrieved from popgenie and treemap realized with REVIGO. B. Annotation of DEGs with expression variation values (log2FoldChange) using GO labels retrieved from popgenie. Blue for downregulated genes and red for upregulated genes. The * indicates hormone related genes found in DEGs. The numbers (1), (31), (8), (25), (19), (17), (35) represent respectively the number of DEGs found in Cell death, Defense & Cell wall, Immune response, Metabolism, Signalization, Transcription factors and Unknown processes respectively. Log2FoldChange = log-ratio of normalized mean read counts in RNAi vs. WT lines.

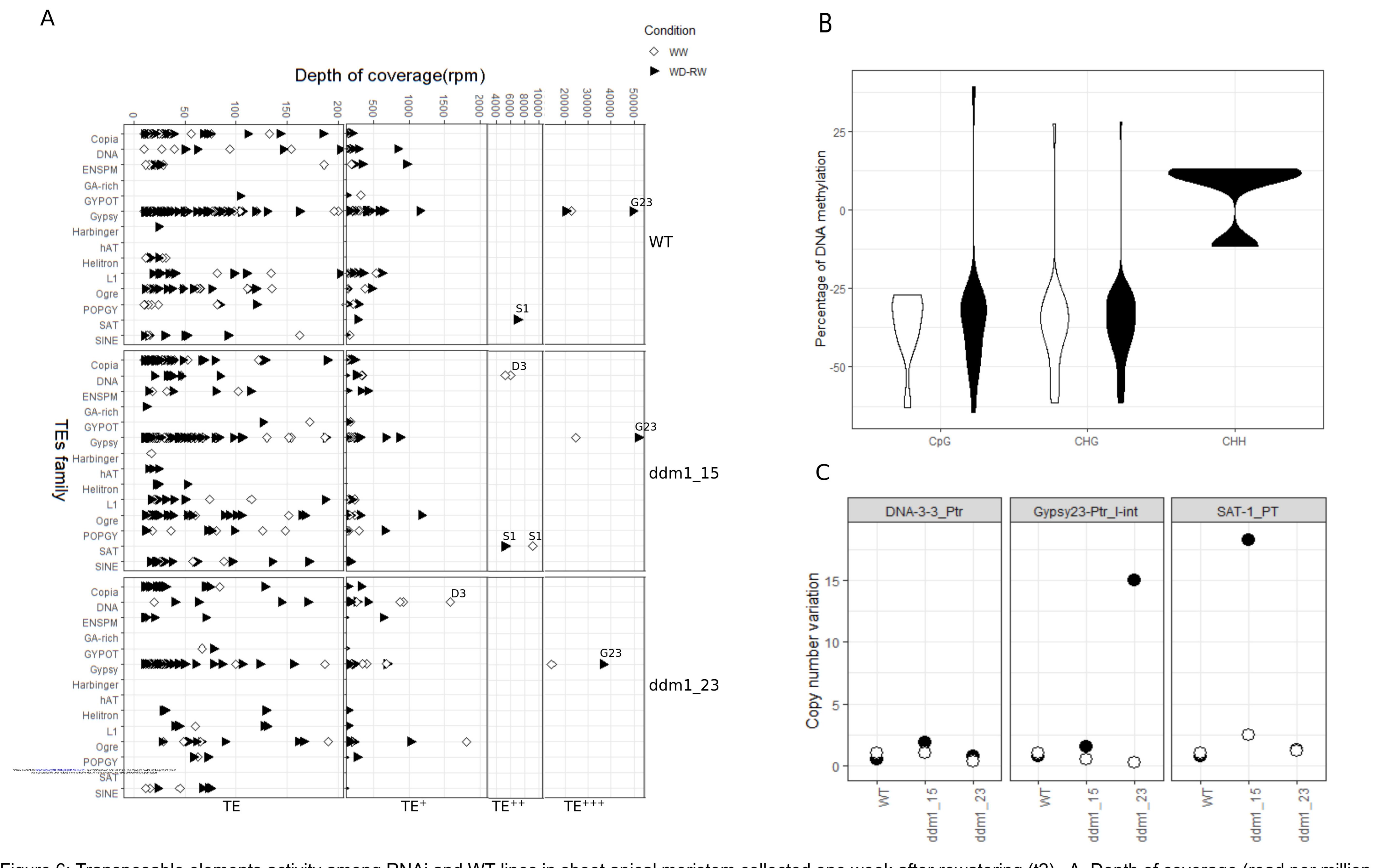


Figure 6: Transposable elements activity among RNAi and WT lines in shoot apical meristem collected one week after rewatering (t2). A. Depth of coverage (read per million, rpm) of different TE families in the three different lines and in both WW (white) and WD-RW (black) regimes. TE, TE+, TE++, TE+++ represent different groups of TE families according to their coverage. TE ranges from 0 to 200X; TE+ = 200X – 2000X; TE++ = 2000X - 10000X; TE+++ = 10000X – 55000X. B. DNA methylation variations in TEs for each context of methylation in WW (white) and WD-RW (black) conditions. C. Copy number variations of three different TEs (DNA-3-3, Gypsy23 and SAT-1) in the three different lines in both WW and WD-RW regimes. White cicles for WW and black circles for WD-RW.

Parsed Citations

Abeysinghe, J. K., Lam, K.-M., & Ng, D. W.-K. (2019). Differential regulation and interaction of homoeologous WRKY18 and WRKY40 in Arabidopsis allotetraploids and biotic stress responses. The Plant Journal, 97(2), 352-367. https://doi.org/10.1111/tpj.14124

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci, A., & Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management, 259(4), 660-684. https://doi.org/10.1016/j.foreco.2009.09.001

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Anderegg, W. R. L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A F. A, Choat, B., & Jansen, S. (2016). Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. Proceedings of the National Academy of Sciences, 113(18), 5024-5029. https://doi.org/10.1073/pnas.1525678113

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Awad, H., Herbette, S., Brunel, N., Tixier, A., Pilate, G., Cochard, H., & Badel, E. (2012). No trade-off between hydraulic and mechanical properties in several transgenic poplars modified for lignins metabolism. Environmental and Experimental Botany, 77, 185-195. https://doi.org/10.1016/j.envexpbot.2011.11.023

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Ayarpadikkannan, S., & Kim, H.-S. (2014). The Impact of Transposable Elements in Genome Evolution and Genetic Instability and Their Implications in Various Diseases. Genomics & informatics, 12, 98-104. https://doi.org/10.5808/GI.2014.12.3.98

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Azooz, M. M., & Youssef, M. M. (2010). Evaluation of Heat Shock and Salicylic Acid Treatments as Inducers of Drought Stress Tolerance in Hassawi Wheat. American Journal of Plant Physiology, 5(2), 56-70. https://doi.org/10.3923/ajpp.2010.56.70

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Badmi, R., Zhang, Y., Tengs, T., Brurberg, M. B., Krokene, P., Fossdal, C. G., Hytönen, T., & Thorstensen, T. (2019). Induced and primed defence responses of Fragaria vesca to Botrytis cinerea infection. BioRxiv, 692491. https://doi.org/10.1101/692491

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Bandurska, H., & Stroi ski, A (2005). The effect of salicylic acid on barley response to water deficit. Acta Physiologiae Plantarum, 27(3), 379-386. https://doi.org/10.1007/s11738-005-0015-5

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Barigah, T. S., Charrier, O., Douris, M., Bonhomme, M., Herbette, S., Améglio, T., Fichot, R., Brignolas, F., & Cochard, H. (2013). Water stress-induced xylem hydraulic failure is a causal factor of tree mortality in beech and poplar. Annals of Botany, 112(7), 1431-1437. https://doi.org/10.1093/aob/mct204

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Basu, S., Ramegowda, V., Kumar, A, & Pereira, A (2016). Plant adaptation to drought stress. F1000Research, 5. https://doi.org/10.12688/f1000research.7678.1

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Baubec, T., Finke, A, Mittelsten Scheid, O., & Pecinka, A (2014). Meristem-specific expression of epigenetic regulators safeguards transposon silencing in Arabidopsis. EMBO Reports, 15(4), 446- 452. https://doi.org/10.1002/embr.201337915

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Bechtold, U., Penfold, C. A., Jenkins, D. J., Legaie, R., Moore, J. D., Lawson, T., Matthews, J. S. A., Vialet-Chabrand, S. R. M., Baxter, L., Subramaniam, S., Hickman, R., Florance, H., Sambles, C., Salmon, D. L., Feil, R., Bowden, L., Hill, C., Baker, N. R., Lunn, J. E., ... Mullineaux, P. M. (2016). Time-Series Transcriptomics Reveals That AGAMOUS-LIKE22 Affects Primary Metabolism and Developmental Processes in Drought-Stressed Arabidopsis. The Plant Cell, 28(2), 345-366. https://doi.org/10.1105/tpc.15.00910

Pubmed: Author and Title

Google Scholar: <u>Author Only Title Only Author and Title</u>

Bertrand, D., & Dufour, É. (2006). La Spectroscopie Infrarouge et ses Applications Analytiques. Tec & Doc / Lavoisier. http://www.lavoisier.fr/notice/fr2743008090.html

