

## 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

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Hypomethylated poplars show higher tolerance to water deficit and highlight
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4 response and genome integrity

5

6 Short title:

- 7 DDM1-dependant DNA methylation in meristem
- 8

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#### 33 Abstract

As fixed and long living organisms subjected to repeated environmental stresses, trees 34 35 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 36 37 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, 38 39 we compared hypomethylated RNAi-*ddm1* lines to wild-type trees for drought tolerance. An integrative analysis was realized with phytohormone balance, methylomes, 40 41 transcriptomes and mobilomes.

Hypomethylated lines were more tolerant when subjected to moderate water 42 43 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 44 45 dependent manner, both in genes and transposable elements. Hypomethylated lines subjected to water deficit showed altered expression of genes involved in phytohormone 46 47 pathways, such as salicylic acid and modified hormonal balance. Several transposable elements showed stress- and/or line-specific patterns of reactivation, and we could 48 detect copy number variations for two of them in stressed *ddm1* lines. 49

50 Overall, our data highlight two major roles for DNA methylation in the shoot apical 51 meristem: control of stress response and plasticity through transduction of hormone 52 signaling and maintenance of genome integrity through the control of transposable 53 elements.

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

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#### 59 INTRODUCTION

As long living organisms, trees are subjected to repeated environmental challenges over 60 61 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; 62 Anderegg et al., 2016). In order to survive, they can adjust rapidly using epigenetic as 63 well as physiological levels of regulation (Nicotra et al., 2015). Epigenetics is defined as 64 65 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 66 67 the role of epigenetic mechanisms (in particular DNA methylation) in plant developmental processes, stress response, plasticity, and adaptation (Slotkin and 68 69 Martienssen, 2007; Colomé-Tatché et al., 2012; Cortijo et al., 2014; Kooke et al., 2015; Raju et al., 2018; Schmid et al., 2018). 70

Although epigenetic processes are commonly regarded as a source of flexibility in 71 perennials like trees (Bräutigam et al., 2013; Zhu et al., 2013; Yakovlev et al., 2012, 72 73 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 74 75 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 76 for the study of the ecophysiological and molecular basis of drought response (Monclus 77 et al., 2006; Street et al., 2006; Bogeat Triboulot et al., 2007; Cohen et al., 2010; 78 Hamanishi et al., 2012; Fichot et al., 2015). For example, differences in global DNA 79 methylation levels among poplar hybrid genotypes have been shown to correlate with 80 biomass production under water deficit (Gourcilleau et al., 2010; Raj et al., 2011; Le Gac 81 82 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 83 84 (Champigny et al., 2019). Lafon-Placette et al. (2018) established that drought preferentially induced changes in the DNA methylation of phytohormone-related genes, 85 apparently elevating phenotypic plasticity (Lafon-Placette et al., 2018). This has raised 86 the question of a possible link between epigenetics and phytohormone signaling / 87 synthesis in order to explain plasticity in plants, in particular in meristematic tissues 88 where development takes place (Maury et al., 2019). Phytohormones are key regulatory 89

elements in plant development and stress response, and their action is often fast and 90 transient. Epigenetic regulations could play a role by modifying the expression of genes 91 in the phytohormone pathways, notably by maintaining them after a hormonal peak, or 92 priming their expression through time to remember the stress episode (i.e., epigenetic 93 memory). In line with this, it has been shown that winter-dormant shoot apical meristems 94 of poplar genotypes grown in field conditions can keep an epigenetic memory of a 95 96 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 97 98 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., 99 100 2017; Yakovlev and Fosdal, 2017).

In plants, DNA methylation occurs in three different contexts (CHH, CHG and 101 CpG, with H=A, C or T), and the methylation or demethylation of cytosines (*de novo* or 102 maintenance during replication) is ensured by different DNA methyltransferases or DNA 103 glycosylases/lyases, respectively (Zemach et al., 2010; Zhang et al., 2018). DNA 104 methylation affects gene expression (Niederhuth and Schmitz, 2017; Bewick and 105 Schmitz, 2017). While methylation in promoters is usually associated with gene 106 silencing, gene-body methylation is more complex, and is often linked to tissue-specific 107 expression or alternative splicing (Vining et al., 2012; Lafon-Placette et al., 2013; Maor 108 109 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 110 and gene expression have used a correlative approach. In poplar, extensive gene-body 111 methylation is found in the open chromatin state, and is linked to structural gene 112 113 characteristics, and correlated with tissue-specific gene expression or stress (Vining et 114 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 115 116 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 117 118 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 119

contribute strongly to genome plasticity in eukaryotes (Lisch, 2012; Avarpadikannan and 120 Kim, 2014; Hirsch and Springer, 2017). In plants, most TEs can be activated, and their 121 contribution to genome size is not negligible, especially for trees with large genomes 122 (Kejnovsky et al., 2012; Lee and Kim, 2014). DNA methylation is required to silence 123 these TEs located in the heterochromatin, and a decrease in DNA methylation level 124 could result in their reactivation (Lippman et al., 2004; Mirouze et al., 2009; Mirouze and 125 126 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 127 understood. 128

DDM1 belongs to the SWI/SNF chromatin remodeling complex, and encodes a 129 chromatin remodeling factor required for the maintenance of DNA methylation. Its 130 depletion affects the distribution of methylation in all sequence contexts (Vongs et al., 131 1993; Jeddeloh et al., 1998; Gendrel et al., 2002; Zhu et al., 2013; Zemach et al., 2013). 132 DDM1 was first identified in Arabidopsis through EMS (ethyl methane sulfonate) 133 treatment, which caused a "decrease in DNA methylation" (Vongs et al., 1993). Vongs et 134 al., showed that Arabidopsis ddm1 mutants displayed a 70 to 75% reduction in cytosine 135 methylation compared to the wild-type (WT). Nonetheless phenotypic variations only 136 appeared several generations after the initial loss of DDM1 activity, notably through 137 reactivation of TEs (Miura et al., 2001). Several studies further characterized ddm1 138 139 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; 140 Sassaki et al., 2011), maize (Li et al., 2014), and rice (Higo et al., 2012; Tan et al., 141 2016). In poplar, RNAi *ddm1* lines have been obtained by targeting the transcripts of the 142 143 two orthologous DDM1 paralogs in Populus tremula × Populus alba cv. INRA 717-1B4 144 (Zhu et al., 2013). Under standard greenhouse conditions, the regenerated lines did not 145 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 146 147 studied under stressed conditions.

148 To investigate whether variation in DNA methylation has the potential to facilitate 149 tree plasticity under stress, we studied these *ddm1* RNAi lines during a water stress

experiment. Here, plasticity is defined as modifications in phenotype (growth, 150 morphology, anatomy, or gene expression) under a drought - re-watering regime for a 151 given genotype (Bradshaw, 2006; Nicotra et al., 2010, 2015). To address this question in 152 a developmental context, we focused our analysis on the shoot apical meristem (SAM, 153 center of plant morphogenesis) one week after re-watering in order to focus on 'stable' 154 post-stress epigenetic events (Lafon-Placette et al., 2018). Previous studies have shown 155 156 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 157 et al., 2018; Le Gac et al., 2018, Sow et al., 2018; Maury et al., 2019). To examine 158 whether plasticity was associated with epigenetic variation within wild type or RNAi lines, 159 160 we combined a fine scale ecophysiological characterization of growth dynamics and water relations with genomics (identification of differentially methylated regions (DMR) 161 162 using whole genome bisulfite sequencing, differentially expressed genes (DEG) using RNA-seq, and active transposable elements using mobilome-seq). We report a 163 164 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 165 variations in water availability. 166

167

#### 168 **RESULTS**

# Phenotypic and physiological differences among lines under well-watered conditions

171 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) 172 and  $\Psi_{pd}$  values remaining above -0.5 MPa (Sup. Fig. 2A). There was no significant 173 difference in either REW or  $\Psi_{pd}$  among lines (Fig. 1 and Sup. Fig. 2A). The WT and 174 175 *ddm1* lines all showed linear growth, and exhibited a similar height growth rate during the experiment (1.27  $\pm$  0.07 cm.day<sup>-1</sup>, P = 0.67; Fig. 2A). However, the WT had a slightly 176 177 higher diameter growth rate than the ddm1 lines (0.11  $\pm$  0.02 vs. 0.08  $\pm$  0.01 mm.day<sup>-1</sup>, P = 0.036; Fig. 2A). Differences among lines were much stronger for total leaf area, with 178

*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  $\Psi_{min}$ , leaf  $\delta^{13}$ 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<sub>50</sub> = -2.16 ± 0.05 MPa), while *ddm1*-23 was the most resistant (P<sub>50</sub> = -2.45 ± 0.04 MPa), and *ddm1*-15 was intermediate (P<sub>50</sub> = -2.28 ± 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 194 and the two RNAi-ddm1 (ddm1-15, ddm1-23) poplar lines in control (well-watered, WW) 195 and stress (moderate water deficit followed by rewatering, WD-RW) treatments. Values 196 are genotypic means  $\pm$  SE (n = 6 per line per treatment). The P50 is the xylem tension 197 inducing 50% loss of hydraulic conductance estimated from vulnerability curves (see 198 Materials and Methods for additional information). S/G corresponds to the ratio between 199 syringyl-like (S) and guaiacyl-like lignin monomeric units (G). Treatment effects were 200 evaluated within each line by using a t-test. Different letters indicate significant 201 differences between genotypes within treatments following Tukey's post hoc test. Levels 202 of significance are \*, 0.01 < P < 0.05; \*\*, 0.001 < P < 0.01; \*\*\*, P < 0.001; ns, non-203 significant; na, not available. 204

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| 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.mm <sup>2</sup> ) - WW                     | 100.61 ± 10.85 | 100.09 ± 5.10  | 112.13 ± 16.67 |
| Xylem vessel density (nb.mm <sup>2</sup> ) - 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-<br>RW                    | 20.56 ± 0.26   | 20.73 ± 0.46   | 19.99 ± 0.27   |
| Tension wood prediction by MIRS (%) -<br>WW                         | 11.05 ± 3.22   | 13.58 ± 2.89   | 14.59 ± 3.68   |
| Tension wood prediction by MIRS (%) -<br>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    |

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#### 208 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  $t_1$ ; re-watering at  $t_1$  increased REW back to control values (Fig. 1). Predawn leaf water potential ( $\Psi_{pd}$ ) at t<sub>1</sub> 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,  $\Psi_{min}$  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<sub>2</sub> for diameter (P < 0.001) while height growth recovered to control values.

218 In response to water deficit, g<sub>s</sub> started to decrease significantly 10 days after drought initiation, *i.e.* once REW had dropped below 40% (P = 0.027 for WT, P = 0.171219 for ddm1 15 and P = 0.021 for ddm1 23 Fig. 1, 2C). The WT and ddm1-23 showed 220 relatively comparable dynamics, and reached almost an 80% decrease relative to 221 222 controls, while stomatal closure was less pronounced in *ddm1-15* (Fig. 2C). A<sub>net</sub> was less impacted than g<sub>s</sub>, especially in *ddm1-15*, in agreement with the moderate intensity 223 of water deficit (Fig. 2C). Therefore, the increase in intrinsic water-use efficiency (*i.e.* the 224 ratio  $A_{net}/g_s$ ) was more pronounced in the WT and *ddm1-23* (Fig. 2C), which was 225 confirmed by a greater  $\delta^{13}$ C increase in these same lines (Sup. Fig. 2B). Total stomatal 226 density was not impacted by water deficit in *ddm1* lines, while it was significantly 227 increased in the WT (P = 0.030, Sup. Fig. 2C). Xylem traits were only seldom affected 228 by water deficit (Table 1). Xylem density was significantly increased in all lines (P < P229 0.001), while the proportion of tension wood increased in the WT only (Table 1). Water 230 231 deficit had no significant effect on the occurrence of mottled or folded leaves (Sup. Fig. 4). 232

#### 233 Phytohormone concentration in SAMs

234 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-235 rewatering, SA increased while zeatin riboside and zeatin -O- glucoside riboside 236 decreased in RNAi lines compared to the WT (Fig. 3). The other type of cytokinin, the 237 238 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 239 trend to WT (Fig. 3). The *ddm1-15* line showed a significant response for one cytokinin 240 only (Fig. 3). ABA and free auxin remained unaffected in all treatments. 241

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

Global DNA methylation content (HPLC analysis) ranged from 17.5 to 21.3 % between 243 244 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 245 246 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 247 248 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. 249 Fig. 1D). 250

Only a few stress-specific DMRs were identified. In contrast, thousands of line-251 specific DMRs were identified, especially for ddm1-15 (Sup. Fig. 5B). The two RNAi 252 lines displayed a different number of DMRs (29785 vs. 30925 for ddm1-15 in WW and 253 WD-RW treatments, respectively, and 11409 vs. 11104 for ddm1-23 in WW and WD-RW 254 255 treatments, respectively). Most of these DMRs were hypomethylated and contextdependent with higher values found in CHG context, especially in ddm1-15 (20310 vs. 256 20847 DMRs in WW and WD-RW treatments, respectively) (Sup. Fig. 5C & 5D). Line-257 specific DMRs were unequally distributed in the three different contexts. In the CpG 258 259 context, DMRs presented a bimodal distribution with both hypo and hypermethylated 260 DMRs (Sup. Fig. 5E). In the CHG context, most DMRs were hypomethylated, while in 261 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 262 263 hypo and hypermethylated states (Fig. 4A). These DMRs were mainly found in CG and CHG contexts (Fig. 4A). 264

