Defective Repression of OLE3::LUC 1 (*DROL1*) is specifically required for the splicing of AT–AC-type introns in Arabidopsis

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Abstract

An *Arabidopsis* mutant named *defective repression of OLE3::LUC 1* (*drol1*) was originally isolated as a mutant with defects in the repression of *OLEOSIN3* (*OLE3*) after seed germination. In this study, we show that DROL1 is an Arabidopsis homolog of yeast DIB1, a subunit of U5 snRNP in the spliceosome, but comprises a subfamily specific to a certain class of eukaryotes. Comprehensive analysis of intron splicing by RNA-Seq analysis of *drol1* mutants revealed reduced splicing of most of the minor introns with AT–AC dinucleotide termini. Thirty-nine genes, including those playing important roles in the response to abiotic stress, exhibited reduced splicing of AT–AC-type introns in *drol1* mutants. In addition, *drol1* mutant seedlings showed growth arrest, similar to that caused by the activation of abscisic acid signaling, as a result of reduced splicing of AT–AC-type introns in some genes. These results indicate that DROL1 is specifically involved in the splicing of introns with AT–AC termini, and splicing of these minor introns plays an important role in plant growth and development.

Introduction

Dramatic changes in gene expression patterns occur during the developmental transition from seed maturation to seed germination; while the former is characterized by the accumulation of large amounts of storage reserves and the acquisition of dormancy and desiccation tolerance, the latter is characterized by the degradation of storage reserves and rapid vegetative growth of seedlings. Many seed-specific genes involved in seed maturation (hereafter referred to as seed maturation genes), such as genes encoding seed storage proteins and oil-body boundary proteins (oleosins), are turned off and repressed during seed germination and eventually silenced in adult plants. Several important factors that control this dramatic transition in the expression of seed maturation genes have been identified. During germination, PICKLE, a SWI/SNF-class chromatin remodeling factor, acts in concert with gibberellin (GA) to repress the embryonic genetic program and promote vegetative growth (Henderson et al., 2004; Li et al., 2005; Ogas et al., 1997, 1999). Two related B3-domain/EAR-motif transcriptional repressors, HSI2 (HIGH-LEVEL EXPRESSION OF SUGAR-INDUCIBLE GENES 2)/VAL1 (VP1/ABI3-LIKE 1) and HSL1 (HSI2-LIKE 1)/VAL2, redundantly function to repress the expression of seed maturation genes during the early stage of seed germination (Suzuki et al., 2007; Tsukagoshi et al., 2007). A trihelix transcriptional repressor ASIL1 binds to conserved *cis* elements in the promoter regions of seed maturation genes and represses target gene expression during germination (Gao et al., 2009). Repression or silencing of seed maturation genes after seed germination is caused by

epigenetic modifications of the chromatin. PICKLE promotes trimethylation of histone H3 lysine 27 (H3K27 me3), a repressive epigenetic mark, in seed maturation genes during seedling growth (Zhang et al., 2008). HISTONE DEACETYLASE 19 (HDA19) and HDA6 repress the embryonic program after germination and promote vegetative growth (Tanaka et al., 2008), and repression of seed maturation genes by HSL1 is mediated in part by its specific interaction with HDA19 (Zhou et al., 2013). On the other hand, HSI2 bound to the chromatin of seed maturation genes specifically recruits HDA6 and MEDIATOR (MED) for the repression of target genes (Chhun et al., 2016).

To further identify factors involved in the repression of seed maturation genes during germination, we screened *Arabidopsis thaliana* mutants post-germination defective in the repression of the *luciferase* (*LUC*) reporter gene expressed under the control of the seed-specific *OLEOSIN3* (*OLE3*) gene promoter (*OLE3::LUC*) (Suzuki et al., 2018). An Arabidopsis mutant, named as *defective repression of OLE3::LUC 1* (*drol1*), exhibited prolonged expression of *OLE3::LUC* after germination to a significantly high level compared with the wild-type (Suzuki et al., 2018). The *DROL1* gene encodes a protein homologous to a subunit of U5 small nuclear ribonucleoprotein particle (snRNP) involved in pre-mRNA splicing. However, the precise role of DROL1 in splicing and how the defect in a splicing factor causes the derepression of *OLE3* during germination remain unknown.

Many eukaryotic genes contain introns, which are excised from pre-mRNAs via a complex process mediated by the spliceosome to form functional mRNAs. The terminal GT–AG dinucleotides represent the most conserved structure of pre-mRNAs in all eukaryotes, and these canonical GT–AG introns are spliced by the major U2-dependent spliceosome, containing U1, U2, U4, U5, and U6 snRNAs and approximately 80 proteins (Wilkinson et al., 2019). In addition to U2-dependent splicing of the canonical GT–AG introns, a small number of unusual introns containing non-consensus AT–AC termini and highly conserved sequences at the 5' splice site and the branch point are spliced by the minor U12-dependent spliceosome (Jackson, 1991; Tarn and Steitz, 1996a, 1996b; Turunen et al., 2013). The U12-dependent spliceosome consists of four unique snRNAs, U11, U12, $U4_{atac}$, and $U6_{atac}$, and only U5 snRNA is shared with the U2-dependent spliceosome (Tarn and Steitz, 1996a, 1996b). The protein composition of each snRNP of the U12-dependent spliceosome is very similar, if not identical, to that of the U2-dependent spliceosome (Schneider et al., 2002; Will et al., 1999).

Although U12 spliceosome-dependent splicing was first identified in the case of AT–AC introns, it was later found that GT–AG are the more common terminal dinucleotides of U12-type introns than AT–AC. The U12-type introns have been identified in various

eukaryotes and represent ≤0.2% of the total pre-mRNA introns (Burge et al., 1998; Szcześniak et al., 2013; Zhu and Brendel, 2003). However, unlike U2-type introns, U12-type introns are absent in certain species, such as the nematode (*Caenorhabditis elegans*) and budding yeast (*Saccharomyces cerevisiae*). The U12-type introns seem to be enriched in genes within certain functional classes, and these genes usually contain only one U12-type intron. Splicing of U12-type introns appears to be significantly slower than that of U2-type introns, and it has been suggested that U12-type introns play a role in regulating the expression of specific sets of genes (Turunen et al., 2013).

In this study, we show that DROL1 is a homolog of yeast DIB1, a protein subunit of U5 snRNP, and the mutation of *DROL1* causes specific retention of AT–AC-type introns but not that of GT–AG-type introns. This increased retention of AT–AC-type introns upregulates the expression of abscisic acid (ABA)-responsive genes and causes growth arrest during germination. These results indicate that the splicing of minor introns plays an important role in plant growth and development.

Results

DROL1 is homologous to yeast DIB1 but comprises a new subfamily

All eukaryotic genome databases searched in this study contained *DROL1* homologs, while no homologous genes were identified among the genomes of prokaryotes. We selected *DROL1* gene homologs of *Arabidopsis thaliana*, rice (*Oryza sativa*), bryophyte (*Physcomitrella patens*), green alga (*Chlamydomonas reinhardtii*), human (*Homo sapiens*), mouse (*Mus musculus*), nematode (*Caenorhabditis elegans*), fission yeast (*Schizosaccharomyces pombe*), and budding yeast (*Saccharomyces cerevisiae*). The predicted amino acid sequences of DROL1 homologs were aligned (Figure 1A) and used for phylogenetic analysis (Figure 1B).

The multiple sequence alignment revealed that DROL1 homologs could be divided into two subfamilies. One subfamily was represented by *S. cerevisiae* DIB1, a subunit of the U5 snRNP (Gottschalk, 1999; Stevens and Abelson, 1999), and is hereafter referred to as the DIB1 subfamily. All members of the DIB1 subfamily contained 142 amino acids (aa), except DIB1 (143 aa), and shared more than 80% sequence identity. All eukaryotes examined in this study contained at least one DIB1 homolog. The other subfamily comprised DROL1 and its close homologs and is hereafter referred to as the DROL1 subfamily. The DROL1 subfamily proteins were variable in length, ranging from 149 to 159 aa, and shared less sequence identity among each other than DIB1 subfamily members; for example, *A. thaliana* DROL1

and *H. sapiens* DLP share approximately 60% sequence identity. Unlike members of the DIB1 subfamily, certain eukaryotes, such as *S. pombe*, *S. cerevisiae*, *C. elegans*, and *C. reinhardtii*, do not contain any protein belonging to the DROL1 subfamily. Further analysis showed that genomes of other eukaryotes, including frog (*Xenopus laevis*), slugfish (*Branchiostoma floridae*), sea urchin (*Strongylocentrotus purpuratus*), octopus (*Octopus bimaculoides*), plasmodial slime mold (*Physarum polycephalum*), and oomycetes (*Globisporangium ultimum* and *Phytophthora kernoviae*), encode both DIB1 and DROL1 subfamily members, whereas those of fruit fly (*Drosophila melanogaster*), western honey bee (*Apis mellifera*), sea squirt (*Ciona intestinalis*), and cellular slime mold (*Dictyostelium discoideum*) encode only DIB1 subfamily members (Supplementary Figure 1). This distribution of DROL1 subfamily is in line with the fact that organisms harboring DROL1 subfamily are known to have U12-dependent spliceosome, except insects and sea squirt, which are reported to harbor U12-dependent spliceosome (Bai et al., 2019; Bartschat and Samuelsson, 2010; Turunen et al., 2013).

Translational initiation site of DROL1

Multiple sequence alignment of the DROL1 subfamily members indicated that DROL1 has a longer N-terminal amino acid sequence than other subfamily members (underlined in Figure 1A). In addition, the *DROL1* nucleotide sequence contained a second ATG codon 24 bp downstream of the first ATG, and translational initiation from the second ATG produced a protein more similar to the other subfamily members. To infer the structure of the 5' end of *DROL1* mRNAs, short-read sequences obtained from wild-type plants by RNA-Seq were aligned to the *DROL1* cDNA sequence. The reads covering each nucleotide of the cDNA sequence were counted (Y-axis) and plotted along to cDNA sequence (X-axis) (Figure 2A). The left most short-read covered second ATG but not the first one.

To confirm the 5' end of *DROL1* mRNA, we performed 5' rapid amplification of cDNA ends (5' RACE). The cDNA fragments amplified by 5' RACE were ligated to adapters and sequenced using next-generation sequencer. The sequence reads thus obtained were aligned to the *DROL1* cDNA sequence, and four major 5' ends (T1–T4) were identified (Figure 2B). The most upstream transcription start site (T1) was located only 6 bp upstream of the first ATG (Figure 2B, orange arrowhead). The second major site (T2) was located between the two ATG codons and 16 bp upstream of the second ATG codon (Figure 2B, red arrowhead). The remaining two transcription start sites (T3 and T4) were located downstream of the second ATG, implying that these transcripts represented degradation products.

To test which ATG codon is important for the functional expression of *DROL1*, we constructed four mutant variants of the *DROL1* gene (1AATG, 1ATGA, 2AATG, and 2ATGA), wherein one adenine (A) nucleotide was inserted upstream or downstream of the first and second ATG codons. When the A nucleotide was cloned upstream of the translation initiation site of *DROL1*, the gene was predicted to maintain its function and complement the *drol1-1* mutant phenotype. Three mutant variants of *DROL1* (1AATG, 1ATGA, and 2AATG) with insertions of A upstream of the second ATG complemented the *drol1-1* mutant phenotype (Figure 2C). On the contrary, the gene with the insertion of A immediately after the second ATG, namely 2ATGA, failed to complement the *drol1-1* mutant phenotype (Figure 2C). These results and those of the multiple sequence alignment suggest that the translation initiation of *DROL1* occurs from the second ATG and not from the first ATG.