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Bewick, A J., & Schmitz, R. J. (2017). Gene body DNA methylation in plants. Current Opinion in Plant Biology, 36, 103-110. https://doi.org/10.1016/j.pbi.2016.12.007

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Bogeat-Triboulot, M.-B., Brosché, M., Renaut, J., Jouve, L., Thiec, D. L., Fayyaz, P., Vinocur, B., Witters, E., Laukens, K., Teichmann, T., Altman, A., Hausman, J.-F., Polle, A., Kangasjärvi, J., & Dreyer, E. (2007). Gradual Soil Water Depletion Results in Reversible Changes of Gene Expression, Protein Profiles, Ecophysiology, and Growth Performance in Populus euphratica, a Poplar Growing in Arid Regions. Plant Physiology, 143(2), 876-892. https://doi.org/10.1104/pp.106.088708

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Bolger, A.M., Lohse, M., & Usadel, B. (2014). Trimmomatic: A flexible trimmer for Illumina sequence data. Bioinformatics (Oxford, England), 30(15), 2114-2120. https://doi.org/10.1093/bioinformatics/btu170

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Bradshaw, A. D. (2006). Unravelling phenotypic plasticity – why should we bother? New Phytologist, 170(4), 644-648. https://doi.org/10.1111/j.1469-8137.2006.01761.x

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Bräutigam, K., Vining, K. J., Lafon-Placette, C., Fossdal, C. G., Mirouze, M., Marcos, J. G., Fluch, S., Fraga, M. F., Guevara, M. Á, Abarca, D., Johnsen, Ø., Maury, S., Strauss, S. H., Campbell, M. M., Rohde, A, Díaz-Sala, C., & Cervera, M.-T. (2013). Epigenetic regulation of adaptive responses of forest tree species to the environment. Ecology and Evolution, 3(2), 399-415. https://doi.org/10.1002/ece3.461

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Brodribb, T. J., & Cochard, H. (2009). Hydraulic Failure Defines the Recovery and Point of Death in Water-Stressed Conifers. Plant Physiology, 149(1), 575-584. https://doi.org/10.1104/pp.108.129783

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Cambiagno, D. A, Nota, F., Zavallo, D., Rius, S., Casati, P., Asurmendi, S., & Alvarez, M. E. (2018). Immune receptor genes and pericentromeric transposons as targets of common epigenetic regulatory elements. The Plant Journal, 96(6), 1178-1190. https://doi.org/10.1111/tpj.14098

Pubmed: <u>Author and Title</u>

Google Scholar: Author Only Title Only Author and Title

Carneros, E., Yakovlev, I., Viejo, M., Olsen, J. E., & Fossdal, C. G. (2017). The epigenetic memory of temperature during embryogenesis modifies the expression of bud burst-related genes in Norway spruce epitypes. Planta, 246(3), 553-566. https://doi.org/10.1007/s00425-017-2713-9

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Champigny, M. J., Unda, F., Skyba, O., Soolanayakanahally, R. Y., Mansfield, S. D., & Campbell, M. M. (s. d.). Learning from methylomes: Epigenomic correlates of Populus balsamifera traits based on deep learning models of natural DNA methylation. Plant Biotechnology Journal, n/a(n/a). https://doi.org/10.1111/pbi.13299

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Chang, S., Puryear, J., & Cairney, J. (1993). A simple and efficient method for isolating RNA from pine trees. Plant Molecular Biology Reporter, 11(2), 113- 116. https://doi.org/10.1007/BF02670468

Pubmed: Author and Title

Google Scholar: <u>Author Only Title Only Author and Title</u>

Chen, C., & Chen, Z. (2002). Potentiation of Developmentally Regulated Plant Defense Response by AtWRKY18, a Pathogen-Induced Arabidopsis Transcription Factor. Plant Physiology, 129(2), 706-716. https://doi.org/10.1104/pp.001057

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Chen, G., Komatsuda, T., Ma, J. F., Li, C., Yamaji, N., & Nevo, E. (2011). A functional cutin matrix is required for plant protection against water loss. Plant Signaling & Behavior, 6(9), 1297-1299. https://doi.org/10.4161/psb.6.9.17507

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Cho, E. J., Choi, S. H., Kim, J. H., Kim, J. E., Lee, M. H., Chung, B. Y., Woo, H. R., & Kim, J.-H. (2016). A Mutation in Plant-Specific SW2/SNF2-Like Chromatin-Remodeling Proteins, DRD1 and DDM1, Delays Leaf Senescence in Arabidopsis thaliana. PLoS ONE, 11(1). https://doi.org/10.1371/journal.pone.0146826

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Choat, B., Brodribb, T. J., Brodersen, C. R., Duursma, R. A, López, R., & Medlyn, B. E. (2018). Triggers of tree mortality under drought. Nature, 558(7711), 531- 539. https://doi.org/10.1038/s41586-018-0240-x

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Chujo, T., Takai, R., Akimoto-Tomiyama, C., Ando, S., Minami, E., Nagamura, Y., Kaku, H., Shibuya, N., Yasuda, M., Nakashita, H., Umemura, K., Okada, A, Okada, K., Nojiri, H., & Yamane, H. (2007). Involvement of the elicitor-induced gene OsWRKY53 in the expression of defense-related genes in rice. Biochimica et Biophysica Acta (BBA) - Gene Structure and Expression, 1769(7), 497-505. https://doi.org/10.1016/j.bbaexp.2007.04.006

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Chwialkowska, K., Nowakowska, U., Mroziewicz, A, Szarejko, I., & Kwasniewski, M. (2016). Water-deficiency conditions differently modulate the methylome of roots and leaves in barley (Hordeum vulgare L.). Journal of Experimental Botany, 67(4), 1109-1121. https://doi.org/10.1093/jxb/erv552

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Cochard, H., Casella, E., & Mencuccini, M. (2007). Xylem vulnerability to cavitation varies among poplar and willow clones and correlates with yield. Tree Physiology, 27(12), 1761- 1767. https://doi.org/10.1093/treephys/27.12.1761

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Cochard, H., Damour, G., Bodet, C., Tharwat, I., Poirier, M., & Glio, T. (2005). Evaluation of a new centrifuge technique for rapid generation of xylem vulnerability curves. Physiologia Plantarum - PHYSIOL PLANT, 124. https://doi.org/10.1111/j.1399-3054.2005.00526.x

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Cohen, D., Bogeat-Triboulot, M.-B., Tisserant, E., Balzergue, S., Martin-Magniette, M.-L., Lelandais, G., Ningre, N., Renou, J.-P., Tamby, J.-P., Le Thiec, D., & Hummel, I. (2010). Comparative transcriptomics of drought responses in Populus: A meta-analysis of genome-wide expression profiling in mature leaves and root apices across two genotypes. BMC Genomics, 11(1), 630. https://doi.org/10.1186/1471-2164-11-630

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Coil, D., Jospin, G., & Darling, A E. (2015). A5-miseq: An updated pipeline to assemble microbial genomes from Illumina MiSeq data. Bioinformatics (Oxford, England), 31(4), 587-589. https://doi.org/10.1093/bioinformatics/btu661

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Colomé-Tatché, M., Cortijo, S., Wardenaar, R., Morgado, L., Lahouze, B., Sarazin, A., Etcheverry, M., Martin, A., Feng, S., Duvernois-Berthet, E., Labadie, K., Wincker, P., Jacobsen, S. E., Jansen, R. C., Colot, V., & Johannes, F. (2012). Features of the Arabidopsis recombination landscape resulting from the combined loss of sequence variation and DNA methylation. Proceedings of the National Academy of Sciences, 109(40), 16240- 16245. https://doi.org/10.1073/pnas.1212955109

Pubmed: Author and Title

Google Scholar: <u>Author Only Title Only Author and Title</u>

Conde, D., Le Gac, A-L., Perales, M., Dervinis, C., Kirst, M., Maury, S., González-Melendi, P., & Allona, I. (2017). Chilling-responsive DEMETER-LIKE DNA demethylase mediates in poplar bud break: Role of active DNA demethylase in trees' bud break. Plant, Cell & Environment, 40(10), 2236-2249. https://doi.org/10.1111/pce.13019

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Corem, S., Doron-Faigenboim, A., Jouffroy, O., Maumus, F., Arazi, T., & Bouché, N. (2018). Redistribution of CHH Methylation and Small Interfering RNAs across the Genome of Tomato ddm1 Mutants. The Plant Cell, 30(7), 1628- 1644. https://doi.org/10.1105/tpc.18.00167

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Correia, B., Pintó-Marijuan, M., Castro, B. B., Brossa, R., López-Carbonell, M., & Pinto, G. (2014). Hormonal dynamics during recovery from drought in two Eucalyptus globulus genotypes: From root to leaf. Plant Physiology and Biochemistry, 82, 151-160. https://doi.org/10.1016/j.plaphy.2014.05.016