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 272 treatments, respectively) were therefore localized in intergenic regions (Sup. Fig. 6A). In 273 the WW treatment, 879 genes were found to be strictly included within the common 274 DMRs (hereafter called DMGs for Differentially Methylated Genes), while 910 DMGs 275 were found in the WD-RW treatment. These numbers increased considerably (up to 276 more than 13,000 genes) when enlarging the windows for DMR identification from 2 kb 277 278 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 279 contexts, DMGs were mostly hypomethylated (Fig. 4C). In the CHH context, DMGs were 280 slightly methylated (between 25 to 50% of difference), compared to the CG and CHG 281 282 contexts (Fig. 4C). Gene Ontology annotation of DMGs revealed significant enrichment in biological functions such as multicellular organism development (including shoot 283 284 system development), negative regulation of biological processes, and response to abiotic stress (including response to hormones) (Sup. Fig. 6C). 285

#### **Transcriptome analysis for the water deficit – rewatering condition**

The identification of DEGs focused on the WD-RW treatment, but revealed clear 287 differences between the WT and the *ddm1*-23 lines. An average of 96 % mapping 288 efficiency was found for the P. tremula x alba reference genome (v1). A total of 32 048 289 genes were analyzed, but only 136 genes were significantly differentially expressed (P < 290 291 0.05). Gene ontology annotation revealed significant enrichment in functions such as defense response, including immune response, response to hormones (SA, Ethylene), 292 response to chitin, and regulation of RNA metabolism (Fig. 5A). The 136 DEGs (76 up-293 regulated and 60 down-regulated) were grouped according to Arabidopsis thaliana gene 294 295 annotation homology into seven main classes: cell death, defense response and cell wall, immune response, metabolism, signalization, transcription factors, and unknown 296 297 function (Fig. 5B). Genes related to immune response were systematically up-regulated 298 (RBOHD, CYP94B1, RLP1, RLP56, RPM1, PLDGAMMA1, PDF1). Most genes related to transcription factors (15/17) were also up-regulated (WRKY, MYB106, ERF, SZF2, 299 PDF2, SVP/AGL22), with only two genes down-regulated (MYB48 and DTA2). Defense 300 301 and cell wall related genes were both up- (18, including CHITIV, KTI1, 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 309 were co-localized with common DMRs among *ddm1* lines. Although only seven DEGs 310 (Potri.001G048700, Potri.001G065300, Potri.002G192400, Potri.009G051300, 311 Potri.016G130900, Potri.T041700, Potri.T085000) overlapped with the DMR genomic 312 locations, 53 were located in the direct vicinity of a DMR (+/- 10 kb) and 98 at +/- 25 kb 313 (Sup. Fig. 7A). A significant and negative rank correlation (Spearman's rho = -0.32, P < 314 0.001) was observed between methylation in the three contexts and expression values 315 when considering at least a +/- 10 kb window for DMRs to reach statistical significance 316 (Sup. Fig. 7B). 317

#### 318 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 319 producing extrachromosomal circular DNAs (eccDNAs), depending on lines and 320 321 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 322 (DNA transposons and retrotransposons) were detected in our mobilome-seg data (Fig. 323 6A). Most of the eccDNAs identified belonged to the annotated Gypsy. Copia. ENSPM. 324 325 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 326 Reads (SRs) coverage ranged from 3X to 4600X (Fig. 6A). Reads spanning the two TE 327 extremities constitute an evidence of a circular TE and were detected using a split reads 328 (SRs) mapping strategy. We detected a high number of SRs with a coverage ranged 329 330 from 3X to 4600X confirming the presence of eccDNAs from TEs (Fig. 6A). The 331 detection of SRs suggested the presence of reads spanning the junction of eccDNAs. 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<sup>+++</sup>"group was exclusively represented by the *Gypsy* superfamily, while the "TE<sup>+++</sup>"group was represented by DNA transposons. In contrast, "TE<sup>++</sup>" and "TE" groups were represented by different superfamilies (Fig. 6A).

338 The most active TE (*Gvpsv23*, 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 339 340 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 341 342 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 343 ddm1-15, in both WW and WD-RW treatments (9000X and 5200X, respectively), and in 344 the WT line only in the WD-RW condition. Two DNA-3-3 TEs with the same name, but 345 different in terms of sequence were also detected in the WW treatment only. The first 346 one (named DNA-3-3 1) was activated in the two RNAi lines (6000X in ddm1-15 and 347 348 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<sup>+</sup>" group 349 that were line- or stress-specific (Fig. 6A). GO annotation of the genes co-localizing with 350 351 TEs (+/- 10 kb of genes) revealed enrichment in functions such as response to stress. 352 including hormone response, multicellular organism development, and negative regulation of cellular processes (Sup. Fig. 8B). The number of genes identified in the 353 vicinity of TEs varied between 45 (TEs inside genes) and 1788 (when considering TEs 354 at +/-25kb of genes) (Sup. Fig. 8C). However, only a few of these genes showed 355 changes in their expression level (seven DEGs when considering the vicinity of +/- 25kb; 356 357 Potri.005G223200, Potri.006G062100, Potri.013G100800, Potri.013G101000, Potri.013G103000, Potri.013G120800, Potri.016G070100). 358

## 359 Methylation of active TEs and estimation of copy number variations for highly 360 active TEs

13

About 21% of the mobilome-seg TE families strictly co-localized within common DMRs. 361 This percentage raised to more than 50% when considering the presence of +/- 25 kb of 362 a DMR in the vicinity (Sup. Fig. 8C). These methylated active TE families were in 363 majority hypomethylated (ca. 92% of the TE families) in ddm1 lines (Fig. 6B). In the WW 364 treatment, active TEs were hypomethylated mostly in CG and CHG contexts, while in 365 the WD-RW treatment, active TEs were hypomethylated in CG and CHG contexts but 366 367 mostly hypermethylated in the CHH context (Fig. 6B). The most active TEs were methylated in CHG context. 368

369 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 370 371 TEs (DNA-3-3 1, Gypsy23 and SAT-1) localized in or near DMRs by gPCR analysis (Fig. 6C). For DNA-3-3\_1, there was no significant variation in the copy number 372 regardless of the lines and treatments (Fig. 6C). In contrast, an increase in copy number 373 was detected in the WD-RW treatment for Gypsy23 in ddm1-23 (15 copies), and for 374 SAT-1 in ddm1-15 (18 copies) (Fig. 6C). Gypsy23 was hypomethylated in the CHG 375 context, while SAT-1 was found in +/- 2kb of DMRs that were CG and CHG 376 377 hypomethylated.

378

#### 379 **DISCUSSION**

## 380 DDM1-dependent DNA methylation plays a role in tree phenotypic plasticity in 381 response to water deficit

#### 382 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

high  $\Psi_{pd}$  (ca. -0.8 MPa) and the small effects on net CO<sub>2</sub> assimilation rates. This avoided 390 rapid growth cessation and instead promoted steady-state acclimation. However, this 391 392 was sufficient to reveal clear differences in drought responses between the wild type and hypomethylated RNA<sub>i</sub>-ddm1 lines. While growth was progressively slowed down in the 393 wild type as REW dropped below 40% (Bogeat-Triboulot et al., 2007), both RNAi-ddm1 394 lines remained unaffected, suggesting improved tolerance to moderate water deficit. 395 396 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 397 398 stomatal closure, at least in *ddm1-15*. The slightly more negative leaf  $\Psi_{min}$  observed in RNA;-ddm1 lines tended to confirm the idea that improved tolerance might have been 399 400 linked partly to a better ability for leaf gas exchange maintenance. In addition, while stomatal density was comparable between the wild type and RNA<sub>i</sub>-ddm1 lines under 401 402 standard conditions, stomatal density increased in response to water deficit in the wild 403 type only. *ddm1* mutants in *Arabidopsis* were reported to have more stomata with 404 modified organization (grouped clusters of two or more stomata) (Vassileva et al., 2016), 405 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 406 also depend on the environmental context. Interestingly, stomatal density seems to be 407 408 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 409 dynamics (Durand et al., 2019). It is therefore possible that the increased stomatal 410 411 density observed in the wild type under water deficit contributed to a higher stomatal 412 sensitivity, providing one possible explanation for constrained leaf gas exchange and 413 growth reduction as compared to RNA<sub>i</sub>-ddm1 lines.

Besides differences in dynamic drought responses, our results also suggest that RNA<sub>i</sub>-*ddm1* lines were intrinsically more tolerant to severe water deficit because of higher xylem resistance to drought-induced cavitation. Xylem resistance to droughtinduced 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

properties such as vessel diameter and density, xylem density, or even xylem 421 biochemical composition were not significantly different from the wild type. However, 422 given the mechanistic understanding of drought-induced cavitation in angiosperms 423 (Choat et al., 2018), it is likely that the increased resistance observed in the RNA<sub>i</sub>-ddm1 424 lines was primarily linked to modifications of the ultrastructure of vessel-vessel bordered 425 pits (Plavcová Hacke, 2011; Awad et al., 2012; Dusotoit-Coucaud et al., 2014; Herbette 426 427 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 428 429 epigenetics might be exploited as such for increasing drought tolerance, remains to be purposely tested. 430

Several DEGs identified in the SAM of RNAi-ddm1 lines could explain at least in 431 part the improved tolerance to moderate water deficit. Indeed, genes involved in the 432 cuticle and waxes (CER8, FLA12) that provide protection from abiotic and biotic stresses 433 were upregulated in RNAi-ddm1 lines. Increased levels of cuticular waxes have been 434 associated with enhanced drought tolerance by preventing uncontrolled water loss 435 (Chen et al., 2011; Wettstein-Knowles, 2016). Similarly, the MYB106 TF, a major 436 regulator of cuticle formation was upregulated in the *ddm1* line (Oshima and Misuda, 437 2013, 2016). Other transcription factors (TFs) (SVP, MYB48, MYB106, WRKY36, 438 WRKY33, WRKY53) associated with drought tolerance in plants were also upregulated 439 in the ddm1 lines (Bechtold et al., 2016; Sun & Yu, 2015; He et al., 2016; Guo et al., 440 2019). Finally, previous studies in Arabidopsis ddm1 mutants and derived epiRILs 441 442 subjected to drought, or more broadly to increased nutrients or salt stress, have provided evidence that variation in DDM1-derived DNA methylation can cause 443 substantial heritable variation in ecologically important plant traits and their plasticity 444 (Reinders et al., 2009; Johannes et al., 2009; Latzel et al., 2013; Cortijo et al., 2014; 445 446 Zhang et al., 2013, Kooke et al., 2015; Cho et al., 2016; Zhang et al., 2018; Furci et al., 2019). 447

448 Hypomethylated poplar RNAi-ddm1 lines show leaf symptoms commonly 449 observed in response to pathogen infection

450 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 451 452 newly formed leaves displayed a mottled phenotype after a dormancy cycle. This is similar to other reports in Arabidopsis and other species, where developmental 453 abnormalities usually appear in later generations (Kakutani, 1997; Tan et al., 2016; 454 Corem et al., 2018; Long et al., 2019). In our RNAi-ddm1 lines we found two distinct leaf 455 phenotypes: "mottled leaves" and "folded leaves." However, the two RNAi lines differed 456 in terms of the quantities of symptomatic leaves, with higher values in ddm1-15 for 457 458 mottled leaves. This was observed even though our stress treatments had no effect on 459 leaf symptom numbers for either line. The alteration of leaf phenotype has already been 460 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 461 462 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 463 464 this phenotype.