Intron retention in *histone deacetylase 2B* (*HD2B*) mRNA in *drol1* mutants

Since Arabidopsis DROL1 is a homolog of *S. cerevisiae* DIB1, a subunit of the U5 snRNP, defects in *DROL1* are predicted to directly affect intron splicing. To discover the changes in the intron splicing patterns of the *drol1* mutant, we attempted to estimate the intron retention levels in mRNAs with RNA-Seq. The original *drol1-1* mutant carries a point mutation at the splice site of the third intron of *DROL1* that interferes with its correct splicing, while the *drol1-2* mutant carries a T-DNA insertion in the *DROL1* gene (Suzuki et al., 2018). Total RNA were extracted from the wild-type, *drol1-1*, and *drol1-2* seedlings at 3, 5, and 7 days after sowing and used to construct cDNA libraries for next-generation sequencing independently three times. Approximately 10 million reads were obtained per library and analyzed.

We collected short reads that did not align with the cDNA and then mapped these reads onto the Arabidopsis genome sequence. The number of short reads spanning exon–intron junctions was counted (Supplementary Figure 2), and intron retention levels were compared between the wild-type and *drol1* mutant plants using edgeR. Out of 124,918 introns, 229 were statistically different between the wild-type and *drol1* mutant plants (false discovery rate [FDR] < 0.01). Among these 229 introns, the third intron of the *HD2B* gene, a member of the *HD2* gene family encoding plant-specific histone deacetylases (Hollender and Liu, 2008), was most significantly retained in 3-day-old *drol1-1* mutant plants.

The compiled reads mapped into the *HD2B* cDNA in the wild-type and *drol1* mutant seedlings are presented in Figure 3A–C. Short reads obtained from 3-day-old wild-type seedlings covered almost the entire cDNA (Figure 3A). All eight exon–intron junctions in the

HD2B gene (Figure 3A, red arrowheads) were covered by short reads similar to other regions. However, in *drol1-1* and *drol1-2* mutants, short reads spanning the third exon–intron junction of *HD2B* were largely decreased in number (Figures 3B and C), indicating decreased fusion of the third and fourth exons of *HD2B* in *drol1* mutants. Short reads that failed to map to cDNA were mapped onto the genomic sequence of *HD2B* (Figures 3D to 3F). A significant number of short reads mapped to the third intron of the *HD2B* gene in *drol1-1* and *drol1-2* mutants (Figure 3E and F), while almost no reads mapped to the third intron of *HD2B* in the wild-type (Figure 3D). These results indicate the retention of the third intron in a substantial number of *HD2B* transcripts in *drol1* mutants. The sequence of the third intron of *HD2B* started with AT and ended with AC and was therefore identified as a U12-dependent intron (Zhu and Brendel, 2003). By contrast, all of the other seven introns of *HD2B* were canonical U2-dependent GT–AG-type introns. This suggests that DROL1 is required for the splicing of AT–AC-type introns.

Introns requiring DROL1 for splicing

To comprehensively analyze the change in the level of intron retention in *drol1* mutants, we counted short reads spanning exon–exon and exon–intron junctions as spliced and retained introns, respectively (Supplementary Figure 2). We compared the number of reads spanning these junctions between wild-type and *drol1* mutant plants using edgeR and calculated the log fold changes in retained ($logFC_{retained}$) and spliced introns ($logFC_{spliced}$) (Figure 4A). In the $logFC_{retained}$ vs. $logFC_{spliced}$ plot shown in Figure 4A, points representing each intron on the right and left side of the Y-axis indicate that the retention of these introns increased or decreased, respectively, in *drol1-1* mutants than the wild-type. The Y-axis indicates the changes in the level of spliced introns, which corresponds to gene expression levels. Of the 229 introns with statistically different retention levels (FDR < 0.01), 170 and 30 introns were located in the first and third quadrants, respectively. Based on the correlation coefficient (0.56), we considered that the levels of spliced and retained introns were positively correlated. Similar tendencies were also observed in 5- and 7-day-old seedlings of *drol1-1* and *drol1-2* mutants (Figure 4B to 4F). Together, these results suggest that the difference in retained introns between the wild-type and *drol1-1* plants were largely caused by the changes in gene expression levels.

On the other hand, 25 introns in the fourth quadrant of Figure 4A showed higher levels of intron retention independent of the changes in the levels of spliced introns between the wild-type and *drol1-1* mutant. Most of those introns (24 out of 25), including the third intron

of *HD2B*, were AT–AC-type (Figure 3); this proportion of AT–AC-type introns (96%) is far greater than the proportion of AT–AC-type introns in the Arabidopsis genome (0.06%; $p < 10^{-15}$). Similar results were obtained in the comparison of intron retention levels between 5- and 7-day-old seedlings of the wild-type and *drol1-1* (Figure 4). The number of differentially retained introns in the *drol1-1* mutant decreased with increasing age. In the comparison between the wild-type and *drol1-2*, most of the introns in the fourth quadrant were also of the AT–AC-type, although the number of differentially retained AT–AC-type introns was less than that in the *drol1-1* (Figure 4).

Next, we calculated the splicing efficiency (SE, defined in Supplementary Figure 2) of 229 differentially retained introns, including 37 AT–AC-type introns and 189 GT–AG-type introns. Most of the GT–AG- and AT–AC-type introns were almost completely spliced in the wild-type (Figure 5A, top row). Similar patterns were observed for GT–AG-type introns in the *drol1-1* mutant (Figure 5A, left middle image). The difference in SE between the wild-type and *drol1-1* mutant (Figure 5A, bottom left panel) was concentrated near the center of the histogram, indicating that the SE of these introns were in the main not affected by DROL1 deficiency. However, the SE of AT–AC-type introns varied in the *drol1-1* mutant (Figure 5A, right middle image), and all differences were negative (Figure 5A, right bottom panel), indicating that the SE of AT–AC-type introns was reduced in the *drol1-1* mutant. These results suggest that DROL1 is specifically required for the splicing of AT–AC-type introns, although the dependence on DROL1 for splicing varied among introns.

All AT–AC-type introns significantly retained in the *drol1* mutant are shown in Figure 5A (black dots) and listed in Table 1. In Table 1, 41 introns belonging to 39 genes are listed, and these introns represent candidates that require DROL1 for their splicing.

DROL1 is required for the splicing of AT–AC-type introns but not U12-dependent introns

Non-canonical AT–AC-type introns are spliced by the minor U12-dependent spliceosome. However, most of the U12-dependent introns contain GT–AG dinucleotide termini, with consensus sequences different from that of canonical U2-dependent introns (Turunen et al., 2013). Therefore, we analyzed the function of DROL1 in the splicing of U12-dependent introns. According to the U12 Intron Database (U12DB; http://genome.crg.es/datasets/u12/), the Arabidopsis genome contains 257 U12-type introns, of which 225 introns present in The Arabidopsis Information Resource (TAIR) database (https://www.arabidopsis.org/) were analyzed. Almost all U12-dependent introns showed nearly 100% SE, independent of the

terminal dinucleotides, in the wild-type (Figure 5B). Although only GT–AG-type U12-dependent introns showed similar SEs in *drol1-1*, a large number of AT–AC-type introns exhibited decreased SE. The difference in SE between the wild-type and *drol1-1* also indicated the specific decrease of SE of AT–AC-type introns in *drol1-1*. These results are consistent with the analysis of differentially retained introns (Figure 5A) and indicated that DROL1 was required only for the splicing of AT–AC-type introns, not U12-dependent introns.

The third intron of *HD2C*, a homolog of *HD2B*, is a U12-dependent AT–AC-type intron, and the SE of this intron was lower in *drol1-1* and *drol1-2* mutants than in the wild-type (Table 1). The entire sequence of the *HD2C* gene, including the promoter, was cloned, and the AT–AC terminal dinucleotide of the third intron was replaced by GT–AG (Figure 6A). The resulting mutant variant of *HD2C* was introduced into the *drol1-2* mutant, and two independent transformants, HD2CgmI/*drol1-2* #5 and #9, were obtained. Total RNA was extracted from both transformants, and intron retention rates (100 - SE) were measured by RNA-Seq. Although retention rates of endogenous AT–AC-type introns (two right gray bars) were higher in the transformants than in the wild-type (left most gray bar), those of GT–AG-type introns transcribed from the transgene (two right white bars) were lower in the transformants than the wild-type (Figure 6B). The low retention rate of endogenous AT–AC-type introns in HD2CgmI/*drol1-2* than in *drol1-2* might be due to feedback repression caused by the accumulation of mature mRNAs of HD2CgmI. This result indicates that the mutation of AT–AC to GT–AG in U12-dependent introns abolished their requirement for DROL1 for splicing and clarified the specific role of DROL1 in the splicing of AT–AC-type introns.

Derepression of seed maturation genes after germination in *drol1* mutants

The Arabidopsis genome contains five genes (*OLE1–5*) that encode seed-specific oleosin proteins (D'Andréa et al., 2007; Miquel et al., 2014). These *OLE* genes exhibit high expression levels during seed maturation (Miquel et al., 2014) but are downregulated approximately 3–4 days after germination (DAG). The *drol1* mutant was originally identified based on the high level of *OLE3:LUC* expression in seedlings at 3–4 DAG (Suzuki et al., 2018).

To compare gene expression levels among germinating seedlings of the wild-type and *drol1-1* and *drol1-2* mutants, we counted the short reads initially mapped to cDNA references in the intron retention analysis and quantified gene expression levels. We first compared the

mRNA levels of *OLE1–5* (Figures 7A to 7E). In wild-type seedlings, levels of all *OLE* mRNAs were very low at 3 DAG. By contrast, significant levels of these *OLE* mRNAs were present in 3-day-old *drol1-1* mutant seedlings, which rapidly decreased at 5 DAG. Similar patterns were observed in *drol1-2* seedlings, although levels of *OLE* mRNAs were lower than those in the *drol1-1* mutant. These changes in the level of *OLE* mRNAs were similar to the expression of the *OLE3:LUC* reporter gene (Suzuki et al., 2018).

The major seed storage proteins in Arabidopsis are 2S albumin and 18S globulin (Fujiwara et al., 2002). Here, we examined the effect of *drol1* mutation on the expression of five 2S albumin genes and three 18S globulin genes after germination (Figures 7F and 7G and Supplementary Figure 3). Similar to *OLE* genes, significant levels of mRNA of these seed storage protein genes were detected in 3-day-old *drol1-1* seedlings than the wild-type, followed by a rapid decline at 5 DAG. However, unlike *OLE* genes, statistically significant differences in the level of expression in *drol1-1* mutant were observed only with genes with the highest levels of expression from each family. Only *at2S1* of five 2S albumin and CRA1 of three 18S globulin were significantly upregulated in *drol1* mutants. *at2S1* is the gene with the highest expression among five 2S albumin. CRA1 is also the highest among the three 18S globulins. The effect of the *drol1-2* mutation on the transcriptomic changes was considerably weaker than *drol1-1* mutation. These results suggest that the defect in DROL1 causes the derepression of genes encoding not only oleosin proteins but also seed storage proteins after germination.

Comprehensive transcriptomic analysis of *drol1* mutants

Genome-wide expression patterns were compared between the wild-type and *drol1* mutants. Short-read counts were analyzed using edgeR (Robinson et al., 2010), and differentially expressed genes (DEGs) were selected (FDR < 0.01). Compared with the wild-type, 1,952 and 3,863 genes were upregulated and downregulated in 3-day-old *drol1-1* mutant seedlings, respectively (Figure 8). The upregulated genes in *drol1-1* mutants were slightly increased in comparison to 5-day-old seedlings but were largely decreased in 7-day-old seedlings. The downregulated genes in *drol1-1* mutants decreased in association with the developmental stage. Similar pattern was observed in the *drol1-2* mutant, although fewer genes were affected than in the *drol1-1* mutant. Most of the DEGs in the *drol1-2* mutant were included to those of *drol1-1* mutants (72%–94%), suggesting that *drol1-2* was weaker than the *drol1-1* mutant in terms of the effects on the transcriptome.