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Cortijo, S., Wardenaar, R., Colome-Tatche, M., Gilly, A., Etcheverry, M., Labadie, K., Caillieux, E., Hospital, F., Aury, J.-M., Wincker, P., Roudier, F., Jansen, R. C., Colot, V., & Johannes, F. (2014). Mapping the Epigenetic Basis of Complex Traits. Science, 343(6175), 1145-1148. https://doi.org/10.1126/science.1248127

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Cotrozzi, L., Pellegrini, E., Guidi, L., Landi, M., Lorenzini, G., Massai, R., Remorini, D., Tonelli, M., Trivellini, A., Vernieri, P., & Nali, C. (2017). Losing the Warning Signal: Drought Compromises the Cross-Talk of Signaling Molecules in Quercus ilex Exposed to Ozone. Frontiers in Plant Science, 8. https://doi.org/10.3389/fpls.2017.01020

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Daviaud, C., Renault, V., Mauger, F., Deleuze, J.-F., & Tost, J. (2018). Whole-Genome Bisulfite Sequencing Using the Ovation® Ultralow Methyl-Seq Protocol. Methods in Molecular Biology (Clifton, N.J.), 1708, 83-104. https://doi.org/10.1007/978-1-4939-7481-8_5

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Dong, X. (2004). NPR1, all things considered. Current Opinion in Plant Biology, 7(5), 547-552. https://doi.org/10.1016/j.pbi.2004.07.005

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Durand, M., Brendel, O., Buré, C., & Le Thiec, D. (2019). Altered stomatal dynamics induced by changes in irradiance and vapour-pressure deficit under drought: Impacts on the whole plant transpiration efficiency of poplar genotypes. New Phytologist, 222. https://doi.org/10.1111/nph.15710

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Dusotoit-Coucaud, A, Brunel, N., Tixier, A, Cochard, H., & Herbette, S. (2014). Hydrolase treatments help unravel the function of intervessel pits in xylem hydraulics. Physiologia Plantarum, 150(3), 388-396. https://doi.org/10.1111/ppl.12092

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Farquhar, G. D., Ehleringer, J. R., & Hubick, K. T. (1989). Carbon Isotope Discrimination and Photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology, 40(1), 503-537. https://doi.org/10.1146/annurev.pp.40.060189.002443

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Farquhar, G., O'Leary, M. H., & Berry, J. (1982). On the Relationship Between Carbon Isotope Discrimination and the Intercellular Carbon Dioxide Concentration in Leaves. Australian Journal of Plant Physiology, 13, 281-292. https://doi.org/10.1071/PP9820121

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Feng, S., Jacobsen, S. E., & Reik, W. (2010). Epigenetic Reprogramming in Plant and Animal Development. Science, 330(6004), 622-627. https://doi.org/10.1126/science.1190614

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Fernando, V. C. D., & Schroeder, D. F. (2016). Role of ABA in Arabidopsis Salt, Drought, and Desiccation Tolerance. Abiotic and Biotic Stress in Plants - Recent Advances and Future Perspectives. https://doi.org/10.5772/61957

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Fichot, R., Barigah, T. S., Chamaillard, S., Thiec, D. L., Laurans, F., Cochard, H., & Brignolas, F. (2010). Common trade-offs between xylem resistance to cavitation and other physiological traits do not hold among unrelated Populus deltoides ×Populus nigra hybrids. Plant, Cell & Environment, 33(9), 1553-1568. https://doi.org/10.1111/j.1365-3040.2010.02164.x

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Fichot, R., Brignolas, F., Cochard, H., & Ceulemans, R. (2015). Vulnerability to drought-induced cavitation in poplars: Synthesis and future opportunities. Plant, Cell & Environment, 38(7), 1233-1251. https://doi.org/10.1111/pce.12491

Pubmed: Author and Title

Google Scholar: <u>Author Only Title Only Author and Title</u>

Forgione, I., Woloszynska, M., Pacenza, M., Chiappetta, A, Greco, M., Araniti, F., Abenavoli, M. R., Van Lijsebettens, M., Bitonti, M. B., & Bruno, L. (2019). Hypomethylated drm1 drm2 cmt3 mutant phenotype of Arabidopsis thaliana is related to auxin pathway impairment. PLANT SCIENCE, 280, 383-396. http://dx.doi.org/10.1016/j.plantsci.2018.12.029

Pubmed: Author and Title

Google Scholar: <u>Author Only Title Only Author and Title</u>

Fujimoto, R., Sasaki, T., Inoue, H., & Nishio, T. (2008). Hypomethylation and transcriptional reactivation of retrotransposon-like sequences in ddm1 transgenic plants of Brassica rapa. Plant Molecular Biology, 66(5), 463- 473. https://doi.org/10.1007/s11103-007-9285-1

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Fujimoto, S. Y., Ohta, M., Usui, A., Shinshi, H., & Ohme-Takagi, M. (2000). Arabidopsis Ethylene-Responsive Element Binding Factors Act as Transcriptional Activators or Repressors of GCC Box–Mediated Gene Expression. The Plant Cell, 12(3), 393-405.

Pubmed: Author and Title

Google Scholar: <u>Author Only Title Only Author and Title</u>

Fultz, D., Choudury, S. G., & Slotkin, R. K. (2015). Silencing of active transposable elements in plants. Current opinion in plant biology, 27, 67-76. https://doi.org/10.1016/j.pbi.2015.05.027

Pubmed: Author and Title

Google Scholar: <u>Author Only Title Only Author and Title</u>

Furci, L., Jain, R., Stassen, J., Berkowitz, O., Whelan, J., Roquis, D., Baillet, V., Colot, V., Johannes, F., & Ton, J. (2019). Identification

and characterisation of hypomethylated DNA loci controlling quantitative resistance in Arabidopsis. ELife, 8, e40655. https://doi.org/10.7554/eLife.40655

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Gagnot, S., Tamby, J.-P., Martin-Magniette, M.-L., Bitton, F., Taconnat, L., Balzergue, S., Aubourg, S., Renou, J.-P., Lecharny, A, & Brunaud, V. (2008). CATdb: A public access to Arabidopsis transcriptome data from the URGV-CATMA platform. Nucleic Acids Research, 36(Database issue), D986-990. https://doi.org/10.1093/nar/gkm757

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Gaillochet, C., & Lohmann, J. U. (2015). The never-ending story: From pluripotency to plant developmental plasticity. Development (Cambridge, England), 142(13), 2237- 2249. https://doi.org/10.1242/dev.117614

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Garg, R., Narayana Chevala, V., Shankar, R., & Jain, M. (2015). Divergent DNA methylation patterns associated with gene expression in rice cultivars with contrasting drought and salinity stress response. Scientific Reports, 5. https://doi.org/10.1038/srep14922

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Gebreselassie, M. N., Ader, K., Boizot, N., Millier, F., Charpentier, J.-P., Alves, A., Simões, R., Rodrigues, J. C., Bodineau, G., Fabbrini, F., Sabatti, M., Bastien, C., & Segura, V. (2017). Near-infrared spectroscopy enables the genetic analysis of chemical properties in a large set of wood samples from Populus nigra (L.) natural populations. Industrial Crops and Products, 107, 159- 171. https://doi.org/10.1016/j.indcrop.2017.05.013

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Gendrel, A-V., Lippman, Z., Yordan, C., Colot, V., & Martienssen, R. A. (2002). Dependence of Heterochromatic Histone H3 Methylation Patterns on the Arabidopsis Gene DDM1. Science, 297(5588), 1871-1873. https://doi.org/10.1126/science.1074950

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Gömöry, D., Hrivnák, M., Krajmerova, D., & Longauer, R. (2017). Epigenetic memory effects in forest trees: A victory of "Michurinian biology? Central European Forestry Journal, 63. https://doi.org/10.1515/forj-2017-0024

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Gourcilleau, D., Bogeat-Triboulot, M.-B., Le Thiec, D., Lafon-Placette, C., Delaunay, A, El-Soud, W. A, Brignolas, F., & Maury, S. (2010). DNA methylation and histone acetylation: Genotypic variations in hybrid poplars, impact of water deficit and relationships with productivity. Annals of Forest Science, 67(2), 208.