The presence of mottled leaves could be suggestive of a hypersensitive response 465 (HR) which could result in the hyperactivation of disease resistance genes (Zhu et al., 466 2013) due to the constitutive hypomethylation in RNAi-ddm1 lines. This is in agreement 467 468 with the recent report of Furci et al., (2019) showing that hypomethylation in Arabidopsis 469 ddm1-epiRILs at selected pericentromeric regions controls quantitative disease resistance against Hyaloperonospora arabidopsidis, which is associated with genome-470 wide priming of defense-related genes. Lesion mimic mutants, characterized by the 471 472 formation of necrotic leaves (hereafter called mottled leaves) in the absence of 473 pathogens have been identified, and most importantly, these mutants show enhanced 474 resistance to pathogen infection. This is probably due to mis-regulation of defense 475 responsive genes (Lorrain et al., 2003; Wu et al., 2008). In poplar RNAi-ddm1 lines, we 476 found an important set of genes involved in defense and immune response that were 477 significantly and differentially expressed in RNAi lines compared to the WT. Immune responsive genes were upregulated in RNAi-ddm1 lines, while defense related genes 478 479 were in majority downregulated. Consequently, genes involved in cell death and leaf senescence (MLO12 and NHL10) were upregulated. The activation of immune response 480

genes in RNAi-ddm1 lines suggests that trees react as if they were attacked by 481 pathogens. This could be particularly important as it could prime *ddm1* lines against 482 483 future pathogen infections (Lopez Sanchez et al., 2016; Furci et al., 2019). Indeed, different TFs (WRKY18, WRKY33, WRKY70, WRKY53 and ERF1) known to be 484 activated during pathogen attack were overexpressed in *ddm1* lines. The WRKY TFs are 485 known to play important roles in plant defense responses that are related to attacks by 486 487 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 488 al., 2004; Wang et al., 2014; Wang et al., 2017; Chujo et al., 2007; Marcel et al., 2010; 489 Chen and Chen, 2002; Abeysinghe et al., 2018). In poplar, overexpression of WRKY18 490 491 (with WRKY35) also activates pathogenesis-related genes, and increases resistance to the biotrophic pathogen *Melampsora* (Jiang et al., 2017). 492

493 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; 494 495 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 496 cis (promoter or nearby TEs) or trans contexts. A few cis-regulated genes can control 497 the induction of several groups of defense genes by DNA (de)methylation, and 498 499 hypomethylation can influence chromatin structure at distant genome loci such as TEs 500 activating the RdDM pathway (Grandbastien, 1998; Makarevitch et al., 2015; Quadrana et al., 2019). This recent data in Arabidopsis have shown that methylation controls 501 502 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 503 overlapping DMRs and DEGs, that only seven DEGs co-localized with DMRs. 504 Expression and methylation values (DEGs at +/-10 kb of DMRs) showed a significant 505 correlation. This suggests that these genes may not be the primary target of DDM1. 506

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-

related genes across the genome via a *trans*-acting mechanism. Quadrana et al., (2019) 512 further showed that in Arabidopsis epiRILs, the insertion of Copia elements preferentially 513 514 targets environmentally responsive genes such as cell death, defense response and immune response, potentially facilitating rapid adaptation. Here, we could detect 515 increased copy numbers for two TE families in the hypomethylated *ddm1* stressed lines. 516 The potential impact of these new insertions on adaptation is unclear. Finally the fact 517 518 that only two TE families showed increased copy number suggests that additional mechanisms prevent genomic insertions of reactivated TEs. 519

520

## 521 Hypomethylated poplar lines exhibit an altered phytohormonal balance in the 522 shoot apical meristem

Phytohormones are key regulators of plant development and response to stress 523 524 (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 525 526 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 527 528 immediately post-rewatering. Although abscisic acid (ABA) (Zhang et al., 2006; 529 Fernando & Schroeder, 2015) and free auxins (Shi et al., 2014; Basu et al., 2016) are 530 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 531 cytokinins (CK) showed significant variations among our *ddm1* lines compared to the 532 533 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 534 *ddm1* lines. This is in agreement with several reports, which found that drought-stressed 535 plants tend to increase the endogenous level of SA promoting tolerance to several 536 stresses including drought (Munne-Bosch and Penuelas, 2003; Bandurska & Stroi ski, 537 2005; Azooz & Youssef 2010; Pandey & Chakraborty, 2015; Sedaghat et al., 2017), and 538 539 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 540 displayed specific hormonal changes for SA and CK. Shoot apices were collected after 541 three weeks of stress (the day of rewatering) to measure the hormonal balance at the 542

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end of the treatment. This timing of sampling could explain why drought-related 543 modifications in ABA or auxin contents were not observed. Correia et al., (2014) have 544 545 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-546 stressed plants reached the same amount of ABA seven days post-drought. This also in 547 agreement with Cotrozzi et al., (2017) who showed a very transient peak of ABA 548 549 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 550 551 condition (memory) one week post-rewatering.

552 DMGs and DEGs nearby active TEs identified in the SAM of *ddm1* stressed lines were mainly involved in development, stress response and phytohormone pathways 553 554 (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 555 556 availability induced changes in DNA methylation preferentially in genes involved in phytohormone metabolism and signaling, potentially promoting phenotypic plasticity. 557 Accordingly, poplar SAMs may also retain an environmental epigenetic memory by 558 targeting hormone-responsive genes (Le Gac et al., 2019). SAMT1, a salicylic acid 559 methyltransferase gene was still up-regulated one week post-stress in RNAi-ddm1 lines 560 compared to the WT, supporting the increase in SA content at the end of the stress. 561 When screening for candidate genes for drought tolerance in *Coffea arabica* cultivars, 562 Mofatto et al., (2016) found that SAMT1 was upregulated under drought conditions. 563 Zhang et al., (2016) have also shown that *DDM1* affects early seedling growth heterosis 564 565 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 566 acid metabolism. They proposed that *DDM1* acts as an epigenetic link between salicylic 567 acid metabolism and heterosis, also protecting plants from pathogens and abiotic stress. 568 569 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 570 571 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). 572

The elevated amount of SA levels in RNAi-ddm1 lines could be suggestive of 573 acquired disease resistance in ddm1 mutants. Similarly, two genes (CYP94B1 and 574 575 OPR2) involved in JA metabolism were upregulated in the RNAi-ddm1 lines. CYP94B1 576 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; 577 Wasternack & Hausse, 2018). Moreover, Latzel et al., (2012) have established a positive 578 579 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 580 581 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 582 583 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 584 585 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 ethylene-586 587 inducible genes as the immune responsive gene PDF1 (Solano et al., 1998; Fujimoto et al., 2000; Heyman et al., 2018). 588

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).

## 595 DDM1-dependent DNA methylation in poplar shoot apical meristem is context 596 dependent and affects both genes and TE activity

#### 597 **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 603 CHG was drastically reduced compared to CpG or CHH contexts, suggesting that in 604 605 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 606 contrasts with Arabidopsis and tomato, where the disruption of DDM1 led to a drastic 607 hypomethylation of the genome, mainly in CpG and CHG contexts (Vongs et al., 1993; 608 609 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 610 611 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 612 CHG, hypermethylation of intergenic regions and genes, and that CHH hypermethylation 613 of TEs only occurred in stressed conditions. The loss of DDM1 has already been 614 615 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 616 regions in tomato and maize (Lippman et al., 2004; Mathieu et al., 2006; Saze & 617 Kakutani, 2007; Zemach et al., 2013; Tan et al., 2016; Corem et al., 2018; Long et al., 618 2019). CHH hypermethylation has also been reported for heterochromatic TEs in rice 619 and tomato (Tan et al., 2016; Corem et al., 2018). Here, we found that extensive CpG 620 621 hypermethylation, notably in genes, was not associated with differential expression level, 622 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 623 proposed that these hypermethylation events are likely to be mediated by different, 624 625 potentially overlapping mechanisms that act as an internal balancing mechanism to 626 compensate for the extensive loss of methylation in other contexts (Zemach et al., 2013; 627 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 stressdependent, and occurs in the shoot apical meristem with possible implications for mitoticand meiotic transmission.

#### 634 **DDM1** impairment of gene methylation has limited effects on gene expression

635 DDM1 decrease in poplar affected the methylation of 879 and 910 genes in WW and 636 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 637 et al., 2012; Lafon-Placette et al., 2013). Despite a strong reduction in genome-wide 638 639 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 640 641 (>90%), whereas in the CpG context an equal number of genes were hypo- or hypermethylated. 642

643 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 60 644 645 downregulated genes. Previous data on Arabidopsis and tomato *ddm1* mutants were of 646 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). 647 Among DEGs, only seven strictly overlapped with DMRs (up to 39% for genes at ~ +/-10 648 kb of DMRs); in agreement with tomato *ddm1* mutants (Corem et al., 2018). This 649 suggests that not all of these DEGs are primary targets of DDM1. A significant negative 650 rank correlation was detected, however, between gene expression and methylation for 651 the 53 DEGs located at less than +/-10 kb of DMRs. Although changes in 5' DNA 652 methylation may influence gene expression (Seymour & Becker, 2017), the role of gene-653 body methylation still remains disputed (Bewick & Schmitz, 2017), and to date it has 654 been difficult to differentiate between direct changes mediated by DNA methylation and 655 secondary effects (Meyer, 2015). In most available studies, no correlation could be 656 657 detected between DNA methylation and expression changes at the genomic level. 658 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 659 stress (Karan et al., 2012; Garg et al., 2015; Chwialkowska et al., 2016, Lafon-Placette 660 661 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).

## 664 **DDM1-dependent DNA methylation favors TEs reactivation and insertion during** 665 **stress**

The role of DNA methylation and DDM1 on TE proliferation is well-established in plants 666 (Miura et al., 2001; Mirouze et al., 2009; Tsukahara et al., 2009). TE proliferation has 667 also been investigated in DDM1-epiRILs in Arabidopsis and tomato (Reinders et al., 668 2009; Johannes et al., 2009; Corem et al., 2018; Quadrana et al., 2019). Here, we 669 reported TE activity in the SAM of WT and RNAi-ddm1 lines using the mobilome-seq 670 workflow (Lanciano et al., 2017). TEs, which represent ~42 % of the genome of poplar 671 (Kejnovski et al., 2012), were evaluated both under control and post water deficit 672 conditions. The pattern of TE methylation varied widely between the different contexts. 673 While most TEs were hypomethylated in CG and CHG contexts, we could not detect any 674 675 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 676 DMR identification, which considered only DMRs with at least 10% of difference and 10X 677 678 of coverage. This is very stringent since CHH methylation level in poplar is very low 679 compared to CG and CHH contexts (~3,25%; Feng et al., 2010). This result also 680 supports a redundant function of CG and non-CG methylation in the transcriptional 681 silencing of the TEs (Ikeda & Nishimura, 2015). The burst of TEs in *ddm1* lines were 682 recorded for the two different classes (DNA transposons and retrotransposons), with a 683 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 684 685 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 686 687 by DDM1 during the stress. Gypsy elements are long terminal repeat (LTR)-flanked retrotransposons that are concentrated in pericentromeric heterochromatin, 688 in comparison to other repeats that are more dispersed e.g.m (Copia, LINE, SINE). Wang 689 et al., (2018) recently reported a constant conflict between Gypsy retrotransposons and 690 691 CHH methylation within a stress-adapted mangrove genome, and found differential

accumulation among classes of LTR TEs mainly due to siRNA-mediated CHH 692 methylation preferentially targeting Gypsy elements. This is consistent with our data as 693 we observed extensive CHH methylation of TEs (such as Gypsy elements) during 694 drought in the *ddm1* lines associated with enrichment in non-coding RNA (ncRNA) GO 695 labels. This may suggest that *ddm1* lines tend to methylate TEs in CHH contexts in 696 order to repress their activity. Wang et al., (2018) subsequently proposed that the 697 698 apparent conflict between TEs activity and repression of integration may enable the maintenance of genetic diversity and thus evolutionary potential during stress 699 700 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., 701 702 (2019) recently proposed that TEs are potent and episodic (epi)mutagens that increase 703 the potential for rapid adaptation. They proposed that this is in large part due to 704 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 705 706 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. 707

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

Our study focused on meristems, previously described as "organs with specific 711 712 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 713 the loci of mitotic and meiotic transmission. Here, we report the detailed characterization 714 from physiological to omics levels of two independent *ddm1* poplar RNAi lines. Both 715 lines exhibited higher tolerance to drought, mottled leaves, and modification of hormonal 716 balance. Our study shows that DDM1-dependent DNA methylation in the shoot apical 717 718 meristem of poplar trees plays two roles: controlling developmental plasticity and 719 enabling stress response through a direct interplay with hormonal pathways (Maury et 720 al., 2019). DDM1-dependent DNA methylation also controls the activation, and probably 721 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 729 730 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 731 adaptation. Further studies are needed to examine the role of stress-induced epigenetic 732 variation and associated mutation that examine a far greater range of stresses, species, 733 and genotypes. This will enable its importance relative to more traditional sources of 734 adaptive and evolutionary variation to be interpreted. Such studies are of particular 735 interest for long-lived organisms in the age of rapid, anthropogenic climate change. 736

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#### 738 METHODS

#### 739 Plant material, experimental design, and control of water deficit

740 Experiments were conducted on two PtDDM1 RNAi lines (ddm1-15 and ddm1-23), and a wild type (WT) line of Populus tremula × Populus alba (clone INRA 717-1B4). These 741 742 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 743 compared to WT, respectively) and *PtDDM1* residual expression (ca. 62% reduction). 744 Six week-old in vitro propagated plantlets were first transferred into small sealed 745 746 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 747 with Osmocote PG Mix (1 kg/m<sup>3</sup> of N-P-K 80/35/60). The experiment was conducted in a 748 greenhouse located at the research station of INRAE Orléans Centre Val-de-Loire 749 750 (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  $t_0$  and lasted three weeks until  $t_1$ . Watering was 756 757 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<sub>i</sub>) were 758 759 converted to soil relative extractable water (REW<sub>i</sub>, %) using the following equation:  $REW_i = (SWC_i - SWC_{wp}) / (SWC_{fc} - SWC_{wp}) \times 100$  where  $SWC_{fc}$  and  $SWC_{wp}$ 760 761 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-762 RW treatment were re-watered to a target value of approx. 40% of REW. At t<sub>1</sub>, plants 763 from the WD-RW treatment were re-watered to field capacity, three blocks were 764 sampled, and the remaining six blocks were maintained watered for one week until t<sub>2</sub>, 765 after which all remaining plants were sampled. The water deficit intensity was evaluated 766 767 at t<sub>1</sub> by measuring the predawn leaf water potential ( $\Psi_{pd}$ , MPa) during the night preceding the re-watering. Measurements were performed on a subset of five randomly 768 769 selected blocks using a pressure chamber (PMS instruments, Albany, OR, USA). 770 Minimum leaf water potential ( $\Psi_{min}$ ) was estimated for the same plants at midday on the 771 day preceding re-watering.