To characterize the upregulated and downregulated genes in *drol1* mutants, we

performed Gene Ontology (GO) analysis using PANTHER (http://go.pantherdb.org/). Of the 428 genes commonly upregulated in *drol1-1* and *drol1-2* mutants (Supplemental Data Set 1), those related to the "maintenance of location," "response to water deprivation," "response to abscisic acid," and "response to salt stress" were overrepresented (Supplemental Data Set 2). The GO term "maintenance of location" refers to a function of oleosin that keeps oil inside oil body, and thus functions as a barrier for oil, and all five *OLE* genes were included in this class of genes. In 3-day-old *drol1* seedlings, the upregulation of genes involved in response to dehydration and ABA implies that these seedlings retain at least part of the seed maturation program, which is consistent with the continued expression of genes encoding oleosin and seed storage proteins.

Among the 842 genes downregulated in 3-day-old *drol1* seedlings compared with the wild-type, those related to "mitotic cell cycle process," "microtubule-based process," "cytokinesis," "mitotic cell cycle phase transition," and "plastid organization" were overrepresented (Supplemental Data Set 3 and 4). Since many genes essential for the rapid vegetative development of seedlings and photosynthetic activity were enriched in these GO terms, their downregulation in *drol1* seedlings is consistent with the abnormal growth of these seedlings.

Defective growth of *drol1* seedlings

In addition to the derepression of *OLE* genes, the *drol1* seedlings showed some developmental defects. The *drol1-1* and *drol1-2* mutant seedlings were smaller in size than wild-type seedlings at 5 days after germination (Figure 9A). While the wild-type cotyledons were curled upward, mutant cotyledons were either flat or occasionally curled downward. In addition, the root length of *drol1* mutant seedlings was approximately 50% or 33% shorter than that of wild-type seedlings at 3 and 5 DAG (Figure 9B). However, root elongation in 5-day-old *drol1* seedlings was similar to that of wild-type seedlings. Leaf development was also delayed in *drol1* mutants than the wild-type; when the wild-type seedlings possessed four leaves, the *drol1* mutant seedlings showed few and small rosette leaves (Figure 2C). These growth defects were observed only when *drol1* seedlings were grown on normal medium (as described in materials and methods section). After planting in soil, the growth defects were rescued, and the fertility of *drol1* mutant seedlings was similar to that of wild-type seedlings.

Since genes involved in the response to dehydration and ABA were upregulated in *drol1* seedlings, the phenotypes involving ABA were surveyed. The germination rate of *drol1*

mutant seeds was lower than that of wild-type seeds (Figure 9C); all wild-type seeds germinated at 2 days after sowing, whereas less than 50% of *drol1* mutant seeds were germinated at this time point, and the rate of germination gradually increased over a week. We also measured the fresh weight of 10-day-old wild-type, *drol1-1*, and *drol1-2* seedlings grown on medium containing various concentrations of salt (Figures 9D and 9E). The results indicated that *drol1* mutants were hypersensitive to salt. Together, these results suggest that growth defects in *drol1* mutants were at least partly caused by extended dormancy of seeds and high osmolarity of the growth medium.

Discussion

DROL1 is required for AT–AC-type intron splicing but is not a component of the spliceosome

In this study, we showed that DROL1 is homologous to yeast DIB1, a highly conserved protein subunit of U5 snRNPs, but a member of another subfamily specific to a certain class of eukaryotes (Figure 1). Defects in DROL1 specifically increased the retention levels of AT–AC-type introns (Figures 3 to 5 and Table 1).

Since *DROL1* is homologous to the *DIB1* gene of *S. cerevisiae* and *DIM1* genes of *S. pombe*, it could be hypothesized that DROL1 mediates AT–AC-type intron splicing as a component of the U5 snRNP. Previous studies on *DLP/hDim2*, the human ortholog of *DROL1*, support this hypothesis. DLP/hDim2 was shown to bind Prp6, a protein subunit of the U5 snRNP that interacts with DIB1 in vitro (Sun et al., 2004). Crystal structure analysis revealed that DLP/hDim2 shares a common structural fold with hDim1, a human ortholog of DIB1 (Simeoni et al., 2005). These results did not deny the possibility that DLP/hDim2 replaced the position of hDim1 in the U5 snRNP.

However, several conflicting results have been reported. A precise structural comparison of hDim1 and DLP/hDim2 revealed that DLP/hDim2 lacks essential structural motifs and residues required for the biological activity of hDim1 (Simeoni et al., 2005). The authors also reported the dimerization of DLP/hDim2 in vitro. It remains unclear whether these structural differences made it difficult to assemble DLP/hDim2 into the U5 snRNP by replacing hDim1.

If a specific form of U5 snRNP containing DROL1 exists, it must be a component of the U12-dependent spliceosome, because almost all AT–AC-type introns are U12-dependent. Attempts to identify protein subunits of U12-dependent spliceosome revealed that some specific protein components were included in U11/U12 di-snRNPs in addition to the commons with U1 and U2 snRNPs (Will et al., 2004, 1999). However, there is currently no

report on unique protein components of $U4_{atac}/U6_{atac}$.U5 tri-snRNPs compared with U4/U6.U5 tri-snRNPs (Schneider et al., 2002). In addition, there has been no report indicating that DLP/hDim2 was identified in U12- and U2-dependent spliceosomes, implying that DLP/hDim2 functions outside the spliceosome.

In the reaction model of the major spliceosome, DIB1 is positioned adjacent to the U6 snRNA at the B complex, which is the pre-catalytic form of the spliceosome for branching and preventing premature spliceosome activation (Plaschka et al., 2017; Schreib et al., 2018; Wilkinson et al., 2019). During the formation of activated B (B^{act}) complex, DIB1 is removed from the spliceosome, thus allowing the U6 snRNA to form a helix with the 5' splice site through the ACAGAGA sequence. When this model is applied to DROL1-containing U12-dependent spliceosome, there is almost no chance for DROL1 to interact with the 5'-AT sequence of the intron.

Together, these results suggest that DROL1 functions outside the spliceosome and recruits AT–AC-type introns to the spliceosome by binding to PRP6. In the current intron splicing model, the splice site was mainly determined by snRNAs, depending on the base pairing among themselves and the pre-mRNA. Although direct interaction between DROL1 and terminal dinucleotide of the intron has not yet been proven, it is evident that DROL1 specifically acts on AT–AC-type introns. It is important to determine whether this function is specific to the Arabidopsis DROL1 or common to all members of the DROL1 subfamily. It would be interesting to test whether knockdown or knockout of *DLP/hDim2* in human cells increases the retention of AT–AC-type introns or has no effect. How DROL1 mediates the splicing of AT–AC-type introns should be investigated in future studies.

Phenotypic effects of defective splicing of AT–AC-type introns

The RNA-Seq analysis showed that many genes were upregulated or downregulated in *drol1* than the wild-type (Supplemental Data Sets 1–4). All five seed-specific *OLE* genes, one of which was used as a reporter for the screening of *drol1-1* mutant, were upregulated in *drol1* mutants (Figure 7), confirming our previous results (Suzuki et al., 2018). These transcriptomic changes were speculated to cause the *drol1* mutant phenotype characterized by developmental defects, low seed germination rate, and hypersensitivity to salt (Figure 9).

The most prominent changes in *drol1* mutants at the transcription level included the upregulation of several ABA-responsive genes, including *ABA INSENSITIVE 5* (*ABI5*; AT2G36270). *ABI5* expression is known to be induced by the application of ABA to germinating embryos, resulting in growth arrest during germination (Lopez-Molina et al.,

2001). The ABI5 protein induces the expression of *AtEm1* and *AtEm6*, which are ordinarily expressed during late embryogenesis (Lopez-Molina et al., 2002), and these inductions were also occurred in *drol1* seedlings (Supplemental Data Set 1). Consistent with the growth arrest, the genes related to mitosis and chloroplast development were downregulated in *drol1* mutants (Supplemental Data Sets 3 and 4). Based on these results, we hypothesized the activation of ABA signaling in *drol1* seedlings, which in turn activated *ABI5* expression, resulting in growth arrest during germination.

The activation of ABA signaling in *drol1* mutants is speculated to be caused by pre-mRNAs of genes harboring AT–AC-type introns. Two candidate genes accountable for the activation of ABA signaling, *NHX5* and *NHX6*, encode endosomal Na^+/H^+ antiporters (Table 1). Both *NHX5* and *NHX6* uniquely contain two AT–AC-type introns, which are conserved in human orthologous genes, *NHE6* and *NHE7* (Zhu and Brendel, 2003). The *NHX5* and *NHX6* genes are involved in salt tolerance in plants, and the *nhx5 nhx6* double mutant plants are shorter than wild-type plants (Bassil et al., 2011). When two AT–AC-type introns were independently retained in the transcriptome of *drol1*, the level of mature *NHX5* and *NHX6* mRNAs was expected to be severely reduced, thus mimicking the hypersensitivity of the *nhx5 nhx6* double mutant to salt. This hypersensitivity might cause the induction of the genes related to the "response to salt stress" and activation of ABA signaling in *drol1* mutants.

The *HD2* gene family is another candidate that could account for the *drol1* mutant phenotype. The *HD2* gene family encodes plant-specific histone deacetylases, which remove the acetyl group from histones H3 and H4 and generally repress gene expression (Hollender and Liu, 2008). The Arabidopsis genome harbors four *HD2* genes, and in three of these genes (except *HD2A*), the third intron is AT–AC type. The *hd2c* mutant exhibits low germination than the wild-type on medium containing ABA and NaCl (Colville et al., 2011; Luo et al., 2012). In addition, since plants overexpressing *HD2D* showed tolerance to NaCl, HD2D is suggested to play a role in the response to high salinity (Han et al., 2016). It was difficult to attribute the *drol1* mutant phenotype to HD2C alone due to the normal development of *hd2c* mutants in the absence of abiotic stress. However, it is possible that the reduced expression of both *HD2C* and *HD2D* increased the sensitivity to ABA and salt stress. It is also possible that reduction in the expression of *HD2C* and *HD2D* enhanced the sensitivity to ABA and salt due to the defects of *NHX5* and *NHX6*.

Some of the genes essential for cell viability also carried AT–AC-type introns. Homozygous mutants of the *NRPA2* gene, which encodes the second largest subunit of the

nuclear RNA polymerase I, were lethal (Onodera et al., 2008). The first intron of *NRPA2* was AT–AC type, and only 9% of the transcripts were spliced. A small amount of the spliced *NRPA2* transcript might rescue the *drol1* phenotype. Moreover, the insertion of polypeptides translated from the retained 96-bp first intron and no stop codon might not disrupt the function of RNA polymerase I. *DPB2* encodes the regulatory subunit of DNA polymerase ε, and homozygous *dpb2* mutants are lethal (Ronceret et al., 2005). The *SMC1* gene, which encodes a subunit of cohesin, is essential for embryogenesis (Liu et al., 2002). These results indicate that a part of the pre-mRNA with an AT–AC-type intron was spliced in the absence of a functional DROL1.

Differences between the transcriptome of wild-type and *drol1* seedlings, in terms of both gene expression and intron retention, gradually decreased with increasing age (Figure 4 and 8). Consistent with these results, *drol1* developmental defects were rescued by planting the seedlings in soil. These results also support that DROL1 is required, but not essential, for the effective splicing of AT–AC-type introns. The time-dependent accumulation of mature mRNAs might help rescue the lethal phenotype of *drol1* mutants.

Materials and methods

Comparison of *DROL1* homologs

Amino acid sequences of DROL1 homologs of different organisms were downloaded from different databases: *Arabidopsis thaliana* homolog from the TAIR database (https://www.arabidopsis.org/), *Oryza sativa* homolog from the Rice Annotation Project Database (RAP-DB; http://rapdb.dna.affrc.go.jp/), *Physcomitrella patens* and *Chlamydomonas reinhardtii* homologs from the Phytozome database (https://phytozome.jgi.doe.g.,ov/), *Caenorhabditis elegans* homolog from WormBase (https://www.wormbase.org/), *Schizosaccharomyces pombe* homolog from PomBase (https://www.pombase.org/), and *Saccharomyces cerevisiae* homolog from the *Saccharomyces* Genome Database (SGD; https://www.yeastgenome.org/). *Mus musculus* and *Homo sapiens* homologs of DROL1 were found in the UniProt database through the DNA Data Bank of Japan (DDBJ) blastp server. Since the *C. reinhardtii* homolog of DROL1 was truncated at the N-terminus, full-length sequences were searched using exonerate (Slater and Birney, 2005), with AtDIB1 (AT5G08290.1) as the query. Multiple sequence alignments and a phylogenetic tree were constructed using ClustalW2 (Larkin et al., 2007) and modified manually.