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Grandbastien, M.-A. (1998). Activation of plant retrotransposons under stress conditions. Trends in Plant Science, 3(5), 181-187. https://doi.org/10.1016/S1360-1385(98)01232-1

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Guo, Y., Ping, W., Chen, J., Zhu, L., Zhao, Y., Guo, J., & Huang, Y. (2019). Meta-analysis of the effects of overexpression of WRKY transcription factors on plant responses to drought stress. BMC Genetics, 20(1), 63. https://doi.org/10.1186/s12863-019-0766-4 Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Ha, S., Vankova, R., Yamaguchi-Shinozaki, K., Shinozaki, K., & Tran, L.-S. P. (2012). Cytokinins: Metabolism and function in plant adaptation to environmental stresses. Trends in Plant Science, 17(3), 172-179. https://doi.org/10.1016/j.tplants.2011.12.005

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Hamanishi, E. T., Thomas, B. R., & Campbell, M. M. (2012). Drought induces alterations in the stomatal development program in Populus. Journal of Experimental Botany, 63(13), 4959-4971. https://doi.org/10.1093/jxb/ers177

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Havlová, M., Dobrev, P. I., Motyka, V., Štorchová, H., Libus, J., Dobrá, J., Malbeck, J., Gaudinová, A, & Vanková, R. (2008). The role of cytokinins in responses to water deficit in tobacco plants over-expressing trans-zeatin O-glucosyltransferase gene under 35S or SAG12 promoters. Plant, Cell & Environment, 31(3), 341-353. https://doi.org/10.1111/j.1365-3040.2007.01766.x

Pubmed: Author and Title

Google Scholar: <u>Author Only Title Only Author and Title</u>

He, G.-H., Xu, J.-Y., Wang, Y.-X., Liu, J.-M., Li, P.-S., Chen, M., Ma, Y.-Z, & Xu, Z-S. (2016). Drought-responsive WRKY transcription factor genes TaWRKY1 and TaWRKY33 from wheat confer drought and/or heat resistance in Arabidopsis. BMC Plant Biology, 16. https://doi.org/10.1186/s12870-016-0806-4

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Herbette, S., Bouchet, B., Brunel, N., Bonnin, E., Cochard, H., & Guillon, F. (2015). Immunolabelling of intervessel pits for polysaccharides and lignin helps in understanding their hydraulic properties in Populus tremula × alba. Annals of Botany, 115(2), 187-199. https://doi.org/10.1093/aob/mcu232

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Heyman, J., Canher, B., Bisht, A, Christiaens, F., & De Veylder, L. (2018). Emerging role of the plant ERF transcription factors in coordinating wound defense responses and repair. Journal of Cell Science, 131(2). https://doi.org/10.1242/jcs.208215

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Higo, H., Tahir, M., Takashima, K., Miura, A, Watanabe, K., Tagiri, A, Ugaki, M., Ishikawa, R., Eiguchi, M., Kurata, N., Sasaki, T., Richards, E., Takano, M., Kishimoto, N., Kakutani, T., & Habu, Y. (2012). DDM1 (Decrease in DNA Methylation) genes in rice (Oryza sativa). Molecular Genetics and Genomics, 287(10), 785-792. https://doi.org/10.1007/s00438-012-0717-5

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Hirsch, C. D., & Springer, N. M. (2017). Transposable element influences on gene expression in plants. Biochimica et Biophysica Acta - Gene Regulatory Mechanisms, 1860(1), 157-165. https://doi.org/10.1016/j.bbagrm.2016.05.010

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Hoffmann, S., Otto, C., Doose, G., Tanzer, A, Langenberger, D., Christ, S., Kunz, M., Holdt, L. M., Teupser, D., Hackermüller, J., & Stadler, P. F. (2014). A multi-split mapping algorithm for circular RNA, splicing, trans-splicing and fusion detection. Genome Biology, 15(2), R34. https://doi.org/10.1186/qb-2014-15-2-r34

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Ikeda, Y., & Nishimura, T. (2015). The role of DNA methylation in transposable element silencing and genomic imprinting. Nuclear Functions in Plant Transcription, Signaling and Development, 13-29. https://doi.org/10.1007/978-1-4939-2386-1 2

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Ito, T., Tarutani, Y., To, T. K., Kassam, M., Duvernois-Berthet, E., Cortijo, S., Takashima, K., Saze, H., Toyoda, A, Fujiyama, A, & others. (2015). Genome-wide negative feedback drives transgenerational DNA methylation dynamics in Arabidopsis. PLoS Genet, 11(4), e1005154.

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Jansson, S., & Douglas, C. J. (2007). Populus: A Model System for Plant Biology. Annual Review of Plant Biology, 58(1), 435-458. https://doi.org/10.1146/annurev.arplant.58.032806.103956

Pubmed: Author and Title

Google Scholar: <u>Author Only Title Only Author and Title</u>

Jeddeloh, J. A, Bender, J., & Richards, E. J. (1998). The DNA methylation locusDDM1 is required for maintenance of gene silencing in Arabidopsis. Genes & Development, 12(11), 1714–1725.

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Jiang, Y., Guo, L., Ma, X., Zhao, X., Jiao, B., Li, C., & Luo, K. (2017). The WRKY transcription factors PtrWRKY18 and PtrWRKY35 promote Melampsora resistance in Populus. Tree Physiology, 37(5), 665- 675. https://doi.org/10.1093/treephys/tpx008

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Johannes, F., Porcher, E., Teixeira, F. K., Saliba-Colombani, V., Simon, M., Agier, N., Bulski, A., Albuisson, J., Heredia, F., Audigier, P., Bouchez, D., Dillmann, C., Guerche, P., Hospital, F., & Colot, V. (2009). Assessing the Impact of Transgenerational Epigenetic Variation on Complex Traits. PLOS Genetics, 5(6), e1000530. https://doi.org/10.1371/journal.pgen.1000530

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Kakutani, T. (1997). Genetic characterization of late-flowering traits induced by DNA hypomethylation mutation in Arabidopsis thaliana. The Plant Journal, 12(6), 1447- 1451. https://doi.org/10.1046/j.1365-313x.1997.12061447.x

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Kakutani, T., Jeddeloh, J. A, & Richards, E. J. (1995). Characterization of an Arabidopsis thaliana DNA hypomethylation mutant. Nucleic acids research, 23(1), 130–137.

Pubmed: <u>Author and Title</u>

Google Scholar: Author Only Title Only Author and Title

Karan, R., DeLeon, T., Biradar, H., & Subudhi, P. K. (2012). Salt Stress Induced Variation in DNA Methylation Pattern and Its Influence on Gene Expression in Contrasting Rice Genotypes. PLoS ONE, 7(6). https://doi.org/10.1371/journal.pone.0040203

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Kawakatsu, T., & Ecker, J. R. (2019). Diversity and dynamics of DNA methylation: Epigenomic resources and tools for crop breeding. Breeding Science, 69(2), 191-204. https://doi.org/10.1270/jsbbs.19005

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Kawakatsu, T., Huang, S. C., Jupe, F., Sasaki, E., Schmitz, R. J., Urich, M. A, Castanon, R., Nery, J. R., Barragan, C., He, Y., Chen, H., Dubin, M., Lee, C.-R., Wang, C., Bemm, F., Becker, C., O'Neil, R., O'Malley, R. C., Quarless, D. X., ... Zhou, X. (2016). Epigenomic Diversity in a Global Collection of Arabidopsis thaliana Accessions. Cell, 166(2), 492-505. https://doi.org/10.1016/j.cell.2016.06.044

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Kawanabe, T., Ishikura, S., Miyaji, N., Sasaki, T., Wu, L. M., Itabashi, E., Takada, S., Shimizu, M., Takasaki-Yasuda, T., Osabe, K., Peacock, W. J., Dennis, E. S., & Fujimoto, R. (2016). Role of DNA methylation in hybrid vigor in Arabidopsis thaliana. Proceedings of the National Academy of Sciences, 113(43), E6704- E6711. https://doi.org/10.1073/pnas.1613372113

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Kejnovsky, E., Hawkins, J. S., & Feschotte, C. (2012). Plant Transposable Elements: Biology and Evolution. In J. F. Wendel, J. Greilhuber, J. Dolezel, & I. J. Leitch (Éd.), Plant Genome Diversity Volume 1 (p. 17-34). Springer Vienna. https://doi.org/10.1007/978-3-7091-1130-7_2

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Koo, A J., Thireault, C., Zemelis, S., Poudel, A N., Zhang, T., Kitaoka, N., Brandizzi, F., Matsuura, H., & Howe, G. A (2014). Endoplasmic reticulum-associated inactivation of the hormone jasmonoyl-L-isoleucine by multiple members of the cytochrome P450 94 family in Arabidopsis. The Journal of Biological Chemistry, 289(43), 29728- 29738. https://doi.org/10.1074/jbc.M114.603084

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Kooke, R., Johannes, F., Wardenaar, R., Becker, F., Etcheverry, M., Colot, V., Vreugdenhil, D., & Keurentjes, J. J. B. (2015). Epigenetic Basis of Morphological Variation and Phenotypic Plasticity in Arabidopsis thaliana. The Plant Cell Online, 27(2), 337-348. https://doi.org/10.1105/tpc.114.133025

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Kopylova, E., Noé, L., & Touzet, H. (2012). SortMeRNA: Fast and accurate filtering of ribosomal RNAs in metatranscriptomic data. Bioinformatics (Oxford, England), 28(24), 3211- 3217. https://doi.org/10.1093/bioinformatics/bts611

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Krueger, F., & Andrews, S. R. (2011). Bismark: A flexible aligner and methylation caller for Bisulfite-Seq applications. Bioinformatics, 27(11), 1571- 1572. https://doi.org/10.1093/bioinformatics/btr167