#### 772 Physiological and phenotypic characterization

#### 773 Growth and leaf symptoms

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). Thesemeasurements were performed on three randomly selected blocks.

## <sup>781</sup> Leaf gas exchange, bulk leaf carbon isotope composition ( $\delta^{13}$ C), and stomatal <sup>782</sup> density

783 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). 784 Measurements were systematically performed on fully mature leaves in the top third of 785 786 the plant in the same five blocks as those used for  $\Psi_{pd}$  and  $\Psi_{min}$ . From the time of drought initiation onwards, net CO<sub>2</sub> assimilation rate (A<sub>net</sub>, µmol m<sup>-2</sup> s<sup>-1</sup>), and stomatal 787 conductance to water vapor ( $q_s$ , mol m<sup>-2</sup> s<sup>-1</sup>) were measured every day between 9 am 788 and 3 pm in order to characterize the dynamic response of the genotypes to water 789 deficit. Measurements were performed at a saturating photosynthetic photon flux density 790 (PPFD) of 2000 µmol m<sup>-2</sup> s<sup>-1</sup>, an ambient CO<sub>2</sub> concentration of 400 ppm, a constant 791 block temperature of 25°C, and a reference vapor pressure deficit (VPD) maintained 792 close to 1kPa. 793

Bulk leaf carbon isotope composition ( $\delta^{13}$ C) was used as a time-integrated surrogate 794 of leaf intrinsic water-use efficiency (Farguhar et al., 1982). Six calibrated discs (3.14 795 796  $cm^2$ ) of leaf lamina were punched from a mature leaf at  $t_2$  on all plants. Leaf disks were oven-dried at 60°C for 48hrs before being ground to a fine powder. One milligram 797 subsamples were then enclosed in tin capsules and combusted at 1200°C. The CO2 798 produced by combustion was purified, and its  ${}^{13}CO_2/{}^{12}CO_2$  ratio was analyzed using 799 800 isotope ratio mass spectrometry (IRMS, Finnigan MAT Delta S, Bremen, Germany). The  $\delta^{13}$ C (‰) was expressed relative to the Vienna Pee Dee Belemnite standard and 801 calculated as  $\delta^{13}C = (R_{sa}-R_{sd})/R_{sd} \times 1000$  where  $R_{sa}$  and  $R_{sd}$  are the  ${}^{13}CO_2/{}^{12}CO_2$  ratios 802 of the sample and the standard, respectively (Farguhar et al., 1989). The accuracy of the 803  $\delta^{13}$ C measurements done by IRMS during the time samples was assessed using 804 referenced standards of ± 0.05 ‰ (SE). All measurements were performed at the 805 INRAE-Nancy technical platform of functional ecology in France. 806

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.

#### 813 Xylem structure, function and biochemical composition

814 Xylem vulnerability to drought-induced cavitation was assessed at t<sub>2</sub> on the well-watered plants of all blocks (INRAE Phenobois Platform, Clermont-Ferrand, France). 815 816 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 817 technique which is well suited to poplars (Cochard et al., 2005, Fichot et al., 2015). In 818 short, the technique uses the centrifugal force to increase xylem tension ( $\Psi_x$ , MPa) in 819 stem segments, while at the same time measuring the percent loss of hydraulic 820 conductance (PLC, %). The dependence of PLC upon  $\Psi_x$  was used to generate 821 vulnerability curves for each stem segment. The following sigmoid function was fitted to 822 data (Cochard et al., 2007): PLC =  $100 / (1 + \exp((s/25) \times (P-P_{50})))$ , where P<sub>50</sub> is the xylem 823 824 tension causing 50% loss of hydraulic conductance (MPa) and s is the slope of the curve at the inflexion point (%. MPa<sup>-1</sup>). Values of  $P_{50}$  were used as proxies for vulnerability to 825 826 xylem drought-induced cavitation.

Xylem histology was performed on stem segments of all plants at t<sub>2</sub>. Stem cross-827 sections 30 µm-thick were obtained using a hand microtome (RM 2155, Leica 828 Microsystems, Vienna, Austria), and stained with safranin (1% in 50% ethanol), and 829 followed by Astra blue (1% in 100% ethanol), before being permanently mounted in 830 Canada Balsam. Stained sections were examined under a light microscope coupled to a 831 Moticam 580 5.0MP digital camera. Pictures covering pith to cambium were taken at a 832 833 10x magnification on three opposite radial sectors in order to estimate vessel diameter  $(\mu m)$ , vessel density  $(mm^{-2})$ , vessel lumen fraction (%), and theoretical xylem specific 834 hydraulic conductivity (Fichot et al., 2010). Image analyses were all performed using the 835 836 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<sup>-3</sup>) 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 842 843 plants by using Fourier-Transform mid-Infrared Spectroscopy (FTIR, Spectrum 400, Perkin Elmer, Massachusetts, USA), and home-made calibration models previously 844 845 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 846 were placed three times on the attenuated total reflectance (ATR) diamond for the scan. 847 Spectra ranged from 650 to 4000 cm<sup>-1</sup> wave numbers with a step of 2 cm<sup>-1</sup>. Spectrum 848 analyses were realized using the R software (R Core Team, 2015). Spectra were first 849 cut and smoothed by using the 'prospectr' package before applying normalization and 850 851 first derivative processing (Bertrand & Dufour, 2006).

#### 852 **Phytohormone quantification**

853 Shoot apices were immediately frozen in liquid nitrogen upon sampling, and later ground 854 to a fine powder in an automatic ball mill (MM 200 Retsch, Germany). Phytohormone 855 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 856 published procedure (OVCM platform, IJPB, INRAE Versailles, France; Li-Marchetti et 857 al., 2015; Trapet et al., 2016). For each sample, 10 mg of dry powder was extracted with 858 0.8 mL of acetone/water/acetic acid (80/19/1 v:v:v). Phytohormone stable labelled 859 isotopes used as internal standards were prepared as described in Roux et al., (2014). 860 Two ng of each and 0,5 ng of cytokinines standard was added to the sample. The 861 extract was vigorously shaken for 1 min, sonicated for 1 min at 25 Hz, shaken for 10 862 minutes at 10°C in a Thermomixer (Eppendorf®), and then centrifuged (8000 g, 10 °C, 863 864 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 (1 865 866 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 867 (50/50 v/v), filtered, and analyzed using a Waters Acquity ultra performance liquid 868 chromatograph coupled to a Waters Xevo Triple quadrupole mass spectrometer TQS 869 (UPLC-ESI-MS/MS). The compounds were separated on a reverse-phase column 870 (Uptisphere C18 UP3HDO, 100\*2.1 mm\*3µm particle size; Interchim, France) using a 871 flow rate of 0.4 ml min<sup>-1</sup>, and a binary gradient: (A) acetic acid 0.1% in water (v/v) and 872 873 (B) acetonitrile with 0.1% acetic acid, and a column temperature of 40°C. Mass spectrometry was conducted using electrospray, and Multiple Reaction Monitoring 874 scanning mode (MRM mode), in either positive ion mode (for the indole-3-acetic acid 875 876 and cytokinins) or negative ion mode (for the other hormones). Relevant instrumental 877 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 878 assist the cone and desolvation (150 L.h<sup>-1</sup> and 800 L.h<sup>-1</sup>, respectively), argon was used 879 as the collision gas at a flow of 0.18 ml.min<sup>-1</sup>. 880

#### 881 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 885 enzymatically hydrolyzed into nucleosides, and analyzed by high-performance liquid 886 chromatography (HPLC), as described by Zhu et al., (2013). Controls for this procedure 887 included co-migration with commercial standards (Sigma-Aldrich), confirmation by 888 enzyme restriction analysis, and tests for RNA contamination based on the HPLC 889 detection of ribonucleosides. Global DNA methyl cytosine percentages (% mC) were 890 estimated as follows:  $\mbox{mC} = (\mbox{mC}/(\mbox{C} + \mbox{mC})) \times 100$ , where 'C' is 2'-déoxycytidine 891 content, and 'mC' is 5-methyl-2'-déoxycytidine content. For each line in each treatment, 892 three biological replicates were randomly chosen out of the six for analyses, with two 893 894 independent genomic DNA extractions per replicate, three hydrolysis replicates and two HPLC runs. 895

## 896 Whole Genome Bisulfite Sequencing (WGBS) and bioinformatic pipeline for 897 methylome characterization

898 An equimolar pool of 2 µg DNA at approximately 100 ng/µl, and extracted from four 899 SAMs was made for each line in each treatment. Whole-genome bisulfite sequencing 900 was performed by the CNRGH laboratory (J. Tost, Evry, France) in accordance with the published procedure (http://www.nugen.com/products/ovation-ultralow-methyl-seg-901 902 library-systems) adapted from Daviaud et al., (2018). The workflow of the library preparation protocol follows the classical library preparation protocol in which methylated 903 adaptors are ligated to the fragmented DNA prior to bisulfite conversion. A total of 200 904 ng of genomic DNA was fragmented to a size of approximately 200 base pairs (bp), and 905 906 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 907 qPCR assay was used to determine the optimal number of PCR amplification cycles 908 (between 10 and 15 cycles) required to obtain a high diversity library with minimal 909 duplicated reads prior to final library amplification. The sequencing was performed with 910 paired ends (2×150bp) on an Illumina HiSeq4000 platform. Raw data were stored in 911 FASTQ files with a minimal theoretical coverage of 30X (SRA record is under the 912 reference PRJNA611484; https://www.ncbi.nlm.nih.gov/sra/PRJNA611484). 913

The bioinformatics pipeline used in this study is adapted from the ENCODE pipeline 914 915 (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 916 917 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 918 919 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-717-920 genome), by using BISMARK (version 0.16.3, Krueger & Andrews, 2011) and bowtie 2 921 tools (version 2.1.0; Langmead et al., 2009) or a bisulfite sequence mapping program 922 (BSMAP version 2.74) (Xi & Li, 2009). The parameters were modified for 'paired-end' 923 924 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 925

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 933 934 tremula x alba genome from the aspendb database. Gene Ontology (GO) term 935 enrichment was assessed for the methylated genes with Revigo (http://revigo.irb.hr/http://revigo.irb.hr/) software, using default parameters. 'TreeMap' 936 view was performed with rectangle size adjusted to reflect the absolute log10 P-value of 937 the GO term, through use of the corresponding poplar model genes from the best v3.0 938 939 blast hits with Arabidopsis TAIR10 annotations.

#### 940 Transcriptomics and bioinformatic pipeline

941 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). Ddm1-23 942 was chosen as the most representative of the two lines as it exhibited a lower decrease 943 in methylation compared to ddm15-7, but nonetheless most of its DMRs were in 944 common among the two lines. In brief, SAMs were ground into fine powder in liquid 945 nitrogen and total RNAs were extracted using a CTAB buffer (Changet al., 1993). RNA 946 947 was precipitated using lithium chloride (10M) and purified using the Macherey Nagel Nucleospin RNA kit (740955). Sequencing was done using the Illumina NexSeq500 948 (IPS2 POPS platform, Saclay, France). RNA-seq libraries were performed by following 949 950 the TruSeq Stranded mRNA SamplePrep Guide 15031047 D protocol (Illumina®, 951 California, USA). The RNA-seq samples have been sequenced in paired-end (PE) with a 952 sizing of 260 bp and a read length of 75 bases. 6 samples by lane of NextSeq500 using 953 individual bar-coded adapters and giving approximately 15 millions of PE reads by 954 sample are generated. To facilitate comparisons, each sample followed the same steps from trimming to counts. RNA-Seg preprocessing included trimming library adapters and 955

performing quality controls. The raw data (fastq) were trimmed with the Trimmomatic 956 (Bolger et al., 2014) tool for Phred Quality Score Qscore >20, read length >30 bases, 957 958 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 959 reads against the Populus tremula x alba hybrid genome (genotype INRA 717-1B4), 960 with the options outSAMprimaryFlag AllBestScore--outFilterMultimapScoreRange 0, to 961 962 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 963 964 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 965 966 with multi-hits were removed.