RNA extraction

Sterilized seeds were sown on 1.5% (w/v) agar plates containing half-strength Murashige and Skoog medium (Wako, Japan) supplemented with 2% sucrose and 0.05% MES-KOH (pH 5.7). Plates were wrapped with aluminum foil and incubated at 4°C for a few days. Then, plates were vertically placed in a growth chamber at 22°C under continuous fluorescent light. Seedlings were collected after 3, 5, and 7 days of incubation, immediately frozen in liquid nitrogen, and ground to a fine powder using a pestle and mortar. Total RNA was extracted from the powder using the NucleoSpin RNA Plant Kit (Takara; http://www.takara-bio.co.jp/), according to the manufacturer's protocol.

5' RACE analysis of DROL1 transcript

The 5' RACE analysis was conducted using the 5'-Full RACE Core Set (Takara), according to the manufacturer's protocol. The cDNAs were reverse transcribed using a 5'-phosphorylated primer (5'-CATTTAGTATGATCC-3') purchased from Eurofins Genomics (https://www.eurofinsgenomics.jp/). The first and second amplifications of cDNA were performed using the following primer pairs: 5'-CACATACACTTGAACATCCTC-3' and 5'-TGATATCACGTTGTTTCCTTCG-3' for the first amplification and 5'-CATCAACCAAAGCTACCTTAGC-3' and 5'-CTTCAATGCGCATCATATGA-3' for the second amplification. The PCR products were purified and ligated to adapters for NextSeq500 (Illumina, http://www.illuminakk.co.jp/). A total of 451,660 reads were obtained, of which 197,822 (44%) contained a reverse-transcription primer sequence. After trimming the primer sequence, reads were aligned to the reference containing a 2-kb promoter and *DROL1* coding sequence using Bowtie (Langmead et al., 2009). The aligned 160,418 reads (81% of trimmed reads) were counted by each position from which they originated.

RNA-Seq analysis

The extracted total RNA was used to construct cDNA libraries with the NEBNext Ultra RNA Library Prep Kit for Illumina, NEBNext Poly(A) mRNA Magnetic Isolation Module, and NEBNext Multiplex Oligos for Illumina (New England BioLabs, https://www.nebj.jp/), according to the manufacturer's protocol. The libraries were sequenced using the NextSeq500 sequencer (Illumina). Raw reads containing adapter sequences were trimmed using bcl2fastq (Illumina), and nucleotides with low-quality (QV < 25) were masked by N using the original script. Reads shorter than 50 bp were discarded, and the remaining reads were mapped to the cDNA reference using Bowtie with the following parameters: "--all --best –strata"

(Langmead et al., 2009). Reads were counted by transcript models. DEGs were selected based on the adjusted *p*-value calculated using edgeR (version 3.20.9) with default settings (Robinson et al., 2010).

Analysis of retained introns

The positions of introns along the chromosome were extracted from XML files downloaded from TAIR. Reads obtained by RNA-Seq analysis that did not map to the cDNA were mapped to the genomic sequence. Among these reads, those spanning the 5' and 3' ends of introns were selected and counted by introns (Supplementary Figure 2). Reads spanning exon–exon junctions were also selected from the reads mapped to cDNA and counted. Changes in the retained and spliced introns in the transcriptome were calculated using edgeR as a log fold change ($logFC_{retained}$ and $logFC_{spliced}$), respectively. The splicing efficiency was calculated as follows: *spliced* / (*spliced* + *retained* / 2) (where *spliced* and *retained* refer to reads spanning the exon–exon and exon–intron junctions, respectively).

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Author contributions

T.S., T.K. T.H. and K.N. designed the research; T.S., T.S., T.N., H.A., S.H., H.T., F.Y., T.K. performed research; T.S. T.K. and K.N. analyzed data; T.S. and K.N. wrote paper.

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Table 1. Genes with AT–AC-type introns showing significant intron retention in *drol1* mutants

Gene	intron	$logFC_{retained}$	FDR	SE (%)	Gene function
AT5G22650	3	7.90	1.47e-105	15	histone deacetylase 2B / HD2B
AT3G62830	1	5.14	4.50e-78	34	UDP-glucuronic acid decarboxylase 2 / UXS2
AT4G13615	1	3.71	6.70e-57	43	Uncharacterised protein family SERF
AT5G22110	4	8.78	1.86e-40	13	DNA polymerase epsilon subunit B / DPB2
AT1G29940	1	6.72	6.82e-32	10	nuclear RNA polymerase A2 / NRPA2
AT5G18410	12	8.45	1.52e-29	19	transcription activators
AT3G53180	2	6.89	5.29e-28	29	glutamate-ammonia ligases
AT1G79610	10 3	4.86 4.81	9.86e-28 3.49e-3	36 85	Na^+/H^+ exchanger 6 / NHX6
AT1G80500	4	4.22	3.68e-27	61	SNARE-like superfamily protein
AT5G63700	8	5.27	2.87e-26	3	zinc ion binding;DNA binding
AT3G21215	8	5.61	4.31e-23	59	RNA-binding (RRM/RBD/RNP motifs) family protein
AT2G27840	3	3.35	3.29e-19	82	histone deacetylase-related / HD-related
AT3G51460	8	5.52	3.05e-17	53	Phosphoinositide phosphatase family protein
AT4G15802	4	2.79	1.59e-16	84	heat shock factor binding protein
AT5G27380	6	2.77	1.79e-15	66	glutathione synthetase 2 / GSH2
AT2G40840	5	6.29	1.86e-13	80	disproportionating enzyme 2 / HD2D
AT4G30900	6	4.03	2.05e-13	39	DNAse I-like superfamily protein
AT5G08430	5	2.90	4.41e-13	9	SWIB/MDM2 domain;Plus-3;GYF
AT3G54670	7	4.56	1.14e-12	11	Structural maintenance of chromosomes family protein / SMC1
AT5G38380	5	5.63	1.54e-12	57	unknown protein
AT1G67960	6	4.44	1.58e-12	25	unknown protein
AT5G03740	3	3.47	1.06e-11	65	histone deacetylase 2C / HD2C
AT1G31660	10	4.25	2.22e-10	70	unknown protein
AT4G38240	13	4.58	3.95e-10	51	α-1,3-mannosyl-glycoprotein ß-1,2-N-acetylglucosaminyltransferase, putative
AT1G73350	4	2.64	5.77e-10	31	unknown protein
AT1G29630	5	4.29	9.19e-10	20	5'-3' exonuclease family protein
AT2G47650	1	3.72	4.49e-8	84	UDP-glucuronic acid decarboxylase 4 / UXS4
AT3G53520	1	6.74	9.78e-8	82	UDP-glucuronic acid decarboxylase 1 / UXS1
AT1G24050	1	3.89	1.17e-7	89	RNA-processing, Lsm domain
AT1G26170	2	6.76	3.60e-7	56	ARM repeat superfamily protein
AT2G39080	5	3.86	9.50e-7	81	NAD(P)-binding Rossmann-fold superfamily protein

AT1G54370	10	2.77	1.26e-6	37	Na^+/H^+ exchanger 5 / NHX5
	3	2.96	4.69e-5	58	
AT2G44270	6	4.28	1.58e-6	76	repressor of lrx1
AT3G24100	1	2.36	2.56e-6	94	Uncharacterised protein family SERF
AT3G22880	14	3.27	1.11e-4	25	DNA repair (Rad51) family protein / DMC1
AT1G80210	2	6.84	1.75e-4	25	Mov34/MPN/PAD-1 family protein / BRCC36A
AT5G44200	4	2.52	4.63e-4	84	CAP-binding protein 20 / CBP20
AT1G77320	6	3.09	1.93e-3	37	transcription coactivators
AT1G73860	14	4.47	7.11e-3	8	P-loop containing nucleoside triphosphate hydrolases superfamily protein

714 Genes are listed ascending to FDR.
715

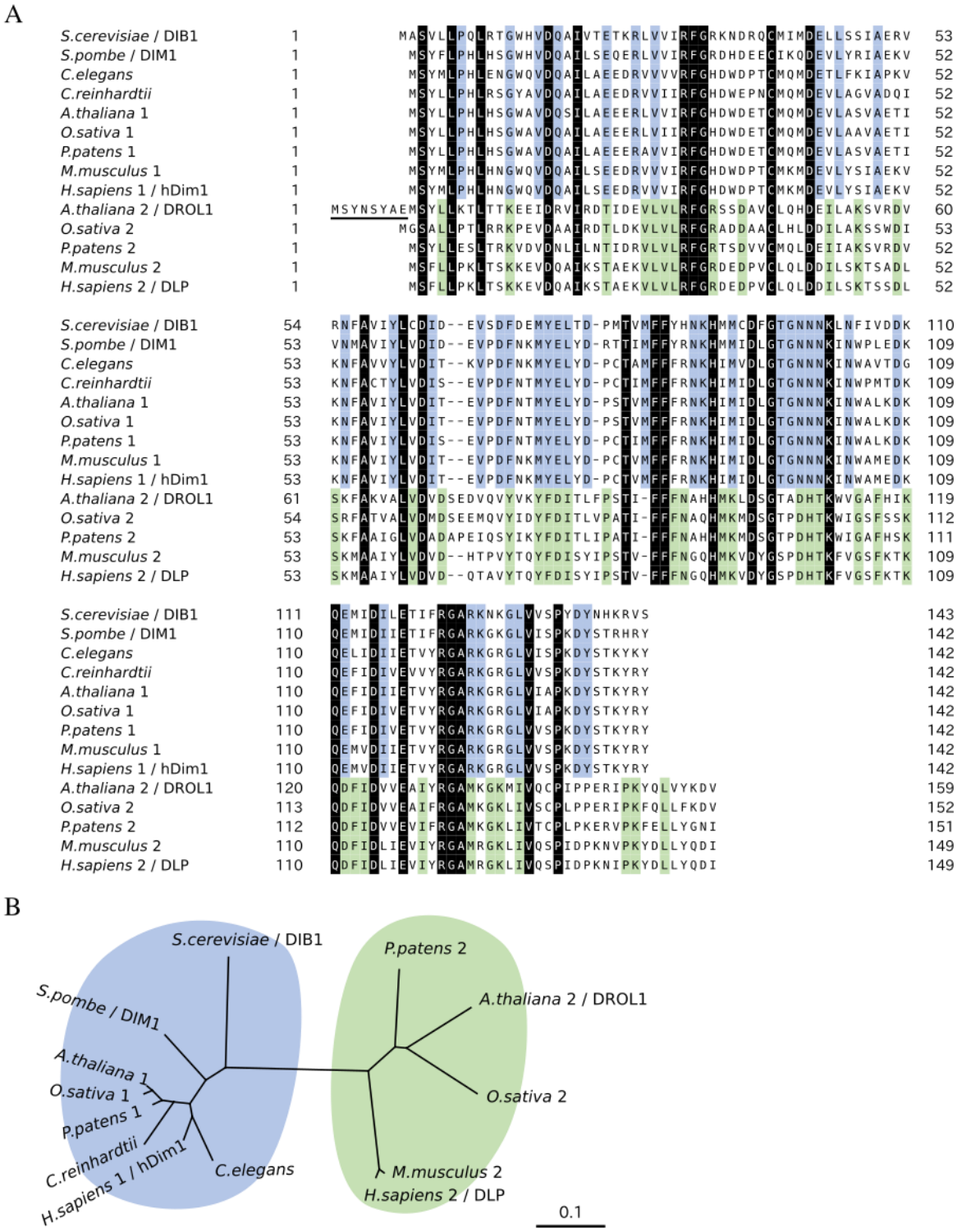


Figure 1. Comparison of DROL1 homologs

(A) Alignment of DROL1 amino acid sequences. Fourteen DROL1 homologs were obtained from nine model organisms. The species name is shown only if it harbors DIB1 subfamily members, and the names were followed by the numbers 1 and 2 when the species has both

DIB1 and DROL1 subfamily members, respectively. Gene IDs and source organisms were as follows: AT5G08290.1, AT3G24730.1 (DROL1): *Arabidopsis thaliana*; Os07t0202300-01, Os11t0297900-01: *Oryza sativa*; Pp1s141_103V6.1, Pp1s12_196V6.1: *Physcomitrella patens*; Cre01.g055416.t1.1: *Chlamydomonas reinhardtii*; TXN4A_MOUSE, TXN4B_MOUSE: *Mus musculus*; TXN4A_HUMAN, TXN4B_HUMAN: *Homo sapiens*; Y54G2A.75.1: *Caenorhabditis elegans*; SPCC16A11.05c: *Schizosaccharomyces pombe*; and YPR082C: *Saccharomyces cerevisiae*. The conserved amino acid residues among all homologs, DIB1 subfamily, and DROL1 subfamily are indicated in black, blue, and green, respectively.