Pubmed: <u>Author and Title</u>

Google Scholar: Author Only Title Only Author and Title

Lafon-Placette, C., Faivre-Rampant, P., Delaunay, A, Street, N., Brignolas, F., & Maury, S. (2013). Methylome of DNase I sensitive chromatin in Populus trichocarpa shoot apical meristematic cells: A simplified approach revealing characteristics of gene-body DNA methylation in open chromatin state. New Phytologist, 197(2), 416-430. https://doi.org/10.1111/nph.12026

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Lafon-Placette, C., Le Gac, A-L., Chauveau, D., Segura, V., Delaunay, A, Lesage-Descauses, M.-C., Hummel, I., Cohen, D., Jesson, B., Le Thiec, D., Bogeat-Triboulot, M.-B., Brignolas, F., & Maury, S. (2018). Changes in the epigenome and transcriptome of the poplar shoot apical meristem in response to water availability affect preferentially hormone pathways. Journal of Experimental Botany, 69(3), 537-551. https://doi.org/10.1093/jxb/erx409

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Lanciano, S., Carpentier, M.-C., Llauro, C., Jobet, E., Robakowska-Hyzorek, D., Lasserre, E., Ghesquière, A, Panaud, O., & Mirouze, M. (2017). Sequencing the extrachromosomal circular mobilome reveals retrotransposon activity in plants. PLoS Genetics, 13(2). https://doi.org/10.1371/journal.pgen.1006630

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Langmead, B., Trapnell, C., Pop, M., & Salzberg, S. L. (2009). Ultrafast and memory-efficient alignment of short DNA sequences to the human genome. Genome Biology, 10(3), R25. https://doi.org/10.1186/gb-2009-10-3-r25

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Latzel, V., Allan, E., Bortolini Silveira, A., Colot, V., Fischer, M., & Bossdorf, O. (2013). Epigenetic diversity increases the productivity and stability of plant populations. Nature Communications, 4. https://doi.org/10.1038/ncomms3875

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Latzel, V., Zhang, Y., Karlsson Moritz, K., Fischer, M., & Bossdorf, O. (2012). Epigenetic variation in plant responses to defence hormones. Annals of Botany, 110(7), 1423-1428. https://doi.org/10.1093/aob/mcs088

Pubmed: Author and Title

Google Scholar: <u>Author Only Title Only Author and Title</u>

Le Gac, A-L., Lafon-Placette, C., Chauveau, D., Segura, V., Delaunay, A., Fichot, R., Marron, N., Le Jan, I., Berthelot, A., Bodineau, G., Bastien, J.-C., Brignolas, F., & Maury, S. (2018). Winter-dormant shoot apical meristem in poplar trees shows environmental epigenetic memory. Journal of Experimental Botany, 69(20), 4821-4837. https://doi.org/10.1093/jxb/ery271

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Le Gac, A-L., Lafon-Placette, C., Delaunay, A, & Maury, S. (2019). Developmental, genetic and environmental variations of global DNA methylation in the first leaves emerging from the shoot apical meristem in poplar trees. Plant Signaling & Behavior, 14. https://doi.org/10.1080/15592324.2019.1596717

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Lee, S.-I., & Kim, N.-S. (2014). Transposable Elements and Genome Size Variations in Plants. Genomics & Informatics, 12(3), 87. https://doi.org/10.5808/GI.2014.12.3.87

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Li, J., Brader, G., & Palva, E. T. (2004). The WRKY70 Transcription Factor: A Node of Convergence for Jasmonate-Mediated and Salicylate-Mediated Signals in Plant Defense. The Plant Cell, 16(2), 319- 331. https://doi.org/10.1105/tpc.016980

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Li, Q., Eichten, S. R., Hermanson, P. J., & Springer, N. M. (2014). Inheritance Patterns and Stability of DNA Methylation Variation in Maize Near-Isogenic Lines. Genetics, 196(3), 667- 676. https://doi.org/10.1534/genetics.113.158980

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Liang, D., Zhang, Z., Wu, H., Huang, C., Shuai, P., Ye, C.-Y., Tang, S., Wang, Y., Yang, L., & Wang, J. (2014). Single-base-resolution methylomes of Populus trichocarpa reveal the association between DNA methylation and drought stress. BMC genetics, 15, S9.

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Li-Marchetti, C., Le Bras, C., Relion, D., Citerne, S., Huché-Thélier, L., Sakr, S., Morel, P., & Crespel, L. (2015). Genotypic differences in architectural and physiological responses to water restriction in rose bush. Frontiers in Plant Science, 6. https://doi.org/10.3389/fpls.2015.00355

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Lippman, Z, Gendrel, A-V., Black, M., Vaughn, M. W., Dedhia, N., Richard McCombie, W., Lavine, K., Mittal, V., May, B., Kasschau, K. D., Carrington, J. C., Doerge, R. W., Colot, V., & Martienssen, R. (2004). Role of transposable elements in heterochromatin and epigenetic control. Nature, 430(6998), 471- 476. https://doi.org/10.1038/nature02651

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Lisch, D. (2012). How important are transposons for plant evolution? Nature Reviews Genetics, 14(1), 49-61. https://doi.org/10.1038/nrg3374

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Liu, G., Ji, Y., Bhuiyan, N. H., Pilot, G., Selvaraj, G., Zou, J., & Wei, Y. (2010). Amino acid homeostasis modulates salicylic acid-associated redox status and defense responses in Arabidopsis. The Plant Cell, 22(11), 3845-3863. https://doi.org/10.1105/tpc.110.079392

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Long, J. C., Xia, A. A., Liu, J. H., Jing, J. L., Wang, Y. Z., Qi, C. Y., & He, Y. (2019). Decrease in DNA methylation 1 (DDM1) is required for the formation of mCHH islands in maize. Journal of Integrative Plant Biology, 61(6), 749-764. https://doi.org/10.1111/jipb.12733

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

López Sánchez, A, Stassen, J. H. M., Furci, L., Smith, L. M., & Ton, J. (2016). The role of DNA (de)methylation in immune responsiveness of Arabidopsis. The Plant Journal, 88(3), 361-374. https://doi.org/10.1111/tpj.13252

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Lorrain, S., Vailleau, F., Balagué, C., & Roby, D. (2003). Lesion mimic mutants: Keys for deciphering cell death and defense pathways in plants? Trends in Plant Science, 8(6), 263-271. https://doi.org/10.1016/S1360-1385(03)00108-0

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Makarevitch, I., Waters, A J., West, P. T., Stitzer, M., Hirsch, C. N., Ross-Ibarra, J., & Springer, N. M. (2015). Transposable Elements Contribute to Activation of Maize Genes in Response to Abiotic Stress. PLoS Genetics, 11(1). https://doi.org/10.1371/journal.pgen.1004915

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Maor, G. L., Yearim, A., & Ast, G. (2015). The alternative role of DNA methylation in splicing regulation. Trends in Genetics, 31(5), 274-280. https://doi.org/10.1016/j.tig.2015.03.002

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Marcel, S., Sawers, R., Oakeley, E., Angliker, H., & Paszkowski, U. (2010). Tissue-Adapted Invasion Strategies of the Rice Blast Fungus Magnaporthe oryzae[W]. The Plant Cell, 22(9), 3177- 3187. https://doi.org/10.1105/tpc.110.078048

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Mauch-Mani, B., Baccelli, I., Luna, E., & Flors, V. (2017). Defense Priming: An Adaptive Part of Induced Resistance. Annual Review of Plant Biology, 68(1), 485-512. https://doi.org/10.1146/annurev-arplant-042916-041132

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Maury, S., Sow, M. D., Le Gac, A-L., Genitoni, J., Lafon-Placette, C., & Mozgova, I. (2019). Phytohormone and Chromatin Crosstalk: The Missing Link For Developmental Plasticity? Frontiers in Plant Science, 10. https://doi.org/10.3389/fpls.2019.00395

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

McCarthy, D. J., Chen, Y., & Smyth, G. K. (2012). Differential expression analysis of multifactor RNA-Seq experiments with respect to biological variation. Nucleic Acids Research, 40(10), 4288- 4297. https://doi.org/10.1093/nar/gks042

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A, Williams, D. G., & Yepez, E. A (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? New Phytologist, 178(4), 719-739. https://doi.org/10.1111/j.1469-8137.2008.02436.x

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Meyer, P. (2015). Epigenetic variation and environmental change: Fig. 1. Journal of Experimental Botany, 66(12), 3541-3548. https://doi.org/10.1093/jxb/eru502

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Mirouze, M., & Paszkowski, J. (2011). Epigenetic contribution to stress adaptation in plants. Current Opinion in Plant Biology, 14(3), 267-274. https://doi.org/10.1016/j.pbi.2011.03.004

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Mirouze, M., Reinders, J., Bucher, E., Nishimura, T., Schneeberger, K., Ossowski, S., Cao, J., Weigel, D., Paszkowski, J., & Mathieu, O. (2009). Selective epigenetic control of retrotransposition in Arabidopsis. Nature, 461(7262), 427- 430. https://doi.org/10.1038/nature08328

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Miura, A., Yonebayashi, S., Watanabe, K., Toyama, T., Shimada, H., & Kakutani, T. (2001). Mobilization of transposons by a mutation abolishing full DNA methylation in Arabidopsis. Nature, 411(6834), 212- 214. https://doi.org/10.1038/35075612