967 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 968 one half of the samples, were discarded. Library size was normalized using the trimmed 969 mean of M-value (TMM) method, and count distribution was modeled with a negative 970 971 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 972 Development Core Team (2005)). Expression differences compared two samples using 973 the likelihood ratio test, and p-values were adjusted by the Benjamini-Hochberg 974 975 procedure to control False Discovery Rate (FDR). A gene was declared differentially expressed if its adjusted p-value was lower than to 0.05. 976

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

#### 982 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

986 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. 987 988 eccDNAs were isolated and libraries were prepared and sequenced following Lanciano et al., (2017). Bioinformatics was carried out on the Populus tremula x alba genome 989 (SPta717 v1.1) by using the same pipelines as described in Lanciano et al., (2017). In 990 order to obtain TE database for Populus tremula x alba genome, we used the TE 991 992 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 993 994 i) mapped against the *P. tremula x alba* reference genome using Bowtie2, ii) mapped for 995 split reads (SR) using segement software (Hoffmann et al., 2014) and iii) de novo 996 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 997 998 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 999 "TE<sup>+</sup>") and comprised TEs with a DOC ranging from 200-1999X. The third group was 1000 named "very active TEs" ("TE<sup>++</sup>") and comprised TEs with a DOC ranging from 2000 to 1001 9999X. The fourth group was named "highly active group" ("TE<sup>+++</sup>"), and comprised TEs 1002 with a DOC ranging from 10000 to 51000X. Raw and processed data are available with 1003 1004 the GEO accession number GSE147934 (https://www.ncbi.nlm.nih.gov/geo/query/acc.cgi?acc=GSE147934). 1005

Copy number variation of TEs was assessed for all studied lines in both 1006 treatments by qPCR using genomic DNA extracted from SAMs. In summary, primers of 1007 TEs were first designed using corresponding FASTA sequences with Eprimer3 and 1008 Netprimer for quality control checking (http://www.bioinformatics.nl/cgi-1009 bin/emboss/eprimer3, http://www.premierbiosoft.com/NetPrimer). Primers that passed 1010 quality control (Gypsy: F=AAC-AAG-CTG-AAG-CCC-AAG-AA, R=TCG-ACC-TCG-AGT-1011 TAG-GTT-CC; DNA-3-3: F=TAG-TGT-GCA-GTG-GAG-CAT-GG, R=AAA-AGC-AGG-1012 GTG-TTT-TGC-TG; SAT-1: F=TCA-CCG-GAA-CCC-ACT-TCT-AC, R=GCA-ACG-ACT-1013 GAG-TTT-CGT-CA) were used with 10 ng/µl of genomic DNA for gPCR analyses 1014 (Platinum<sup>™</sup> SYBR<sup>™</sup> Green gPCR SuperMix-UDG, Invitrogen<sup>™</sup> kit). A standard cycling 1015 program was applied (50 °C for 2 min, 95 °C for 2 min, and 40 cycles of 95 °C for 15 sec 1016

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).

## 1020 Statistical analyses

Statistical analyses were performed with R statistical software under R Studio integrated 1021 development environment (R Core Team, 2015, RStudio: Integrated Development for R. 1022 RStudio, Inc., Boston, MA URL http://www.rstudio.com/). Means are expressed with their 1023 standard errors (SE). Differences between lines and treatments for phenotypic traits 1024 were evaluated by analysis of variance (ANOVA) on individual values adjusted for block 1025 effects. Tukey's post-hoc test was used to identify differences between groups when 1026 ANOVAs indicated significant effects. Statistical tests were considered significant at P < P1027 0.05. 1028

## 1029 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; 1032 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 1033 1034 A.L.L.G and M.D.S. HPLC analysis was done by A.D and S.M. RNA-seg 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 1038 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 1040 manuscript. All authors approved the final version of the manuscript.

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## 1694 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 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 1705 for WD-RW. Values are genotypic means  $\pm$  SE. A. Time course of stem height and diameter (n = 6 per 1706 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<sub>2</sub> assimilation rate,  $g_s$ , stomatal 1709 conductance to water vapour, WUE<sub>i</sub>, intrinsic water-use efficiency computed as A<sub>net</sub>/g<sub>s</sub>). Values presented 1710 are those of WD-RW plants relative to WW controls (n = 5 per line per treatment). Treatment effects were 1711 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.

**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 ± 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).

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 RNAi lines (ddm1 15 & ddm1 23) vs. the WT lines in all contexts (CG, CHG & CHH) and in WW and WD-1722 1723 RW conditions. Black bars for hypomethylated DMRs and grev 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 1724 context of methylation. Only DMRs with at least a 25 % difference were kept except for CHH where a 1725 1726 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

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1729 expressed genes (genes with an adjusted p-value by FDR, false discovery rate < 0.05 = 136 DEGs 1730 identified) between ddm1-23 and the WT line. GO labels were retrieved from popgenie and treemap 1731 realized with REVIGO. B. Annotation of DEGs with expression variation values (log2FoldChange) using 1732 GO labels retrieved from popgenie. Blue for downregulated genes and red for upregulated genes. The \* 1733 indicates hormone related genes found in DEGs. The numbers (1), (31), (8), (25), (19), (17), (35) 1734 represent respectively the number of DEGs found in Cell death, Defense & Cell wall, Immune response, 1735 Metabolism, Signalization, Transcription factors and Unknown processes respectively. Log2FoldChange = 1736 log-ratio of normalized mean read counts in RNAi vs. WT lines.

1737 Figure 6: Transposable elements activity among RNAi and WT lines in shoot apical meristem collected 1738 one week after rewatering (t2). A. Depth of coverage (read per million, rpm) of different TE families in the 1739 three different lines and in both WW (white) and WD-RW (black) regimes. TE, TE+, TE++, TE+++ 1740 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 1741 1742 TEs for each context of methylation in WW (white) and WD-RW (black) conditions. C. Copy number 1743 variations of three different TEs (DNA-3-3, Gypsy23 and SAT-1) in the three different lines in both WW 1744 and WD-RW regimes. White cicles for WW and black circles for WD-RW.

1745 **Table 1:** Xylem structural, functional and biochemical traits measured for the wild type and the two RNAi-1746 ddm1 (ddm1-15, ddm1-23) poplar lines in control (well-watered, WW) and stress (moderate water deficit 1747 followed by rewatering, WD-RW) treatments. Values are genotypic means  $\pm$  SE (n = 6 per line per treatment). The P<sub>50</sub> is the xylem tension inducing 50% loss of hydraulic conductance estimated from 1748 1749 vulnerability curves (see Materials and Methods for additional information). S/G corresponds to the ratio 1750 between syringyl-like (S) and guaiacyl-like lignin monomeric units (G). Treatment effects were evaluated 1751 within each line by using a t-test. Different letters indicate significant differences between genotypes within 1752 treatments following Tukey's post hoc test. Levels of significance are \*, 0.01 < P < 0.05; \*\*, 0.001 < P <1753 0.01; \*\*\*, *P* < 0.001; ns, non-significant; na, not available.

## 1754 Supplemental materials:

1755 Supplemental Figure 1: Strategies for methylome bioinformatic analysis A. Impact of different types of 1756 quality controls on the percentage of mapped reads on two distinct genomes: P. trichocarpa and P. 1757 tremula × P. alba. Dots shapes are quality control specific. 1. Circles for quality control with trimming. 2. 1758 Triangular for sample with only trimming control and 3. Squared for sample without any quality control. 1759 Colors are distinct between the two genomes (black for *P. trichocarpa* and white for *P. tremula* × *P.alba*). 1760 On the left, the results for Well-Watered (WW) conditions and on the other side Water Deficit and 1761 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 1762 1763 are for BISMARK and light bars for BSMAP software. On the left, the results for Well-Watered (WW)

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1764 conditions and on the other side Water Deficit and ReWatering (WD-RW). Values are 'QC' means quality 1765 control with trimming and filtering. **C**. Percentages of cytosine considered by BISMARK after quality 1766 control and 10X minimal coverage filtering on the two genomes: *P. trichocarpa* and *P. tremula* × *P. alba*. 1767 Bars are for methylation percentage and dots are for coverage values. Black color is for Well-Watered 1768 (WW) conditions and white for Water Deficit and Re-Watering one (WD-RW). **D**. Percentages of cytosine 1769 considered by BISMARK after quality control and 10X minimal coverage filtering for the three methylation 1770 contexts (CG, CHG and CHH) for *P. tremula* × *P. alba*.

1771 Supplemental Figure 2: Phenotypic and physiological characterization of the wild type and the two RNAi-1772 ddm1 (ddm1-15, ddm1-23) poplar lines in control (well-watered, WW) and stress (moderate water deficit 1773 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 ± SE. A. Predawn and minimum leaf water potential 1774 measured before rewatering (n = 5 per line per treatment). **B**. Bulk leaf carbon isotope composition ( $\delta^{13}$ C) 1775 1776 measured on leaves sampled at the end of the experiment (n = 6 per line in WW, n = 12 per line in WD-1777 RW). C. Total stomatal density measured at the end of the experiment (n = 3 per line per treatment). 1778 Treatment effects were evaluated within each line using a t-test. Levels of significance are \*, 0.01 < P <1779 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</p>
- **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, wellwatered 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

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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.

1806 Supplemental figure 6: Identification of differentially methylated genes. A. Annotation of the common 1807 DMRs between the RNAi and the WT lines in WW and WD-RW regimes. Gene annotation was retrieved 1808 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 1809 against P. tremula x P. reference genome. B. Identification of common differentially methylated genes 1810 1811 (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 1812 1813 DMR, 10 kb = Genes in +/- 10 kb of DMR and 25 kb = Genes that are found in +/- 25 kb of DMR. C. 1814 Genes Ontology (GO) annotation of the common DMRs in WD-RW regimes for all contexts. GO labels 1815 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.

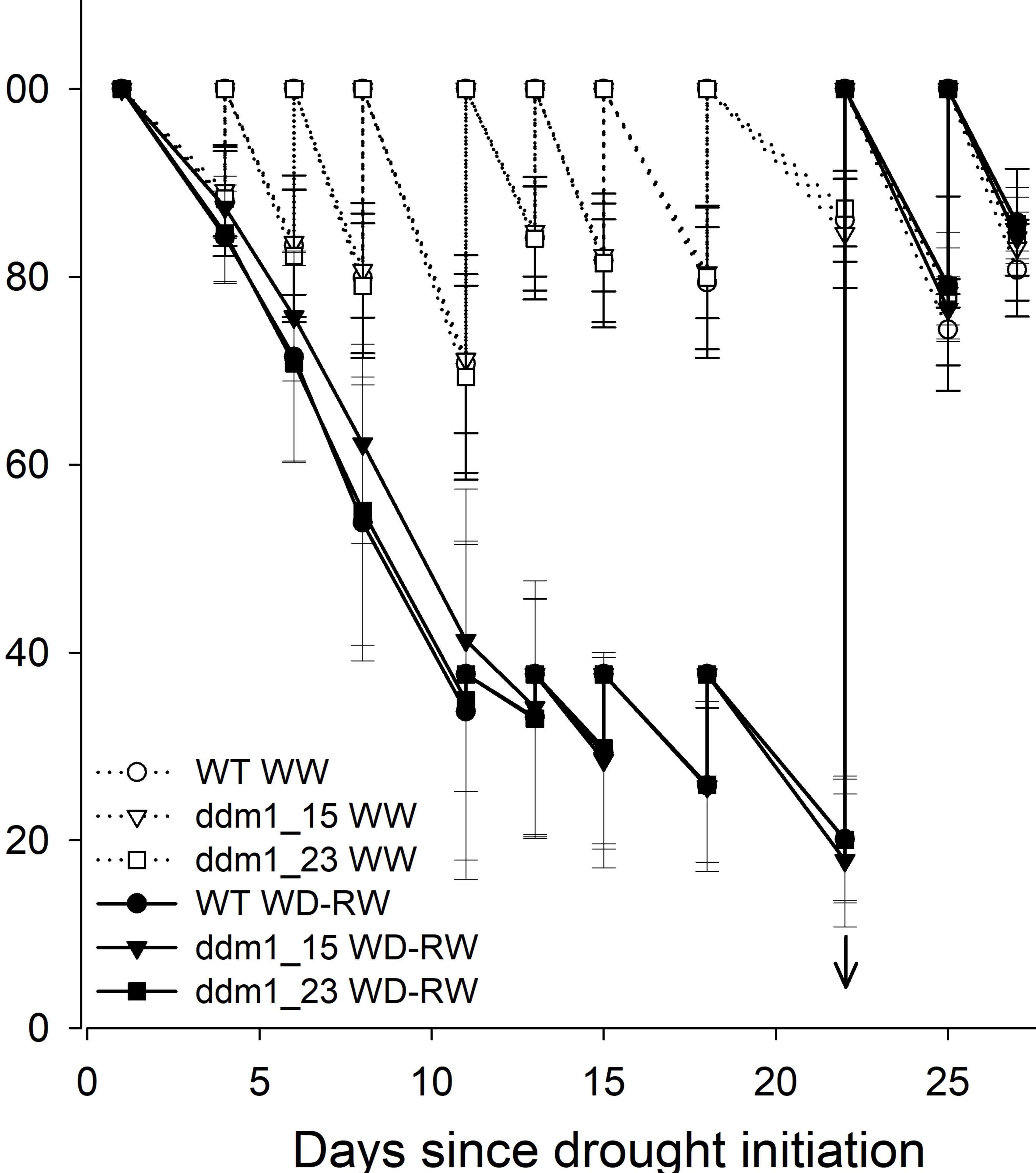
Supplemental Table 1: Mean methylation level in ddm1 and WT lines in both WW and WD-RW
conditions, Values are the average of methylation (in %) for each lines in the three different contexts (CG,
CHG and CHH).