(B) Phylogenetic tree of DROL1 homologs. Since mouse (TXN4A_MOUSE) and human (TXN4A_HUMAN) DROL1 homologs have the same amino acid sequences, the node corresponding to mouse DROL1 was omitted.

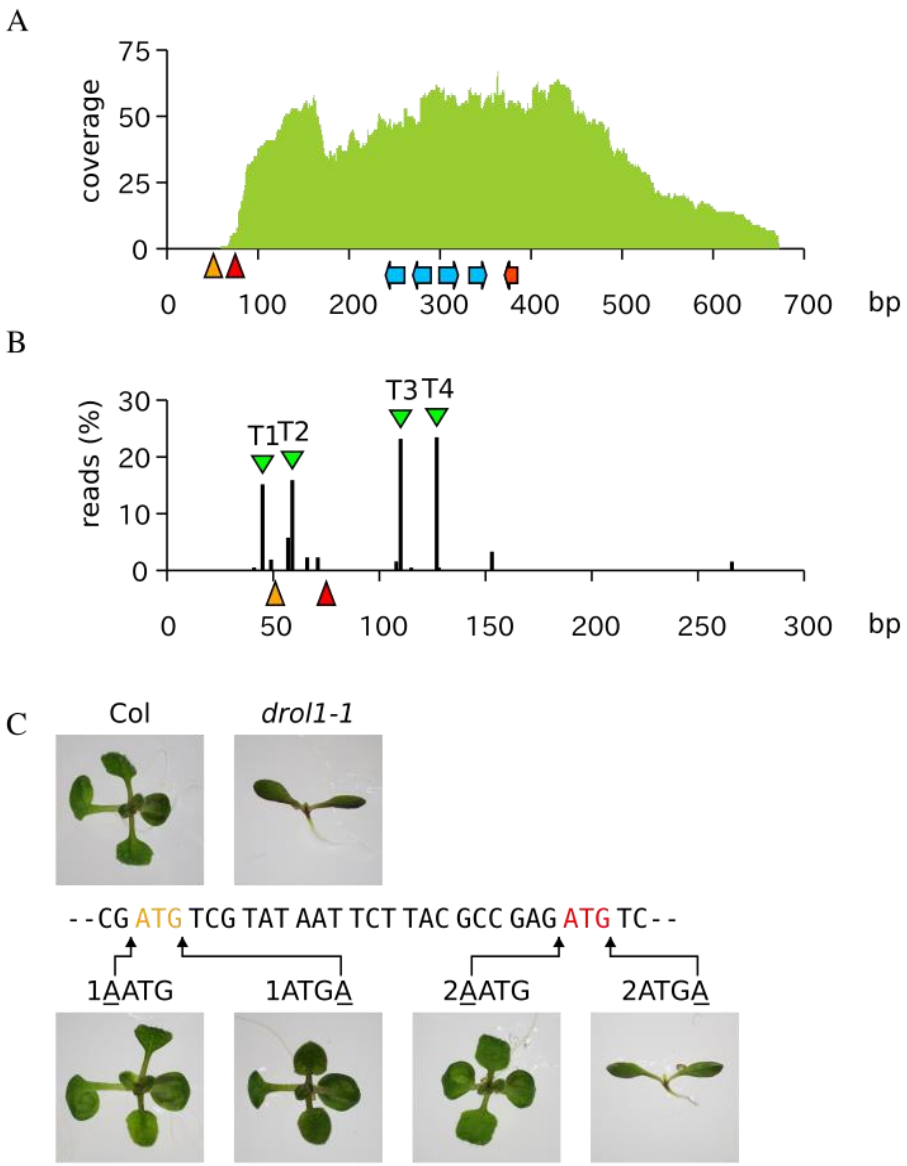


Figure 2. Analysis of the transcription and translation start site of *DROL1*

(A) RNA-Seq analysis of *DROL1*. Total RNAs extracted from 3-day-old wild-type plants were subjected to cDNA library construction for next-generation sequencing. The reads obtained were aligned to the *DROL1* cDNA reference. The X-axis represents the reference sequences, and the Y-axis indicates the coverage of short reads. Orange and red arrowheads indicate the putative translational start sites. The red arrow indicates the reverse-transcription primer, and the blue arrows indicate 5' RACE primers. (B) Transcription start sites determined by 5' RACE. The 5' ends of the aligned reads obtained by 5' RACE were counted and plotted. Orange and red arrowheads indicate the putative translational start sites, as described above. Four major peaks of 5' ends are indicated by green triangles. (C) Analysis of the translational start site. Nucleotide sequences corresponding to the longer N-terminal

amino acid sequences of DROL1 and two ATG codons (orange and red) are indicated. The insertion sites of adenine (A) nucleotide in four mutant variants of the *DROL1* gene (1AATG, 1ATGA, 2AATG, and 2ATGA) are indicated by arrows. Images of 10-day-old seedlings of the wild-type (Col) and *drol1-1* mutant and four transformants are shown. More than three independent lines were tested for each mutated gene.

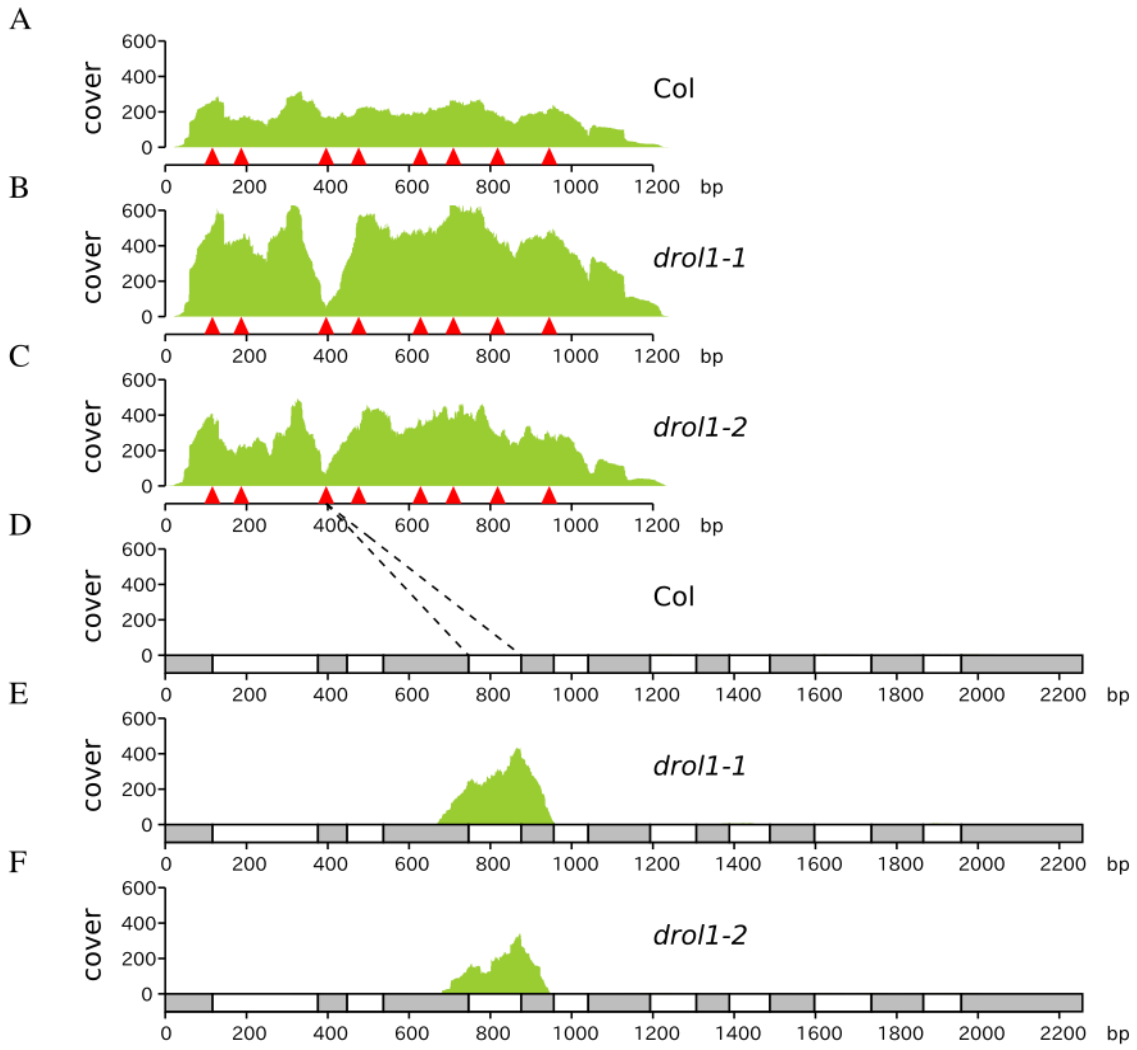
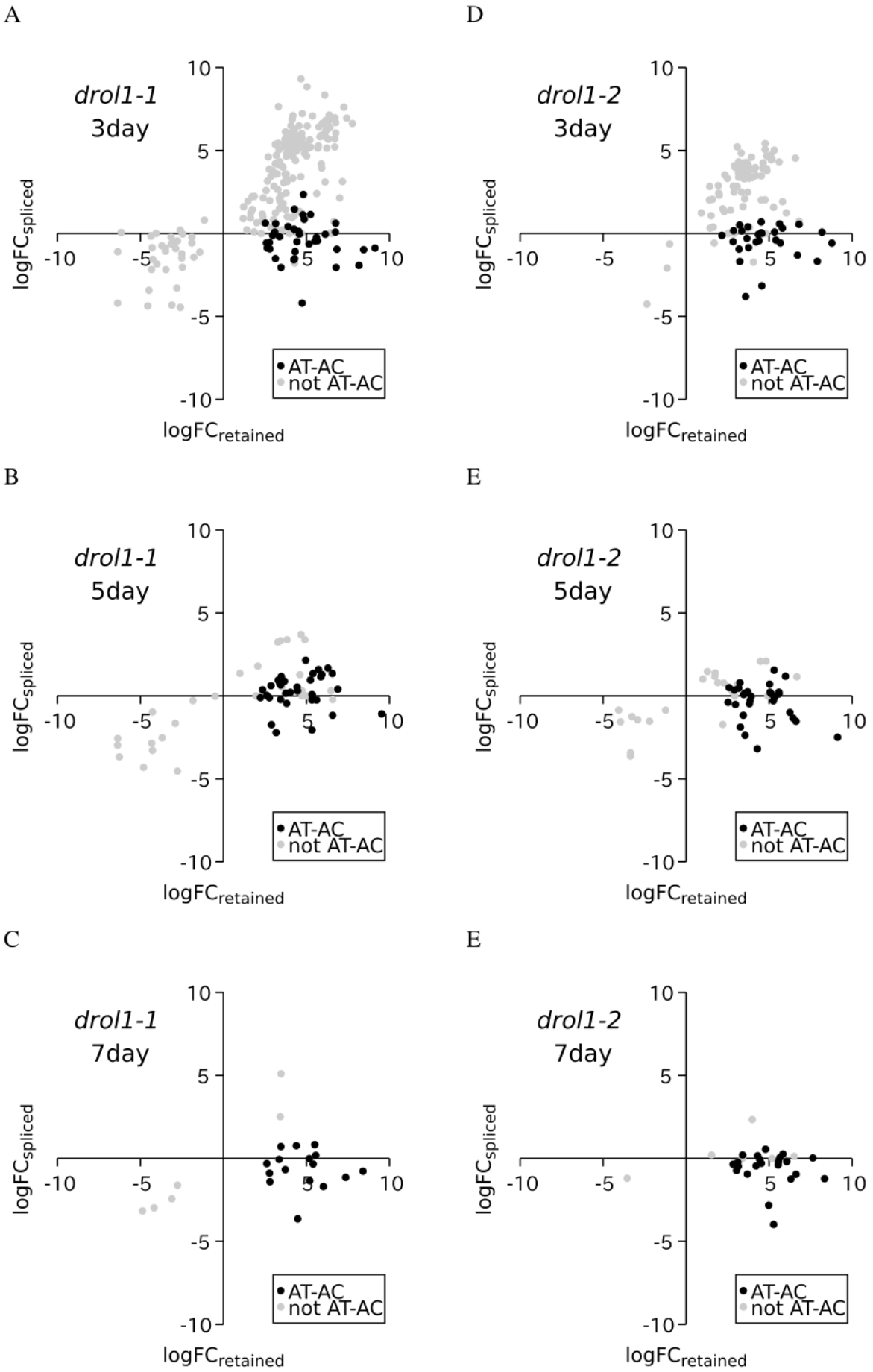