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Mofatto, L. S., Carneiro, F. de A, Vieira, N. G., Duarte, K. E., Vidal, R. O., Alekcevetch, J. C., Cotta, M. G., Verdeil, J.-L., Lapeyre-Montes, F., Lartaud, M., Leroy, T., De Bellis, F., Pot, D., Rodrigues, G. C., Carazzolle, M. F., Pereira, G. A. G., Andrade, A. C., & Marraccini, P. (2016). Identification of candidate genes for drought tolerance in coffee by high-throughput sequencing in the shoot apex of different Coffea arabica cultivars. BMC Plant Biology, 16. https://doi.org/10.1186/s12870-016-0777-5

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Monclus, R., Dreyer, E., Villar, M., Delmotte, F. M., Delay, D., Petit, J.-M., Barbaroux, C., Le Thiec, D., Bréchet, C., & Brignolas, F. (2006). Impact of drought on productivity and water use efficiency in 29 genotypes of Populus deltoides×Populus nigra. New Phytologist, 169(4), 765-777. https://doi.org/10.1111/j.1469-8137.2005.01630.x

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Munné-Bosch, S., & Peñuelas, J. (2003). Photo- and antioxidative protection, and a role for salicylic acid during drought and recovery

in field-grown Phillyrea angustifolia plants. Planta, 217(5), 758-766. https://doi.org/10.1007/s00425-003-1037-0

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Nicotra, A.B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., Poot, P., Purugganan, M. D., Richards, C. L., Valladares, F., & van Kleunen, M. (2010). Plant phenotypic plasticity in a changing climate. Trends in Plant Science, 15(12), 684-692. https://doi.org/10.1016/j.tplants.2010.09.008

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Nicotra, Adrienne B., Segal, D. L., Hoyle, G. L., Schrey, A W., Verhoeven, K. J. F., & Richards, C. L. (2015). Adaptive plasticity and epigenetic variation in response to warming in an Alpine plant. Ecology and Evolution, 5(3), 634-647. https://doi.org/10.1002/ece3.1329

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Niederhuth, C. E., & Schmitz, R. J. (2017). Putting DNA methylation in context: From genomes to gene expression in plants. Biochimica et Biophysica Acta (BBA) - Gene Regulatory Mechanisms, 1860(1), 149-156. https://doi.org/10.1016/j.bbagrm.2016.08.009

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Nishiyama, R., Watanabe, Y., Fujita, Y., Le, D. T., Kojima, M., Werner, T., Vankova, R., Yamaguchi-Shinozaki, K., Shinozaki, K., Kakimoto, T., Sakakibara, H., Schmülling, T., & Tran, L.-S. P. (2011). Analysis of cytokinin mutants and regulation of cytokinin metabolic genes reveals important regulatory roles of cytokinins in drought, salt and abscisic acid responses, and abscisic acid biosynthesis. The Plant Cell, 23(6), 2169- 2183. https://doi.org/10.1105/tpc.111.087395

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Ojolo, S. P., Cao, S., Priyadarshani, S. V. G. N., Li, W., Yan, M., Aslam, M., Zhao, H., & Qin, Y. (2018). Regulation of Plant Growth and Development: A Review From a Chromatin Remodeling Perspective. Frontiers in Plant Science, 9. https://doi.org/10.3389/fpls.2018.01232

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Ong-Abdullah, M., Ordway, J. M., Jiang, N., Ooi, S.-E., Kok, S.-Y., Sarpan, N., Azimi, N., Hashim, A. T., Ishak, Z., Rosli, S. K., Malike, F. A., Bakar, N. A. A., Marjuni, M., Abdullah, N., Yaakub, Z., Amiruddin, M. D., Nookiah, R., Singh, R., Low, E.-T. L., ... Martienssen, R. A. (2015). Loss of Karma transposon methylation underlies the mantled somaclonal variant of oil palm. Nature, 525(7570), 533-537. https://doi.org/10.1038/nature15365

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Oshima, Y., & Mitsuda, N. (2013). The MIXTA-like Transcription factor MYB16 is a major regulator of cuticle formation in vegetative organs. Plant Signaling & Behavior, 8(11). https://doi.org/10.4161/psb.26826

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Oshima, Y., & Mitsuda, N. (2016). Enhanced cuticle accumulation by employing MIXTA-like transcription factors. Plant Biotechnology, 33, 161-168. https://doi.org/10.5511/plantbiotechnology.16.0627a

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Pandey, S., & Chakraborty, D. (2015). Salicylic Acid and Drought Stress Response: Biochemical to Molecular Crosstalk. In B. N. Tripathi & M. Müller (Éd.), Stress Responses in Plants: Mechanisms of Toxicity and Tolerance (p. 247- 265). Springer International Publishing. https://doi.org/10.1007/978-3-319-13368-3 10

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Pandey, S. P., Srivastava, S., Goel, R., Lakhwani, D., Singh, P., Asif, M. H., & Sane, A. P. (2017). Simulated herbivory in chickpea causes rapid changes in defense pathways and hormonal transcription networks of JA/ethylene/GA/auxin within minutes of wounding. Scientific Reports, 7(1), 1-14. https://doi.org/10.1038/srep44729

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Plavcová, L., & Hacke, U. G. (2011). Heterogeneous distribution of pectin epitopes and calcium in different pit types of four angiosperm species. New Phytologist, 192(4), 885-897. https://doi.org/10.1111/j.1469-8137.2011.03842.x

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Plomion, C., Bastien, C., Bogeat-Triboulot, M.-B., Bouffier, L., Déjardin, A, Duplessis, S., Fady, B., Heuertz, M., Le Gac, A-L., Le Provost, G., Legué, V., Lelu-Walter, M.-A, Leplé, J.-C., Maury, S., Morel, A, Oddou-Muratorio, S., Pilate, G., Sanchez, L., Scotti, I., ... Vacher, C. (2016). Forest tree genomics: 10 achievements from the past 10 years and future prospects. Annals of Forest Science, 73(1), 77-103. https://doi.org/10.1007/s13595-015-0488-3

Pubmed: Author and Title

Google Scholar: <u>Author Only Title Only Author and Title</u>

Quadrana, L., & Colot, V. (2016). Plant Transgenerational Epigenetics. Annual Review of Genetics, 50, 467-491. https://doi.org/10.1146/annurev-genet-120215-035254

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Quadrana, L., Etcheverry, M., Gilly, A., Caillieux, E., Madoui, M.-A., Guy, J., Bortolini Silveira, A., Engelen, S., Baillet, V., Wincker, P., Aury, J.-M., & Colot, V. (2019). Transposition favors the generation of large effect mutations that may facilitate rapid adaption. Nature Communications, 10(1), 1-10. https://doi.org/10.1038/s41467-019-11385-5

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Qüesta, J. I., Fina, J. P., & Casati, P. (2013). DDM1 and ROS1 have a role in UV-B induced- and oxidative DNA damage in A thaliana. Frontiers in Plant Science, 4. https://doi.org/10.3389/fpls.2013.00420

Pubmed: Author and Title

Google Scholar: <u>Author Only Title Only Author and Title</u>

Raj, S., Bräutigam, K., Hamanishi, E. T., Wilkins, O., Thomas, B. R., Schroeder, W., Mansfield, S. D., Plant, A L., & Campbell, M. M. (2011). Clone history shapes Populus drought responses. Proceedings of the National Academy of Sciences, 108(30), 12521–12526.

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Raju, S. K. K., Shao, M.-R., Sanchez, R., Xu, Y.-Z., Sandhu, A., Graef, G., & Mackenzie, S. (2018). An epigenetic breeding system in soybean for increased yield and stability. Plant Biotechnology Journal, 16(11), 1836-1847. https://doi.org/10.1111/pbi.12919

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Reinders, J., Wulff, B. B. H., Mirouze, M., Marí-Ordóñez, A, Dapp, M., Rozhon, W., Bucher, E., Theiler, G., & Paszkowski, J. (2009). Compromised stability of DNA methylation and transposon immobilization in mosaic Arabidopsis epigenomes. Genes & Development, 23(8), 939-950. https://doi.org/10.1101/gad.524609

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Richards, C. L., Alonso, C., Becker, C., Bossdorf, O., Bucher, E., Colomé-Tatché, M., Durka, W., Engelhardt, J., Gaspar, B., Gogol-Döring, A., Grosse, I., van Gurp, T. P., Heer, K., Kronholm, I., Lampei, C., Latzel, V., Mirouze, M., Opgenoorth, L., Paun, O., ... Verhoeven, K. J. F. (2017). Ecological plant epigenetics: Evidence from model and non-model species, and the way forward. Ecology Letters, 20(12), 1576- 1590. https://doi.org/10.1111/ele.12858

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Rigaill, G., Balzergue, S., Brunaud, V., Blondet, E., Rau, A., Rogier, O., Caius, J., Maugis-Rabusseau, C., Soubigou-Taconnat, L., Aubourg, S., Lurin, C., Martin-Magniette, M.-L., & Delannoy, E. (2018). Synthetic data sets for the identification of key ingredients for RNA-seq differential analysis. Briefings in Bioinformatics, 19(1), 65-76. https://doi.org/10.1093/bib/bbw092