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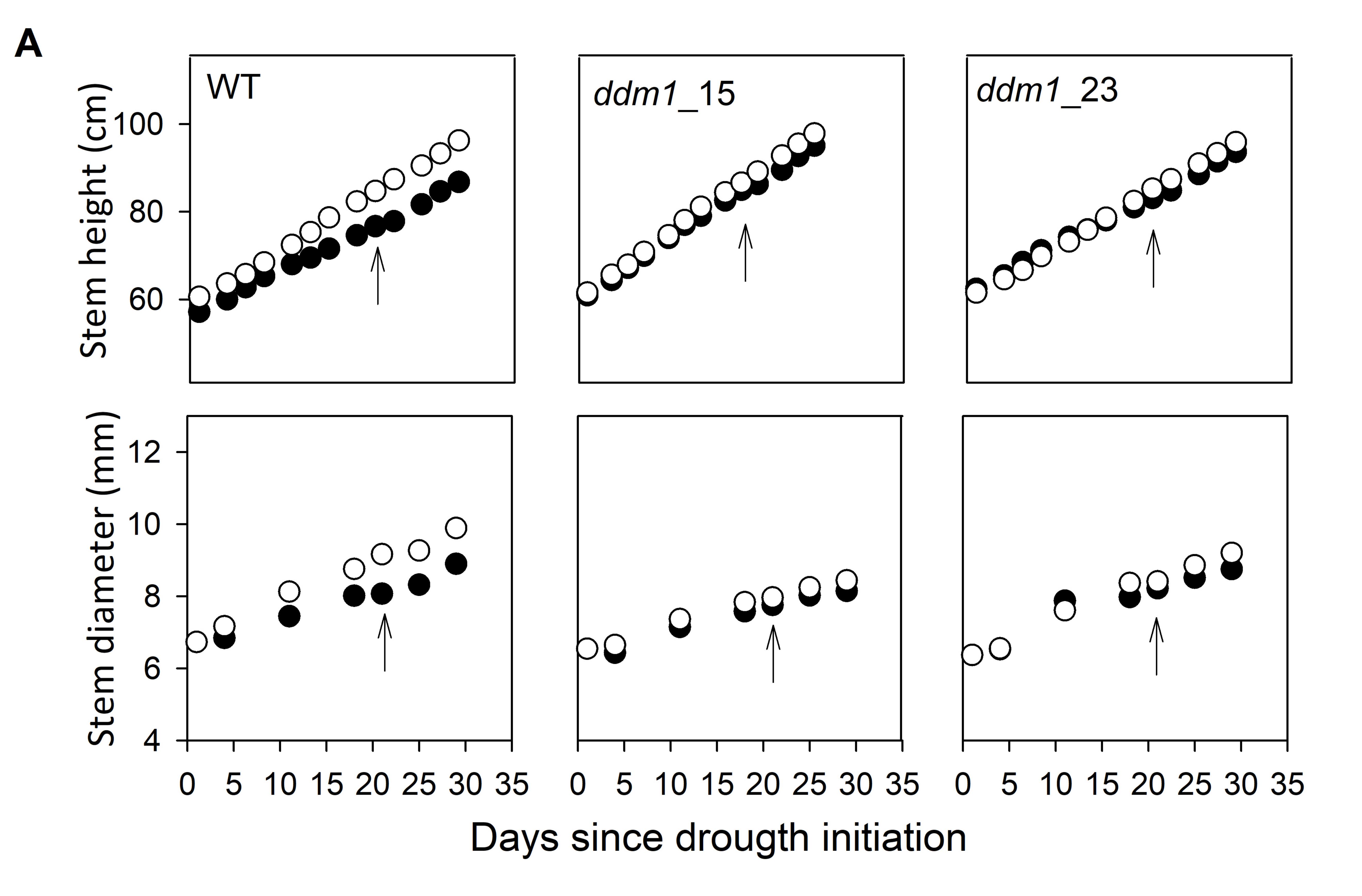
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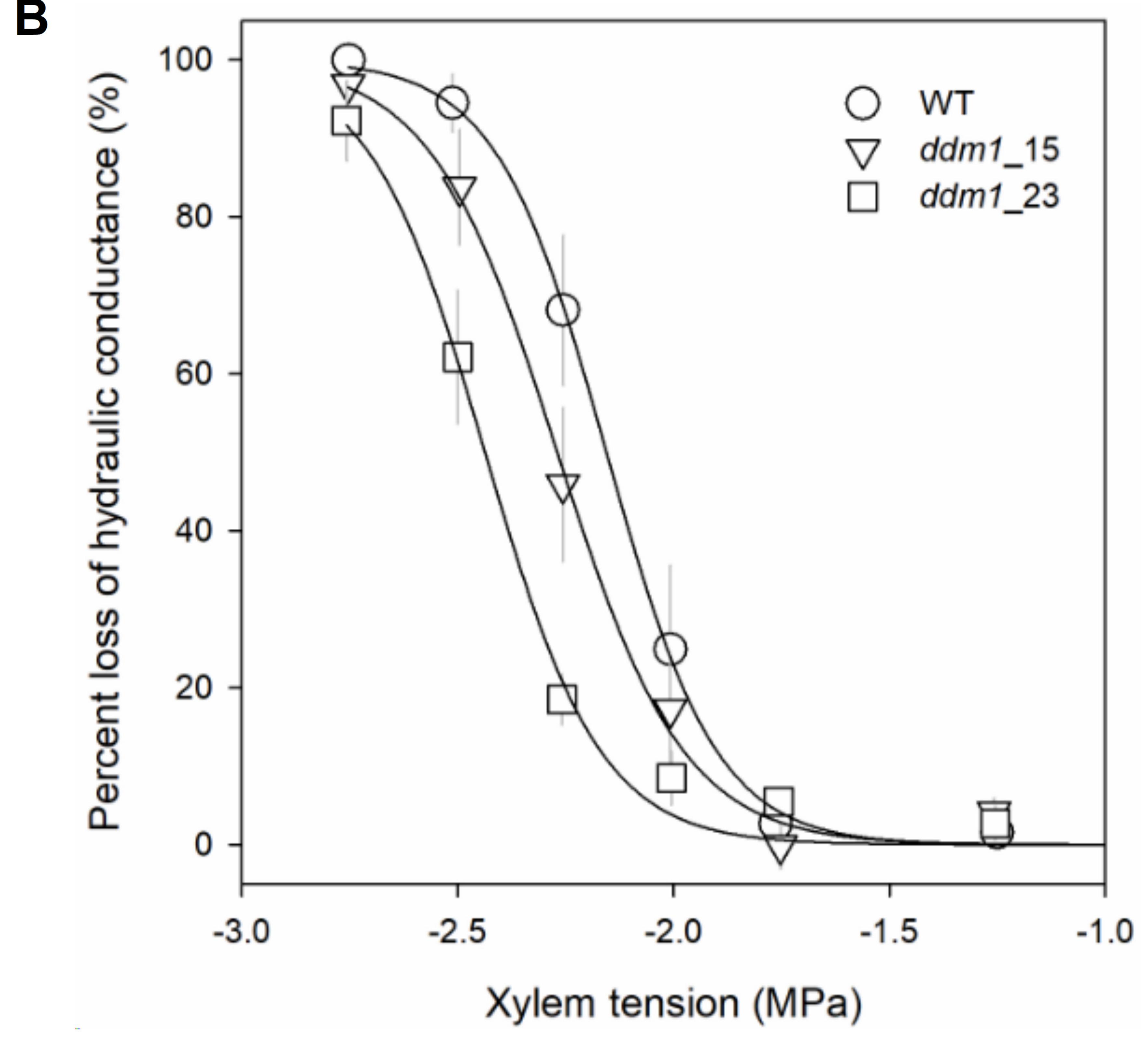
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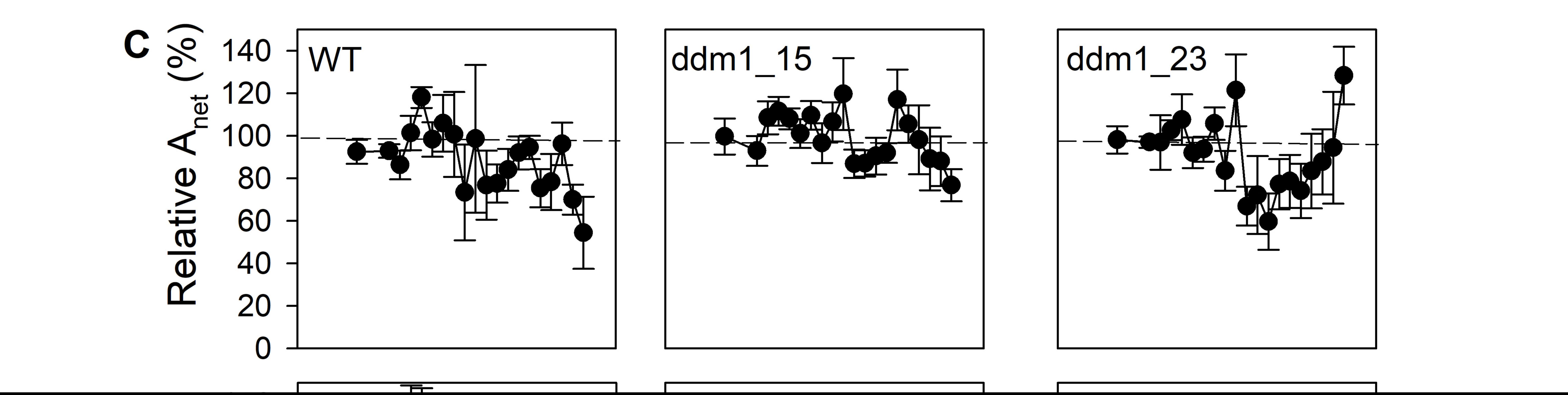
Figure 1: Time course of soil relative extractable water (REW) during the experiment for the wild type and the two RNAiddm1 (ddm1-15, ddm1-23) poplar lines in control (well-watered, WW) and stress (moderate water deficit followed by rewatering, WD-RW) treatments. Open symbols and dashed lines for WW 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).