Figure 3. RNA-Seq analysis for *HD2B*

(A–C) Short reads of 3-day-old wild-type (A), *drol1-1* (B), and *drol1-2* (C) seedlings obtained by RNA-Seq and mapped to cDNA of *HD2B*. Red arrowheads indicate the positions of exon junctions. (D–F) Transcribed region of *HD2B* in wild-type (D), *drol1-1* (E), and *drol1-2* (F) seedlings. Gray and white boxes represent exons and introns, respectively.


A
drol1-1
3day
D
drol1-2
3day
B
drol1-1
5day
E
drol1-2
5day
C
drol1-1
7day
E
drol1-2
7day
logFC_spliced
logFC_retained
AT-AC
not AT-AC
10
5
-5
-10

761

Figure 4. Analysis of retained introns in the *drol1-1* and *drol1-2* mutant

(A) Scatter plot of logFC values of retained and spliced introns. Introns with FDR < 0.01 were selected, and logFC values were plotted along the X-axis. The Y-axis represents the logFC values of spliced introns. AT–AC-type introns and other types of introns (mostly GT–AG) are plotted as black and gray spots, respectively.

Scatter plots of logFC values of retained and spliced introns. (A–C) Comparison between the wild-type and *drol1-1* at 3-, 5-, and 7-day-old seedlings, respectively. Only significantly (FDR < 0.01) increased retained introns in *drol1-1* than the wild-type are plotted. Subpanel A is the same as that shown in Figure 4A. (D–F) Comparison between the wild-type and *drol1-2* at 3-, 5-, and 7-day-old seedlings, respectively. Black and gray points indicate AT–AC- and GT–AG-type introns, respectively.

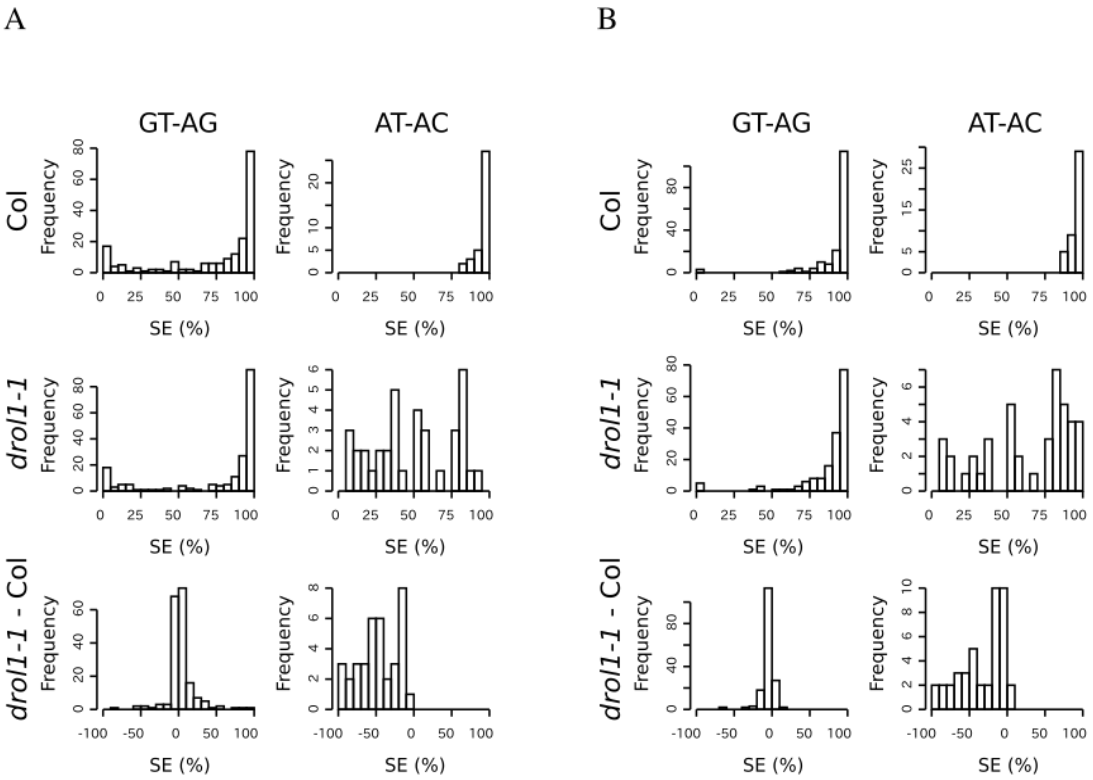


Figure 5. Histogram of splicing efficiency (SE) of introns

(A) SE histogram for GT–AG- and AT–AC-type introns significantly retained in *drol1-1* mutant. SE are grouped by their spliced ratio are plotted in the left and right columns, respectively. The first and second rows represent the observed spliced ratios in the wild-type (Col) and *drol1-1*, respectively. The third row represents the differences in spliced ratio between the wild-type and *drol1-1*. (B) SE histograms of histograms for GT–AG- and AT–AC-type U12-dependent introns are shown in left and right columns, respectively.

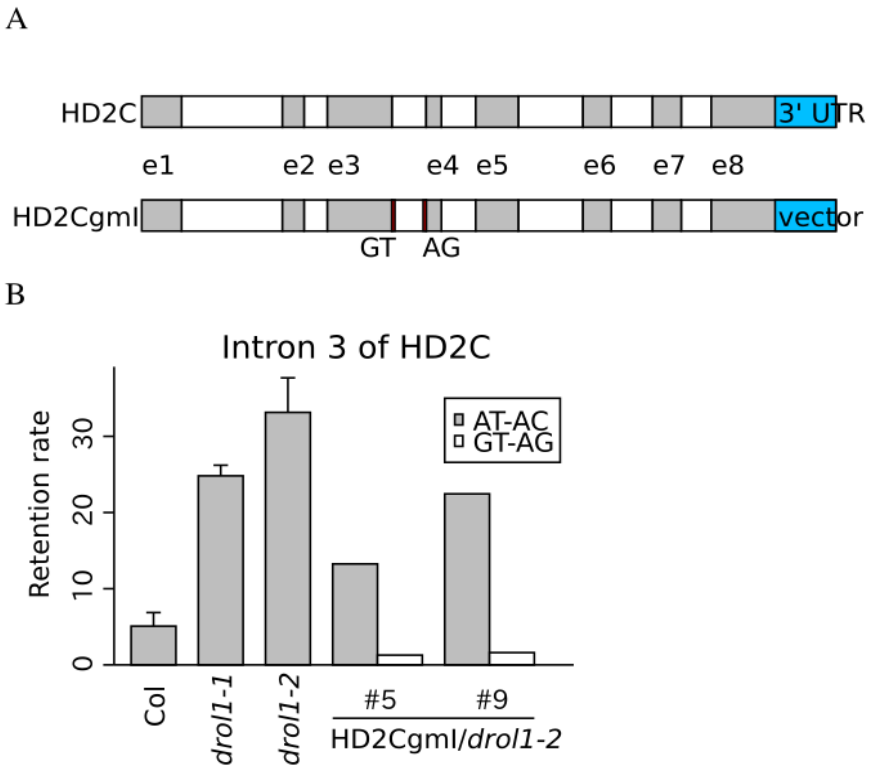


Figure 6. Retention rates of introns converted from AT–AC-type to GT–AG-type in *drol1-2*

(A) Gene structure of endogenous and modified *HD2C*. Eight exons (e1–8) and 3' untranslated region (3'UTR) in exon 8 are shown as gray and blue boxes, respectively. Two point mutations used to convert AT–AC-type to GT–AG-type introns are indicated by red bars. *HD2CgmI* is recombined to vector at the stop codon. (B) Retention rate of the third intron of *HD2C*. The retention rate of the AT–AC-type and GT–AG-type third intron in HD2CgmI is shown as gray and white boxes, respectively.