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Roux, B., Rodde, N., Jardinaud, M.-F., Timmers, T., Sauviac, L., Cottret, L., Carrère, S., Sallet, E., Courcelle, E., Moreau, S., Debellé, F., Capela, D., de Carvalho-Niebel, F., Gouzy, J., Bruand, C., & Gamas, P. (2014). An integrated analysis of plant and bacterial gene expression in symbiotic root nodules using laser-capture microdissection coupled to RNA sequencing. The Plant Journal: For Cell and Molecular Biology, 77(6), 817-837. https://doi.org/10.1111/tpj.12442

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Roux, F., Colomé-Tatché, M., Edelist, C., Wardenaar, R., Guerche, P., Hospital, F., Colot, V., Jansen, R. C., & Johannes, F. (2011). Genome-Wide Epigenetic Perturbation Jump-Starts Patterns of Heritable Variation Found in Nature. Genetics, 188(4), 1015-1017. https://doi.org/10.1534/genetics.111.128744

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Russo, V. E. A, Riggs, A D., & Martienssen, R. A (1996). Epigenetic mechanisms of gene regulation. Cold Spring Harbour, NY: Cold Spring Harbour Laboratory Press. https://trove.nla.gov.au/version/27736760

Pubmed: <u>Author and Title</u>

Google Scholar: Author Only Title Only Author and Title

Sasaki, T., Kobayashi, A., Saze, H., & Kakutani, T. (2012). RNAi-independent de novo DNA methylation revealed in Arabidopsis mutants of chromatin remodeling gene DDM1. The Plant Journal, 70(5), 750-758. https://doi.org/10.1111/j.1365-313X.2012.04911.x

Pubmed: Author and Title

Google Scholar: <u>Author Only</u> <u>Title Only</u> <u>Author and Title</u>

Saze, H., & Kakutani, T. (2007). Heritable epigenetic mutation of a transposon-flanked Arabidopsis gene due to lack of the chromatin-remodeling factor DDM1. The EMBO Journal, 26(15), 3641–3652.

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Schmid, M. W., Giraldo-Fonseca, A., Rövekamp, M., Smetanin, D., Bowman, J. L., & Grossniklaus, U. (2018). Extensive epigenetic

reprogramming during the life cycle of Marchantia polymorpha. Genome Biology, 19(1). https://doi.org/10.1186/s13059-017-1383-z

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Schmittgen, T. D., & Livak, K. J. (2008). Analyzing real-time PCR data by the comparative C(T) method. Nature Protocols, 3(6), 1101-1108. https://doi.org/10.1038/nprot.2008.73

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Schneider, C. A, Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. Nature Methods, 9(7), 671-675. https://doi.org/10.1038/nmeth.2089

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Sedaghat, M., Tahmasebi-Sarvestani, Z., Emam, Y., & Mokhtassi-Bidgoli, A. (2017). Physiological and antioxidant responses of winter wheat cultivars to strigolactone and salicylic acid in drought. Plant Physiology and Biochemistry, 119, 59-69. https://doi.org/10.1016/j.plaphy.2017.08.015

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Seymour, D. K., & Becker, C. (2017). The causes and consequences of DNA methylome variation in plants. Current Opinion in Plant Biology, 36, 56-63. https://doi.org/10.1016/j.pbi.2017.01.005

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Shi, H., Chen, L., Ye, T., Liu, X., Ding, K., & Chan, Z. (2014). Modulation of auxin content in Arabidopsis confers improved drought stress resistance. Plant Physiology and Biochemistry, 82, 209-217. https://doi.org/10.1016/j.plaphy.2014.06.008

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Slotkin, R. K., & Martienssen, R. (2007). Transposable elements and the epigenetic regulation of the genome. Nature Reviews. Genetics, 8(4), 272-285. https://doi.org/10.1038/nrg2072

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Solano, R., Stepanova, A, Chao, Q., & Ecker, J. R. (1998). Nuclear events in ethylene signaling: A transcriptional cascade mediated by ETHYLENE-INSENSITIVE3 and ETHYLENE-RESPONSE-FACTOR1. Genes & Development, 12(23), 3703-3714.

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Song, J. T., Lu, H., McDowell, J. M., & Greenberg, J. T. (2004). A key role for ALD1 in activation of local and systemic defenses in Arabidopsis. The Plant Journal, 40(2), 200- 212. https://doi.org/10.1111/j.1365-313X.2004.02200.x

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Sow, M. D., Allona, I., Ambroise, C., Conde, D., Fichot, R., Gribkova, S., Jorge, V., Le-Provost, G., Pâques, L., Plomion, C., Salse, J., Sanchez-Rodriguez, L., Segura, V., Tost, J., & Maury, S. (2018). Epigenetics in Forest Trees. In Advances in Botanical Research (Vol. 88, p. 387-453). Elsevier. https://doi.org/10.1016/bs.abr.2018.09.003

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Sow, M. D., Segura, V., Chamaillard, S., Jorge, V., Delaunay, A., Lafon-Placette, C., Fichot, R., Faivre-Rampant, P., Villar, M., Brignolas, F., & Maury, S. (2018). Narrow-sense heritability and PST estimates of DNA methylation in three Populus nigra L. populations under contrasting water availability. Tree Genetics & Genomes, 14(5). https://doi.org/10.1007/s11295-018-1293-6

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Springer, N. M., & Schmitz, R. J. (2017). Exploiting induced and natural epigenetic variation for crop improvement. Nature Reviews Genetics, 18(9), 563-575. https://doi.org/10.1038/nrg.2017.45

Pubmed: Author and Title

Google Scholar: <u>Author Only Title Only Author and Title</u>

Stokes, T. L., Kunkel, B. N., & Richards, E. J. (2002). Epigenetic variation in Arabidopsis disease resistance. Genes & Development, 16(2), 171-182. https://doi.org/10.1101/gad.952102

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Street, N. R., Skogström, O., Sjödin, A., Tucker, J., Rodríguez-Acosta, M., Nilsson, P., Jansson, S., & Taylor, G. (2006a). The genetics and genomics of the drought response in Populus. The Plant Journal, 48(3), 321-341. https://doi.org/10.1111/j.1365-313X.2006.02864.x

Street, N. R., Skogström, O., Sjödin, A., Tucker, J., Rodríguez-Acosta, M., Nilsson, P., Jansson, S., & Taylor, G. (2006b). The genetics and genomics of the drought response in Populus. The Plant Journal, 48(3), 321-341. https://doi.org/10.1111/j.1365-313X.2006.02864.x

Sun, Y., & Yu, D. (2015). Activated expression of AtWRKY53 negatively regulates drought tolerance by mediating stomatal movement.

Plant Cell Reports, 34(8), 1295-1306. https://doi.org/10.1007/s00299-015-1787-8

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Tan, F., Zhou, C., Zhou, Q., Zhou, S., Yang, W., Zhao, Y., Li, G., & Zhou, D.-X. (2016). Analysis of Chromatin Regulators Reveals Specific Features of Rice DNA Methylation Pathways. Plant Physiology, 171(3), 2041-2054. https://doi.org/10.1104/pp.16.00393

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Trapet, P., Avoscan, L., Klinguer, A, Pateyron, S., Citerne, S., Chervin, C., Mazurier, S., Lemanceau, P., Wendehenne, D., & Besson-Bard, A (2016). The Pseudomonas fluorescens Siderophore Pyoverdine Weakens Arabidopsis thaliana Defense in Favor of Growth in Iron-Deficient Conditions. Plant Physiology, 171(1), 675- 693. https://doi.org/10.1104/pp.15.01537

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Tsukahara, S., Kobayashi, A, Kawabe, A, Mathieu, O., Miura, A, & Kakutani, T. (2009). Bursts of retrotransposition reproduced in Arabidopsis. Nature, 461(7262), 423-426. https://doi.org/10.1038/nature08351

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Tuskan, G. A, DiFazio, S., Jansson, S., Bohlmann, J., Grigoriev, I., Hellsten, U., Putnam, N., Ralph, S., Rombauts, S., Salamov, A, Schein, J., Sterck, L., Aerts, A, Bhalerao, R. R., Bhalerao, R. P., Blaudez, D., Boerjan, W., Brun, A, Brunner, A, ... Rokhsar, D. (2006). The Genome of Black Cottonwood, Populus trichocarpa (Torr. & Gray). Science, 313(5793), 1596- 1604. https://doi.org/10.1126/science.1128691

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Vassileva, V., Hollwey, E., Todorov, D., & Meyer, P. (s. d.). Leaf epidermal profiling as a phenotyping tool for DNA methylation mutants.

Vining, K. J., Pomraning, K. R., Wilhelm, L. J., Priest, H. D., Pellegrini, M., Mockler, T. C., Freitag, M., & Strauss, S. H. (2012). Dynamic DNA cytosine methylation in the Populus trichocarpa genome: Tissue-level variation and relationship to gene expression. Bmc Genomics, 13(1), 27.