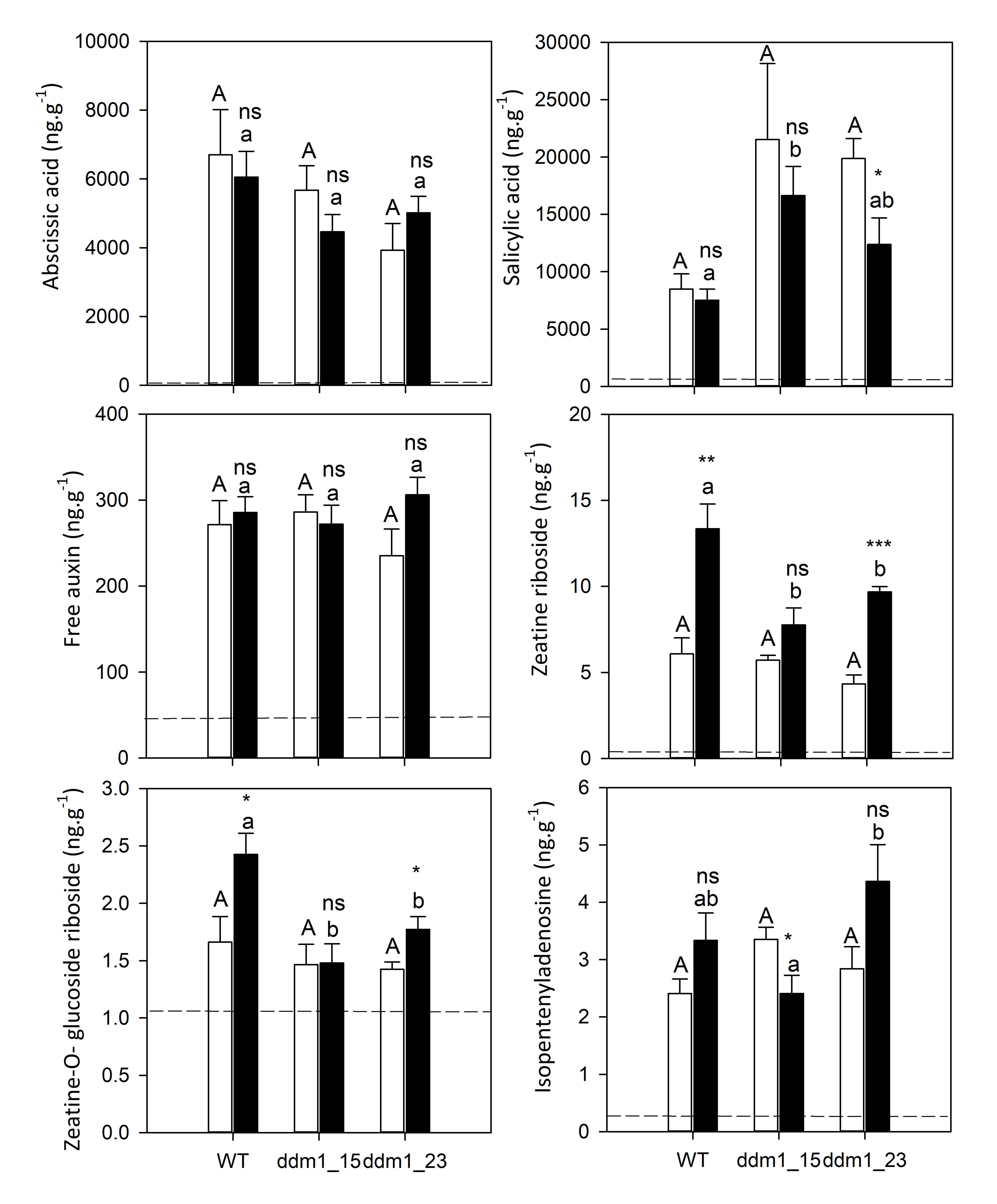




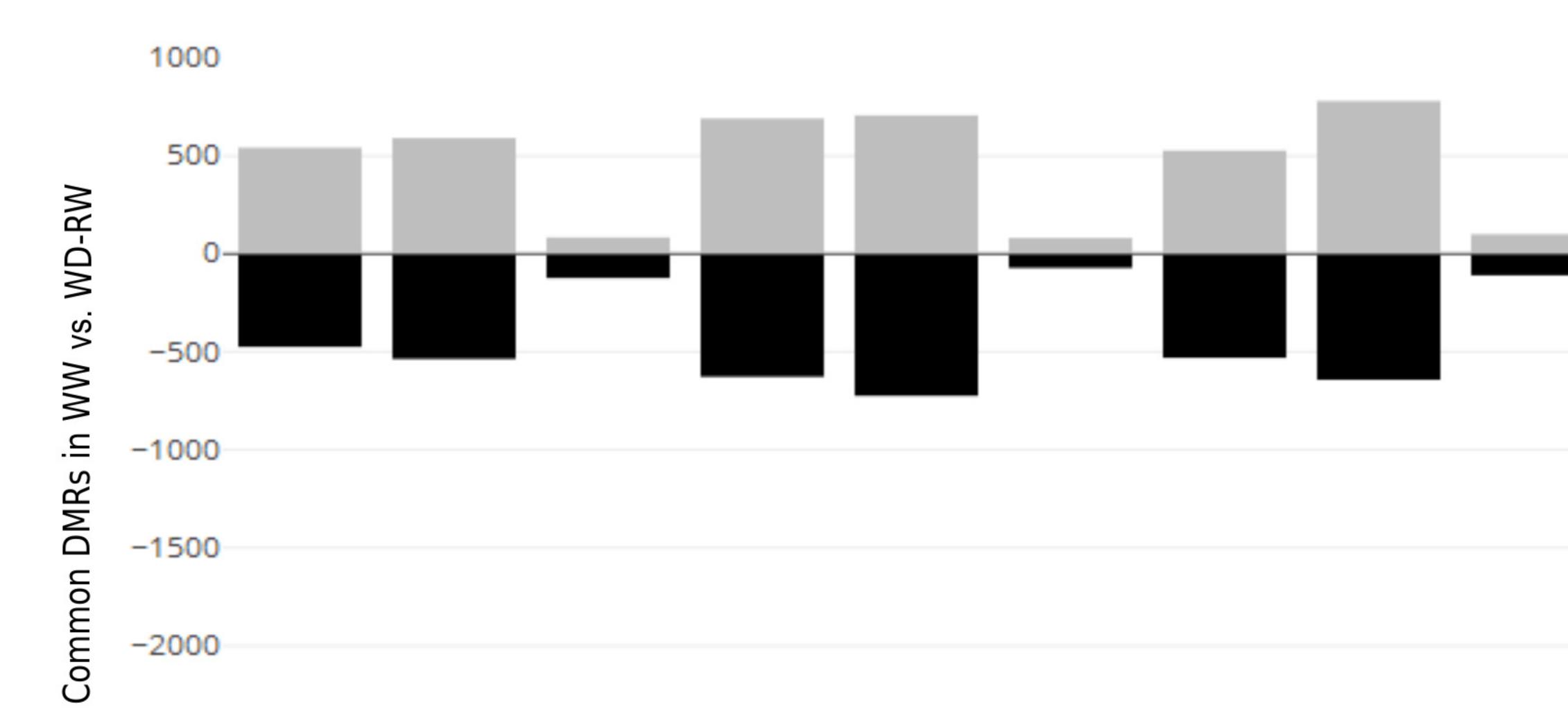


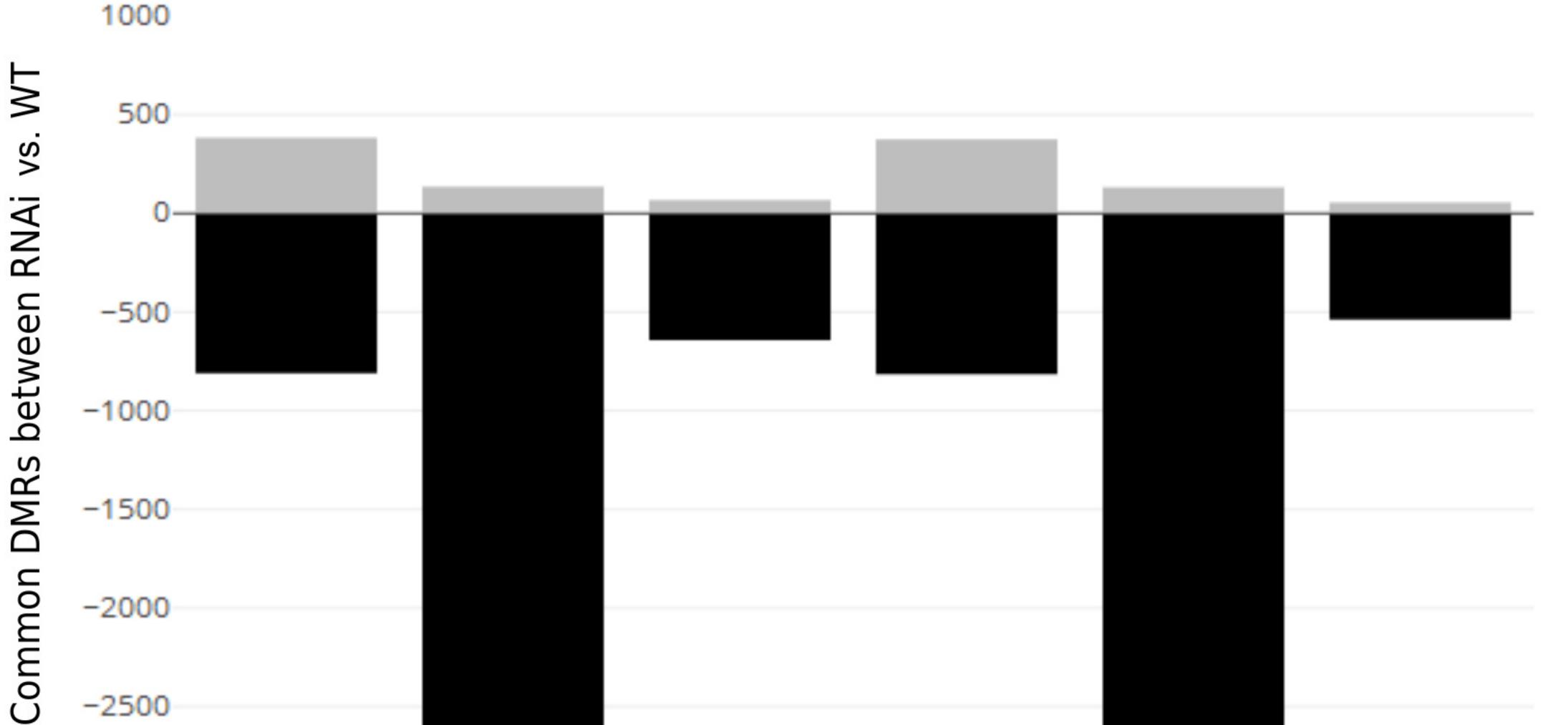






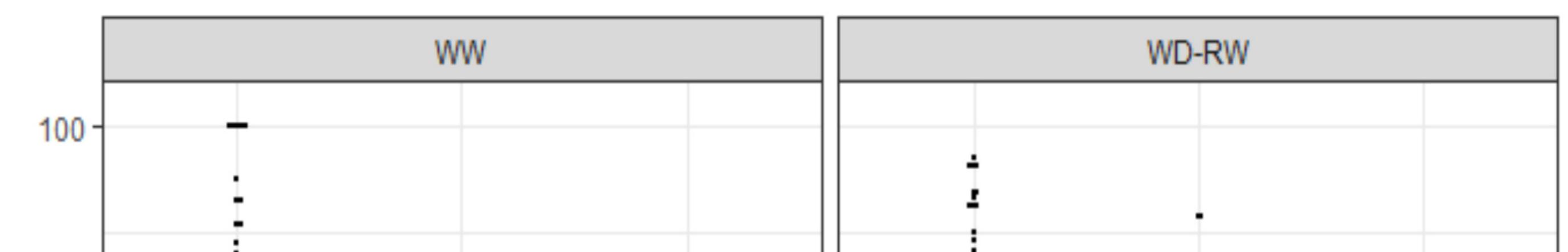
**Figure 3**: Phytohormone contents (cytokinins, abscisic acid, salicylic acid and free auxin) measured in shoot apex just after rewatering ( $t_1$ ). Values are genotypic means ± SE (n = 3 per line in WW and in WD-RW). Treatment effects were evaluated within each line by using t-test. Levels of significance 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).