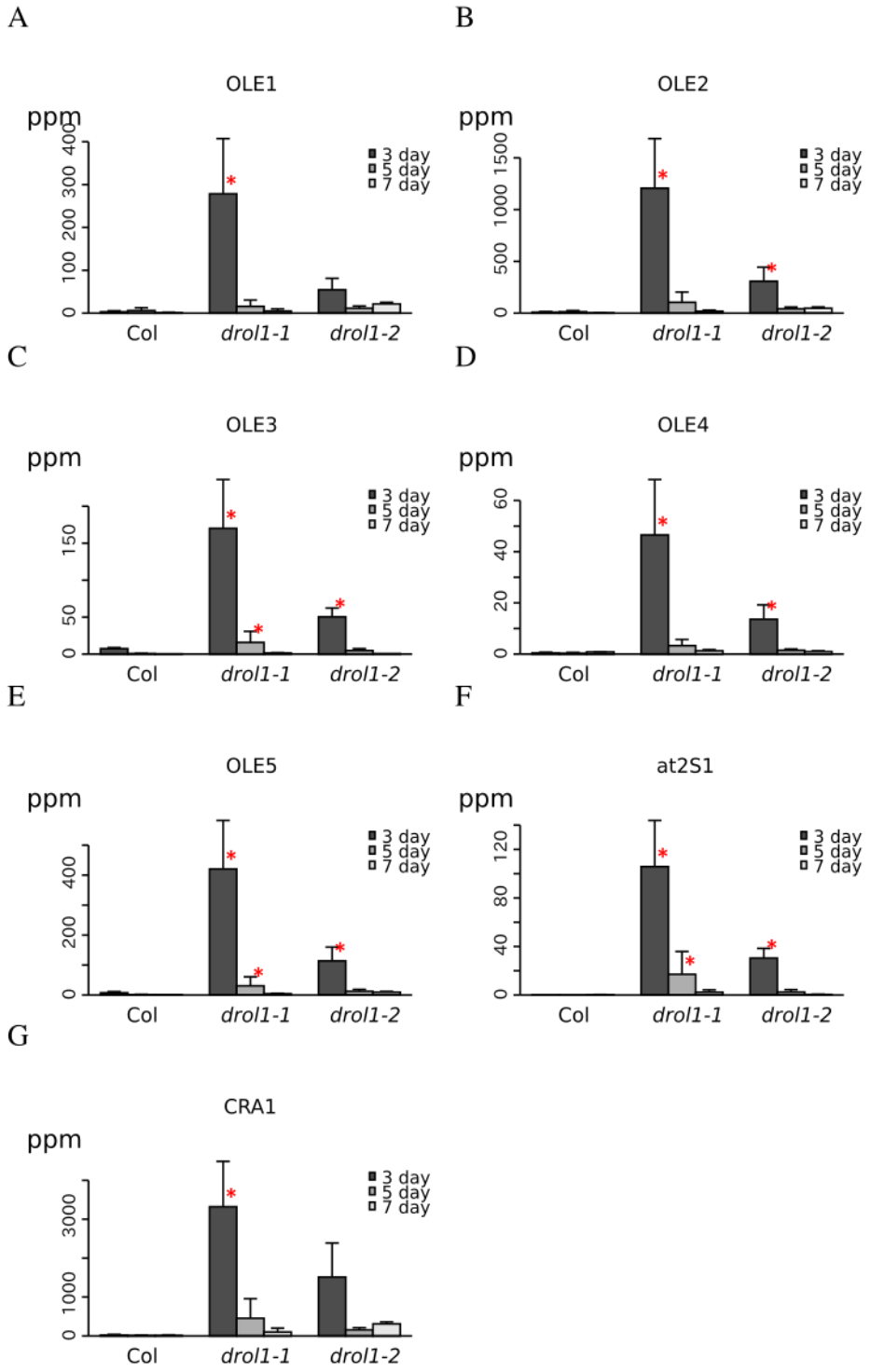


Figure 7. Differentially expressed genes (DEGs) in *drol1* mutants

(A–E) Expression levels of five *OLEOSIN* (*OLE*) genes in the wild-type and *drol1-1* and *drol1-2* mutants. Error bars indicate standard deviation (SD; n = 3). Red asterisks indicate significantly increased expression compared with the wild-type (FDR < 0.01). (F, G)

Expression levels of 2S albumin (At2S1) and 18S globulin (CRA1), respectively.

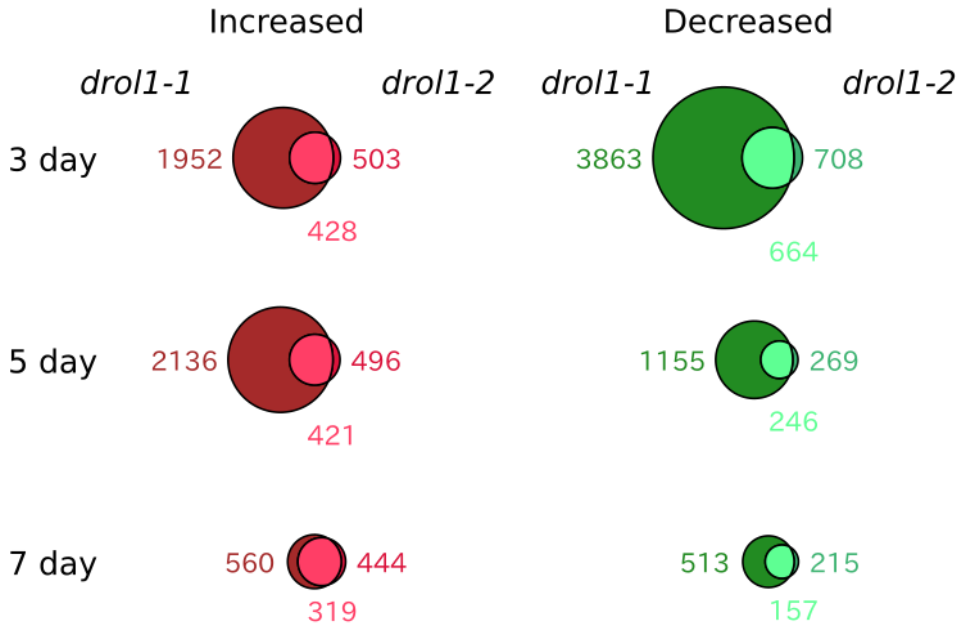


Figure 8. Differentially expressed genes (DEGs) in *drol1* mutants

DEGs were counted and displayed in circles. Red and green circles indicate upregulated and downregulated genes, respectively, in seedlings of *drol1* mutants compared with the wild-type. Genes are also indicated by numbers besides the circles and overlaps.

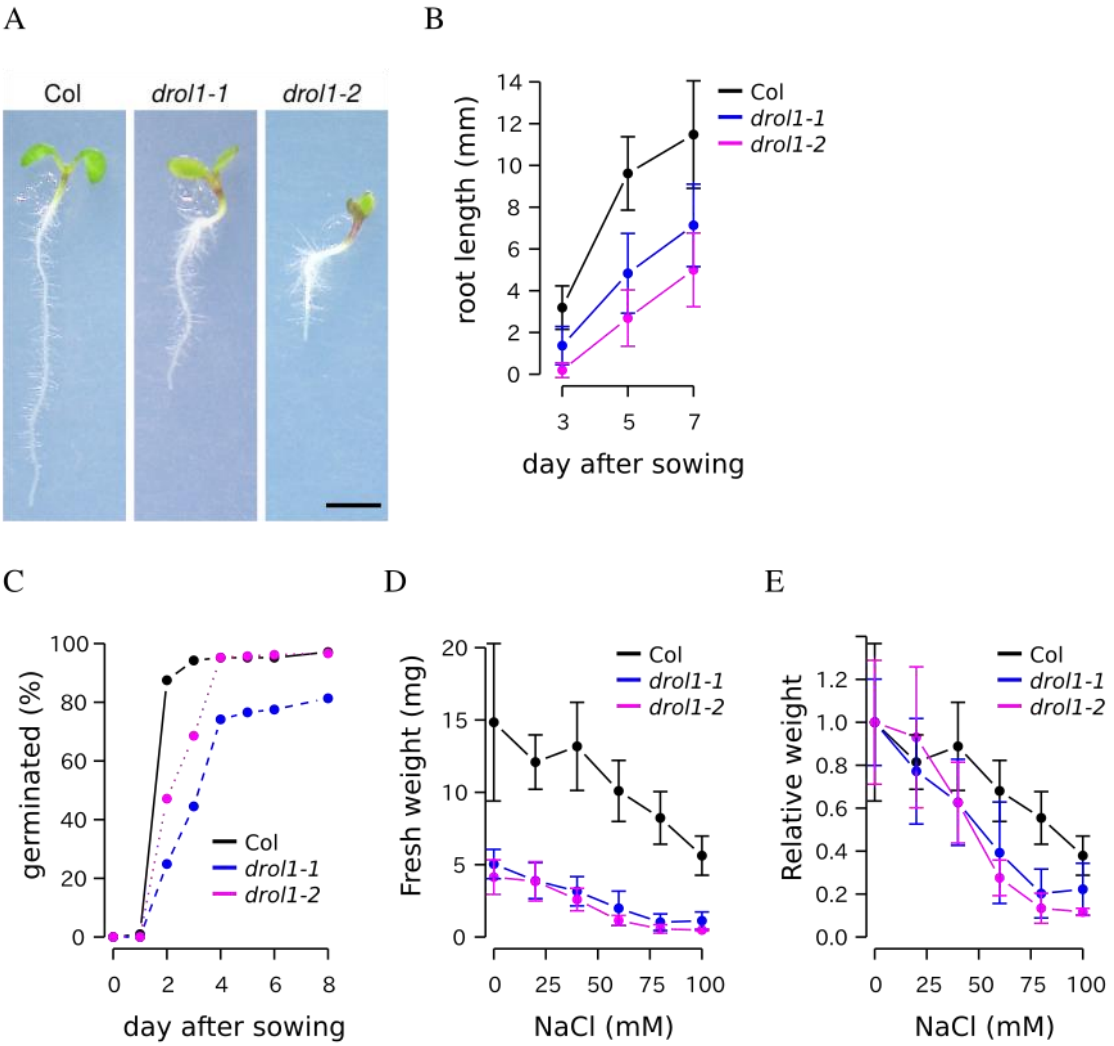
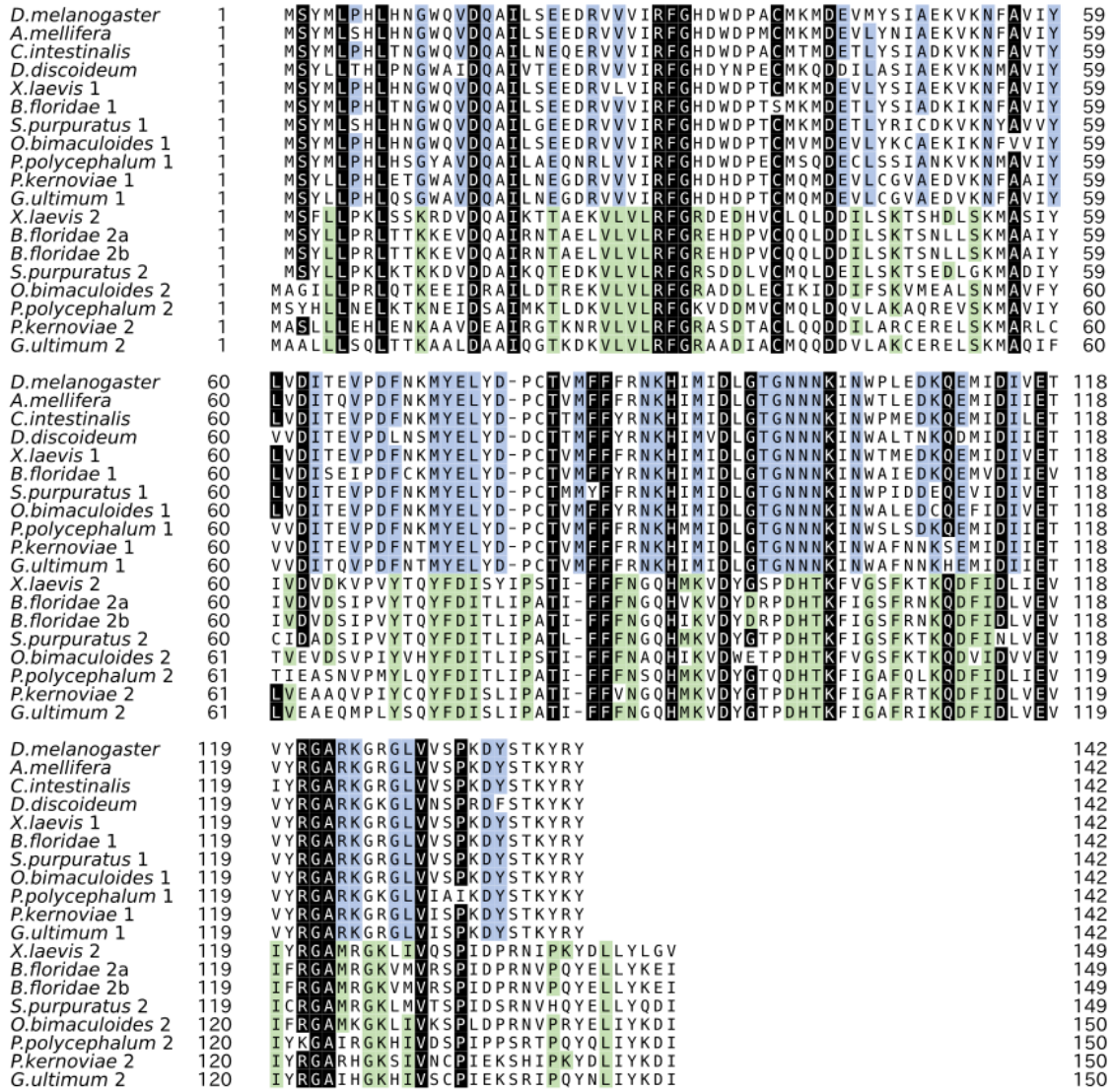