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Volaire, F., Lens, F., Cochard, H., Xu, H., Chacon-Doria, L., Bristiel, P., Balachowski, J., Rowe, N., Violle, C., & Picon-Cochard, C. (2018). Embolism and mechanical resistances play a key role in dehydration tolerance of a perennial grass Dactylis glomerata L. Annals of Botany, 122(2), 325- 336. https://doi.org/10.1093/aob/mcy073

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Vongs, A, Kakutani, T., Martienssen, R. A, & Richards, E. J. (1993). Arabidopsis thaliana DNA methylation mutants. Science (New York, N.Y.), 260(5116), 1926-1928. https://doi.org/10.1126/science.8316832

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Wang, J., Tao, F., An, F., Zou, Y., Tian, W., Chen, X., Xu, X., & Hu, X. (2017). Wheat transcription factor TaWRKY70 is positively involved in high-temperature seedling plant resistance to Puccinia striiformis f. Sp. Tritici. Molecular Plant Pathology, 18(5), 649-661. https://doi.org/10.1111/mpp.12425

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Wang, Yan, Wang, Q., Liu, M., Bo, C., Wang, X., Ma, Q., Cheng, B., & Cai, R. (2017). Overexpression of a maize MYB48 gene confers drought tolerance in transgenic arabidopsis plants. Journal of Plant Biology, 60(6), 612- 621. https://doi.org/10.1007/s12374-017-0273-y

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Wang, Yushuai, Liang, W., & Tang, T. (2018). Constant conflict between Gypsy LTR retrotransposons and CHH methylation within a stress-adapted mangrove genome. New Phytologist, 220(3), 922-935. https://doi.org/10.1111/nph.15209

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Wang, Zhen, Wang, F., Hong, Y., Yao, J., Ren, Z., Shi, H., & Zhu, J.-K. (2018). The Flowering Repressor SVP Confers Drought Resistance in Arabidopsis by Regulating Abscisic Acid Catabolism. Molecular Plant, 11(9), 1184-1197. https://doi.org/10.1016/j.molp.2018.06.009

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Wang, Zheng, Fang, H., Chen, Y., Chen, K., Li, G., Gu, S., & Tan, X. (2014). Overexpression of BnWRKY33 in oilseed rape enhances resistance to Sclerotinia sclerotiorum. Molecular Plant Pathology, 15(7), 677- 689. https://doi.org/10.1111/mpp.12123

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Wasternack, C., & Hause, B. (2018). A Bypass in Jasmonate Biosynthesis – the OPR3-independent Formation. Trends in Plant Science,

23(4), 276- 279. https://doi.org/10.1016/j.tplants.2018.02.011

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Wettstein-Knowles, P. von. (2016). Plant Waxes. In ELS (p. 1-13). American Cancer Society. https://doi.org/10.1002/9780470015902.a0001919.pub3

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Wu, C., Bordeos, A, Madamba, Ma. R. S., Baraoidan, M., Ramos, M., Wang, G., Leach, J. E., & Leung, H. (2008). Rice lesion mimic mutants with enhanced resistance to diseases. Molecular Genetics and Genomics, 279(6), 605-619. https://doi.org/10.1007/s00438-008-0337-2

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Xi, Y., & Li, W. (2009). BSMAP: Whole genome bisulfite sequence MAPping program. BMC Bioinformatics, 10, 232. https://doi.org/10.1186/1471-2105-10-232

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Xu, Z, & Zhou, G. (2008). Responses of leaf stomatal density to water status and its relationship with photosynthesis in a grass. Journal of Experimental Botany, 59(12), 3317- 3325. https://doi.org/10.1093/ixb/ern185

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Yakovlev, I. A., Carneros, E., Lee, Y., Olsen, J. E., & Fossdal, C. G. (2016). Transcriptional profiling of epigenetic regulators in somatic embryos during temperature induced formation of an epigenetic memory in Norway spruce. Planta, 243(5), 1237- 1249. https://doi.org/10.1007/s00425-016-2484-8

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Yakovlev, I. A., & Fossdal, C. G. (2017). In Silico Analysis of Small RNAs Suggest Roles for Novel and Conserved miRNAs in the Formation of Epigenetic Memory in Somatic Embryos of Norway Spruce. Frontiers in Physiology, 8. https://doi.org/10.3389/fphys.2017.00674

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Yakovlev, I. A., Lee, Y., Rotter, B., Olsen, J. E., Skrøppa, T., Johnsen, Ø., & Fossdal, C. G. (2014). Temperature-dependent differential transcriptomes during formation of an epigenetic memory in Norway spruce embryogenesis. Tree Genetics & Genomes, 10(2), 355-366. https://doi.org/10.1007/s11295-013-0691-z

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Yakovlev, I., Fossdal, C. G., Skrøppa, T., Olsen, J. E., Jahren, A. H., & Johnsen, Ø. (2012). An adaptive epigenetic memory in conifers with important implications for seed production. Seed Science Research, 22(02), 63-76. https://doi.org/10.1017/S0960258511000535

Pubmed: Author and Title

Google Scholar: <u>Author Only Title Only Author and Title</u>

Yamamuro, C., Zhu, J.-K., & Yang, Z. (2016). Epigenetic modifications and plant hormone action. Molecular plant, 9(1), 57-70. https://doi.org/10.1016/j.molp.2015.10.008

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Yao, Y., Bilichak, A., Golubov, A., & Kovalchuk, I. (2012). Ddm1 plants are sensitive to methyl methane sulfonate and NaCl stresses and are deficient in DNA repair. Plant Cell Reports, 31(9), 1549-1561. https://doi.org/10.1007/s00299-012-1269-1

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Yona, A. H., Frumkin, I., & Pilpel, Y. (2015). A Relay Race on the Evolutionary Adaptation Spectrum. Cell, 163(3), 549-559. https://doi.org/10.1016/j.cell.2015.10.005

Pubmed: <u>Author and Title</u>

Google Scholar: <u>Author Only Title Only Author and Title</u>

Zemach, A, Kim, M. Y., Hsieh, P.-H., Coleman-Derr, D., Eshed-Williams, L., Thao, K., Harmer, S. L., & Zilberman, D. (2013). The Arabidopsis Nucleosome Remodeler DDM1 Allows DNA Methyltransferases to Access H1-Containing Heterochromatin. Cell, 153(1), 193-205. https://doi.org/10.1016/j.cell.2013.02.033

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Zemach, A, McDaniel, I. E., Silva, P., & Zilberman, D. (2010). Genome-Wide Evolutionary Analysis of Eukaryotic DNA Methylation. Science, 328(5980), 916-919. https://doi.org/10.1126/science.1186366

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Zhang, J., Jia, W., Yang, J., & Ismail, A M. (2006). Role of ABA in integrating plant responses to drought and salt stresses. Field Crops Research, 97(1), 111-119. https://doi.org/10.1016/j.fcr.2005.08.018

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Zhang, Q., Li, Y., Xu, T., Srivastava, A K., Wang, D., Zeng, L., Yang, L., He, L., Zhang, H., Zheng, Z., Yang, D.-L., Zhao, C., Dong, J., Gong, Z., Liu, R., & Zhu, J.-K. (2016). The chromatin remodeler DDM1 promotes hybrid vigor by regulating salicylic acid metabolism. Cell Discovery, 2, 16027. https://doi.org/10.1038/celldisc.2016.27

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Zhang, Y.-Y., Fischer, M., Colot, V., & Bossdorf, O. (2013). Epigenetic variation creates potential for evolution of plant phenotypic plasticity. New Phytologist, 197(1), 314- 322. https://doi.org/10.1111/nph.12010

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Zhang, Y.-Y., Latzel, V., Fischer, M., & Bossdorf, O. (2018). Understanding the evolutionary potential of epigenetic variation: A comparison of heritable phenotypic variation in epiRILs, RILs, and natural ecotypes of Arabidopsis thaliana. Heredity, 121(3), 257- 265. https://doi.org/10.1038/s41437-018-0095-9

Pubmed: Author and Title

Google Scholar: <u>Author Only Title Only Author and Title</u>

Zhu, H., Wang, G., & Qian, J. (2016). Transcription factors as readers and effectors of DNA methylation. Nature Reviews Genetics, 17(9), 551-565. https://doi.org/10.1038/nrg.2016.83

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Zhu, L.-Y., Zhu, Y.-R., Dai, D.-J., Wang, X., & Jin, H.-C. (2018). Epigenetic regulation of alternative splicing. American Journal of Cancer Research, 8(12), 2346-2358.

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title

Zhu, R., Shevchenko, O., Ma, C., Maury, S., Freitag, M., & Strauss, S. H. (2013). Poplars with a PtDDM1-RNAi transgene have reduced DNA methylation and show aberrant post-dormancy morphology. Planta, 237(6), 1483-1493. https://doi.org/10.1007/s00425-013-1858-4

Pubmed: Author and Title

Google Scholar: Author Only Title Only Author and Title