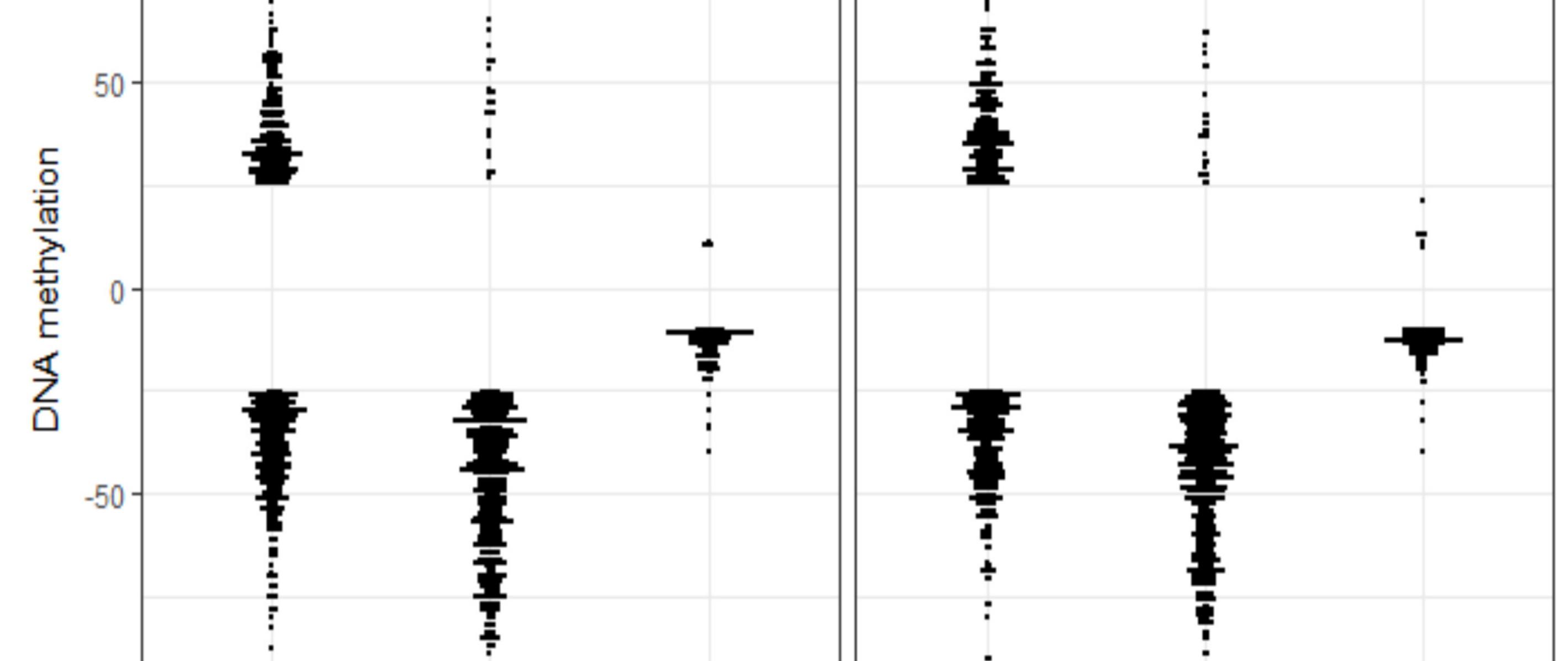






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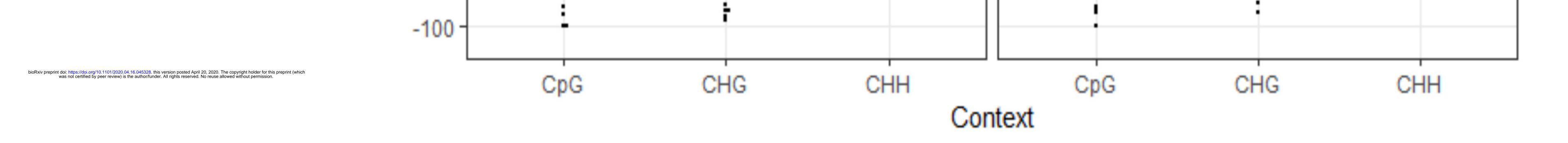
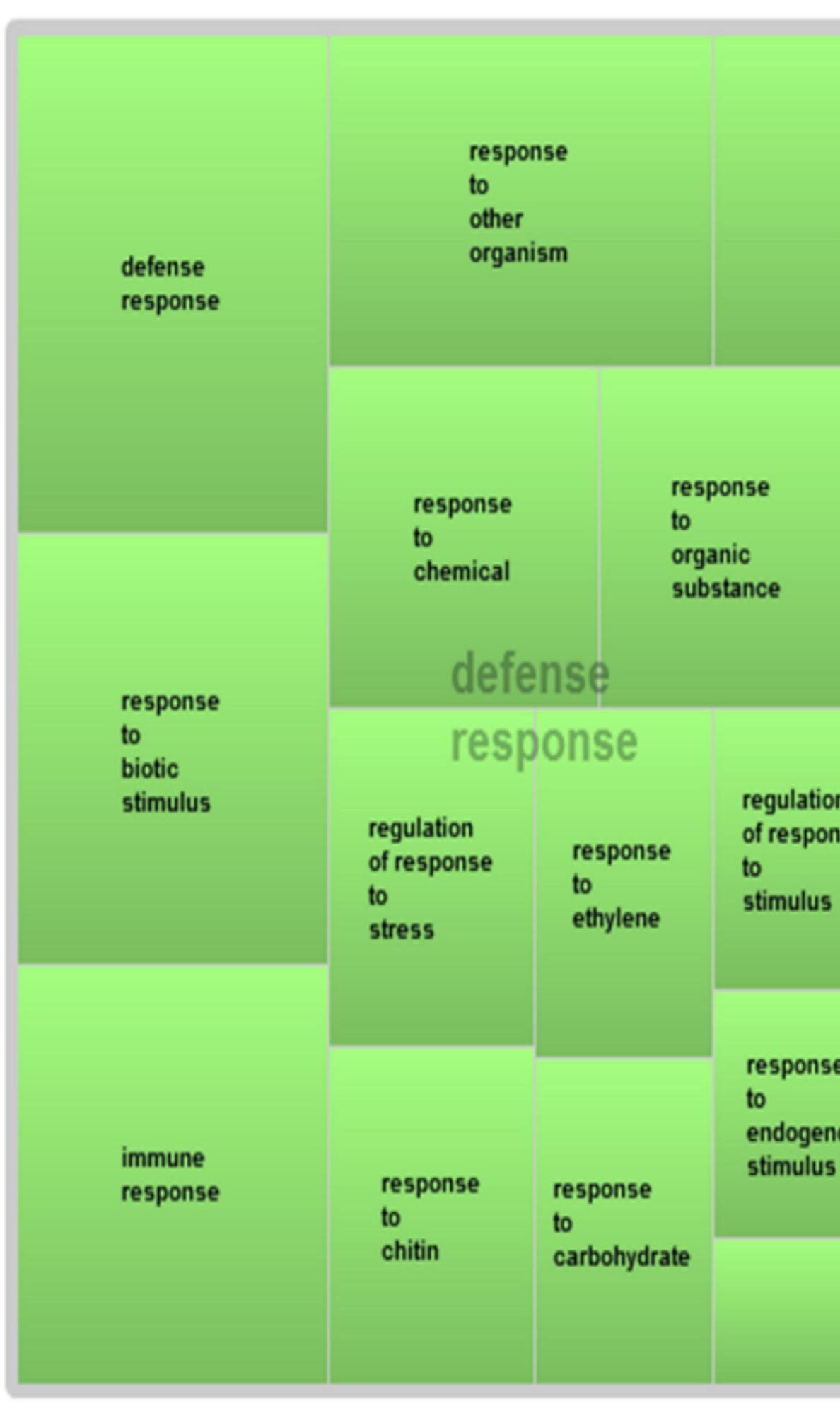


Figure 4: Variations in DNA methylation among RNAi and WT lines in shoot apical meristem one week after rewatering (t2). A. Common DMRs between WW and WD-RW conditions. Black bars for hypomethylated DMRs and grey bars for hypermethylated DMRs. B. Common DMRs between the two RNAi lines (ddm1\_15 & ddm1\_23) vs. the WT lines in all contexts (CG, CHG & CHH) and in WW and WD-RW conditions. Black bars for 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

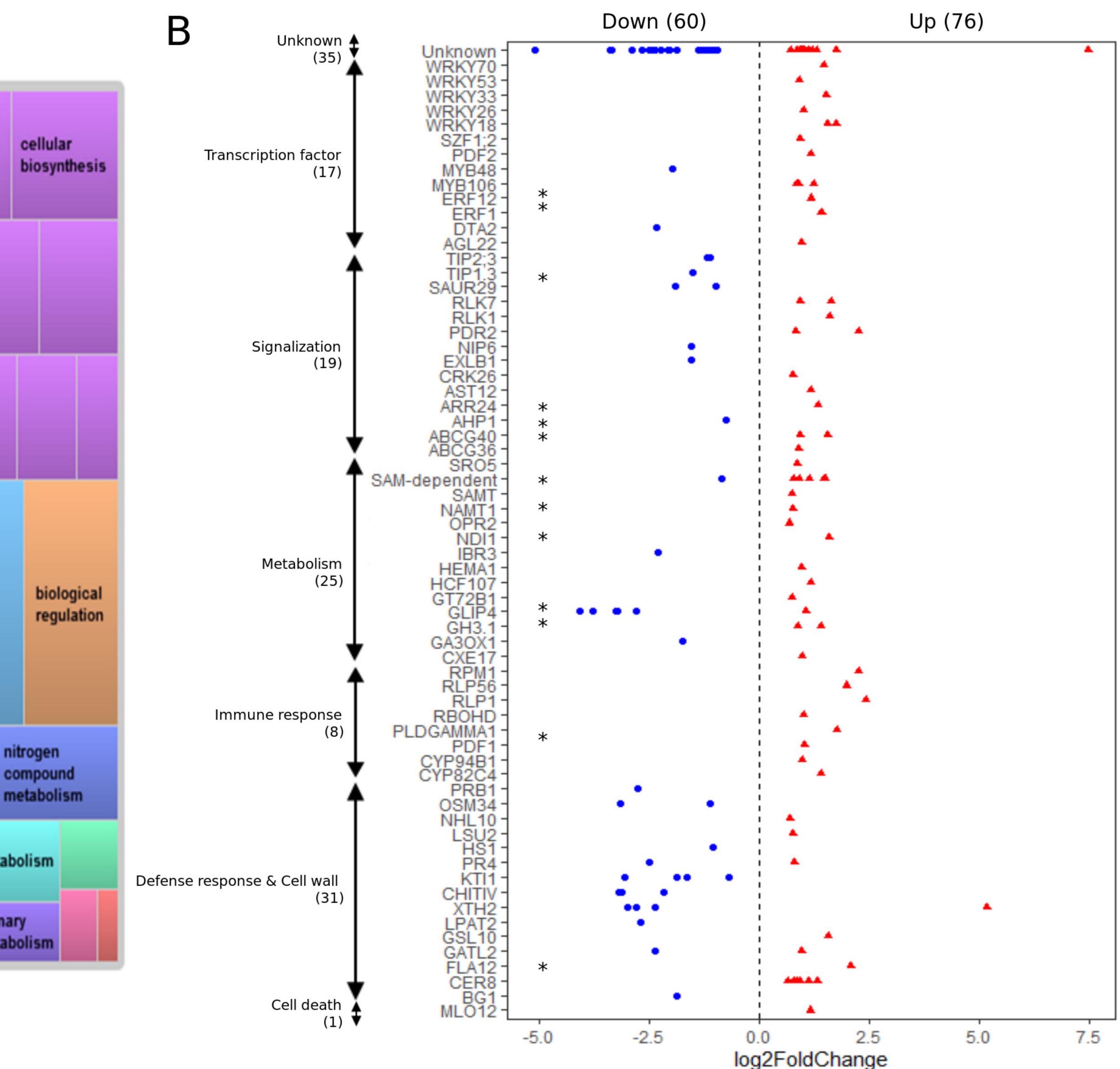
CHH where a threshold of 10% was applied due to the low proportion of DMRs in that context.



Α

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.

| response<br>to<br>stress                     |                                     | regulation<br>of RNA<br>metabolism        | regulation<br>of cellular<br>process | regulation<br>of metabolism |                         |
|--|-------------------------------------|---|--------------------------------------|-----------------------------|-------------------------|
|  | response<br>to<br>salicylic<br>acid | RNA<br>biosynthesis                       | regul<br>of RN<br>metabolism         |                             |                         |
| n cellular<br>nse response<br>to<br>stimulus |                                     | response<br>to to<br>stimulus<br>stimulus |                                      | multi-organism<br>process   |                         |
| e<br>Ious                                    | response<br>to<br>salt<br>stress    | immune<br>Sysystem<br>process<br>process  |                                      | cellular<br>process         |                         |
|  |                                     |   |                                      | biosynthesis                | metal<br>prima<br>metal |



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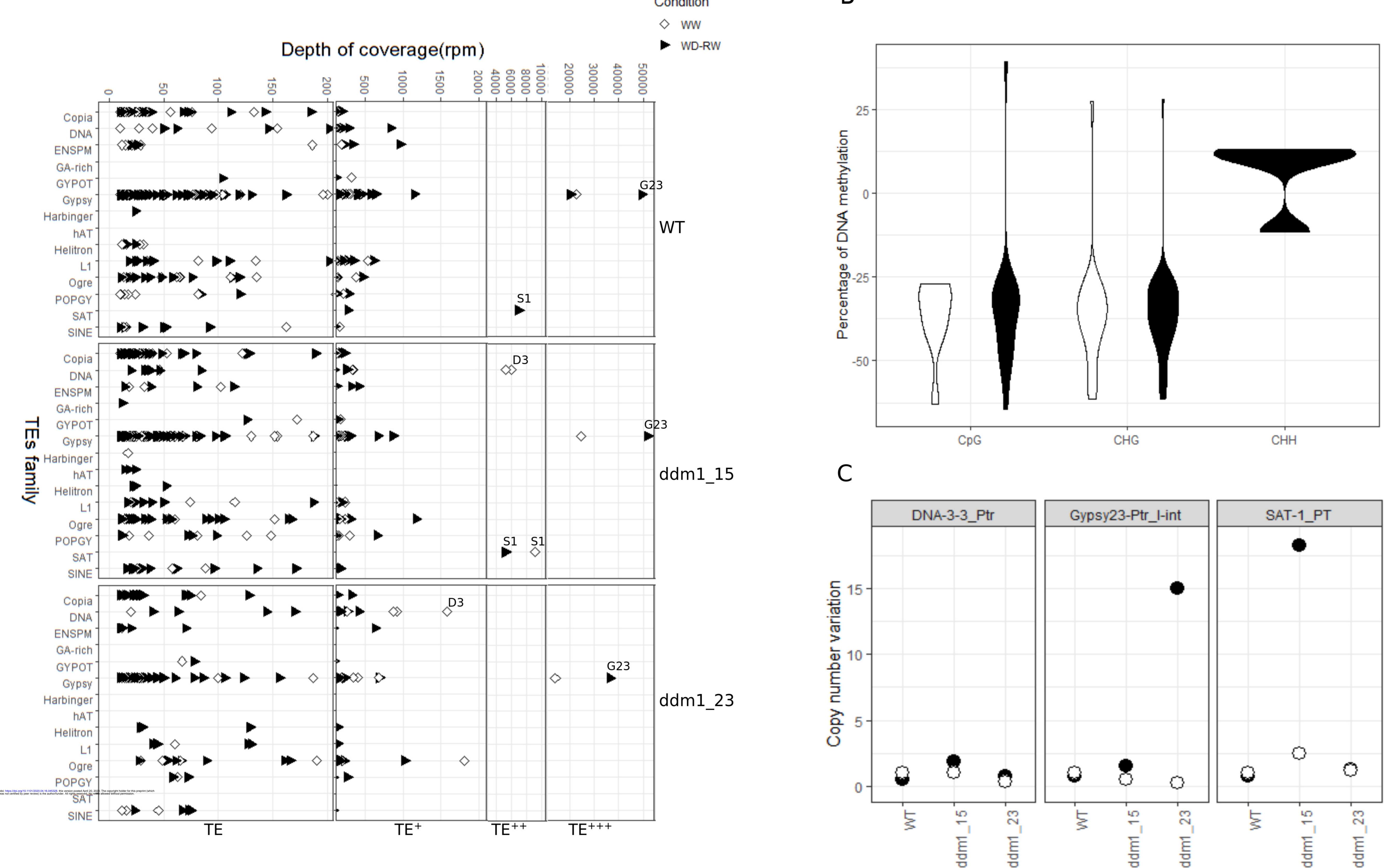






Figure 6: Transposable elements activity among RNAi and WT lines in shoot apical meristem collected one week after rewatering (t2). A. Depth of coverage (read per million, rpm) of different TE families in the three different lines and in both WW (white) and WD-RW (black) regimes. TE, TE+, TE++, TE+++ represent different groups of TE families according to their coverage. TE ranges from 0 to 200X; TE+ = 2000X - 2000X; 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.

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