Figure 9. Phenotypes of the *drol1* mutant related to intron retention

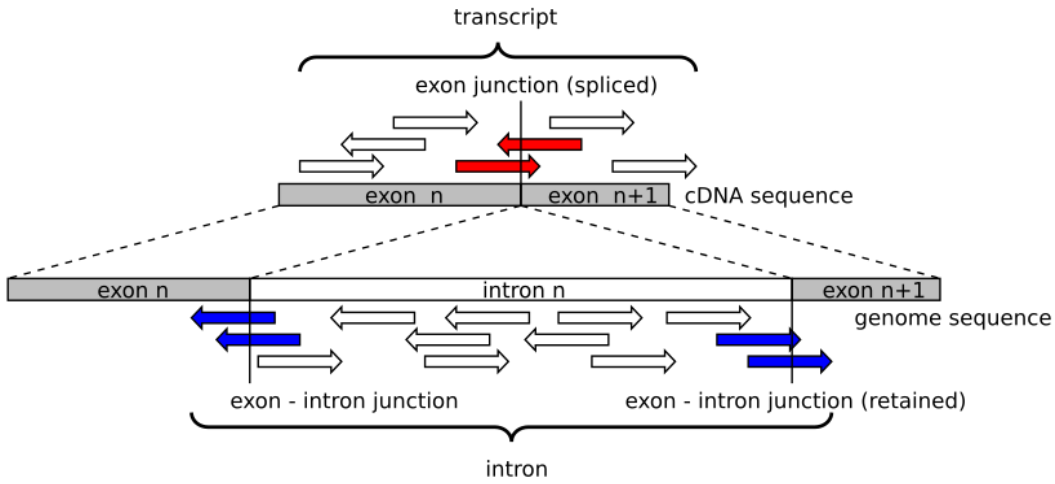
(A) Photographs of 5-day-old wild-type (Col), *drol1-1*, and *drol1-2* seedlings (from left to right). Scale bar = 2 mm. (B) Root length of 3–7-day-old seedlings. Error bars represent SD (n = 23–35). (C) Seed germination rate (n = 18–33). (D) Fresh weight of seedlings grown on medium supplemented with various concentrations of salt (NaCl) (n = 4–15). (E) Relative fresh weight for D.



Supplementary Figure 1. Multiple sequence alignment of DROL1 homologs

Sources of DROL1 amino acid sequences were as follows: *Drosophila melanogaster* (Q8SZ87_DROME in UniProt; https://www.uniprot.org/), *Xenopus laevis* (rna22650 rna37839 in Xlaevis 9.2; http://ftp.xenbase.org), *Apis mellifera* (genome assemblies from ftp://ftp.ensemblgenomes.org), *Ciona intestinalis* and *Branchiostoma floridae* (genome assemblies from https://genome.jgi.doe.g.,ov), *Strongylocentrotus purpuratus*, *Physarum polycephalum*, *Phytophthora kernoviae*, and *Globisporangium ultimum*: genome assemblies GCF_000002235.4, GCA_000413255.3, GCA_008080845.1, and GCA_000143045.1, respectively, from https://www.ncbi.nlm.nih.gov/. Open reading frames were identified in genome assemblies using tblastn and exonerate. Short reads of

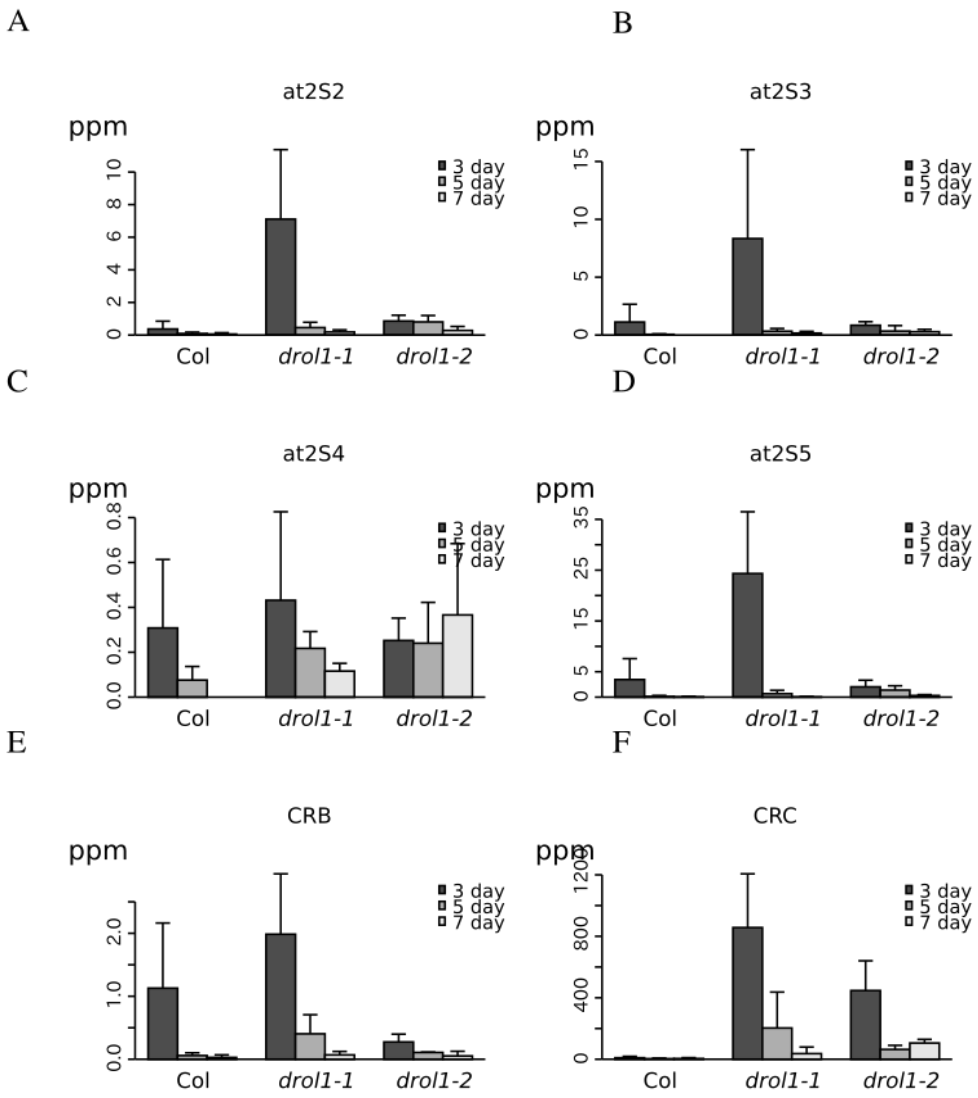
Octopus bimaculoides and *Dictyostelium discoideum* from the Short-Read Archive database (https://www.ncbi.nlm.nih.gov/sra) were assembled by Trinity. The rules for naming and coloring are consistent with those used in Figure 1.



$$Splicing\ efficiency = \frac{spliced}{spliced + retained/2} \times 100$$

Supplementary Figure 2. Scheme for the analysis of retained and spliced introns

Short reads obtained by RNA-Seq were first mapped to the cDNA reference and then counted by transcript to represent the transcript level. Reads spanning the exon–exon junctions (red arrows) were counted to represent the spliced level. Reads that did not map to cDNA reference were mapped to the genome reference. Among these reads, those spanning the exon–intron junction (blue arrows) were counted to determine the intron retention level. Splicing efficiency (SE) was calculated for each intron.



Supplementary Figure 3. Increased expression of genes encoding seed storage proteins in *drol1* seedlings

Expression levels of four 2S albumin and two 18S globulin genes, as determined by RNA-Seq, are shown. Error bars indicate standard deviation (SD; n = 3). Red asterisks indicate significantly increased expression compared with the wild-type (FDR < 0.01).

Supplemental Data Set 1. Upregulated genes in *drol1* seedlings at 3 days after germination (DAG)

Supplemental Data Set 2. Downregulated genes in *drol1* seedlings at 3 DAG

Supplemental Data Set 3. Gene Ontology (GO) analysis of upregulated genes in *drol1* mutants

Supplemental Data Set 4. GO analysis of downregulated genes in *drol1* mutants

Supplementary Data Set 1.

Upregulated genes in *drol1* seedlings at 3 days after germination (DAG)

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT2G19320	9.86	7.17	unknown protein	
AT4G27140	9.48	7.68	seed storage albumin 1	
AT1G32710	8.85	6.89	Cytochrome c oxidase, subunit Vib family protein	
AT4G31830	7.81	5.09	unknown protein	
AT5G62800	7.67	4.54	Protein with RING/U-box and TRAF-like domains	
AT3G13280	7.35	7.32	Putative endonuclease or glycosyl hydrolase	
AT4G18920	7.35	5.44	Protein of unknown function (DUF1264)	
AT3G22490	7.33	4.84	Seed maturation protein	
AT3G15280	7.15	4.92	unknown protein	
AT5G10000	7.11	5.12	ferredoxin 4	
AT2G42560	7.10	5.33	late embryogenesis abundant domain-containing protein / LEA domain-containing protein	
AT3G24220	7.08	5.80	nine-cis-epoxycarotenoid dioxygenase 6	
AT5G40420	6.96	4.99	oleosin 2	GO:0051235
AT1G07645	6.79	4.50	dessication-induced 1VOC superfamily protein	
AT2G15010	6.67	5.45	Plant thionin	
AT3G27660	6.60	4.83	oleosin 4	GO:0051235
AT5G01300	6.59	4.78	PEBP (phosphatidylethanolamine-binding protein) family protein	
AT2G05915	6.55	6.10	unknown protein	
AT1G27990	6.49	4.76	unknown protein	
AT5G09640	6.43	4.63	serine carboxypeptidase-like 19	
AT4G25580	6.36	4.58	CAP160 protein	GO:0009737
AT1G80090	6.32	4.72	Cystathionine beta-synthase (CBS) family protein	
AT3G51810	6.22	4.15	Stress induced protein	GO:0009737
AT2G44470	6.18	5.06	beta glucosidase 29	GO:0009651
AT5G51760	6.17	4.03	Protein phosphatase 2C family protein	GO:0009737
AT1G56600	6.14	4.42	galactinol synthase 2	GO:0009414
				GO:0009737
				GO:0009651
AT2G18540	6.11	4.47	RmlC-like cupins superfamily protein	
AT2G19900	6.07	4.51	NADP-malic enzyme 1	
AT2G40170	6.06	3.92	Stress induced protein	GO:0009737
AT5G52300	6.01	4.53	CAP160 protein	GO:0009414
				GO:0009737
				GO:0009651
AT1G48130	5.98	4.03	1-cysteine peroxiredoxin 1	GO:0009414
AT2G21490	5.92	4.11	dehydrin LEA	GO:0009414
				GO:0009737
AT3G17520	5.82	4.32	Late embryogenesis abundant protein (LEA) family protein	
AT3G01570	5.81	3.92	Oleosin family protein	GO:0051235
AT4G01970	5.79	3.90	stachyose synthase	
AT3G21370	5.77	4.58	beta glucosidase 19	GO:0009651
AT4G36600	5.76	4.16	Late embryogenesis abundant (LEA) protein	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT2G21820	5.72	3.93	unknown protein	
AT3G54940	5.66	3.93	Papain family cysteine protease	
AT1G02700	5.63	3.73	unknown protein	
AT1G52690	5.63	4.51	Late embryogenesis abundant protein (LEA) family protein	GO:0009414
AT2G25890	5.63	3.85	Oleosin family protein	GO:0051235
AT5G47130	5.55	4.37	Bax inhibitor-1 family protein	
AT5G18450	5.54	4.21	Integrase-type DNA-binding superfamily protein	
AT2G47770	5.53	3.80	TSPO(outer membrane tryptophan-rich sensory protein)-related	GO:0009737
				GO:0009651
AT5G66400	5.50	3.60	Dehydrin family protein	GO:0009414
				GO:0009737
AT3G15670	5.49	3.98	Late embryogenesis abundant protein (LEA) family protein	
AT2G35590	5.48	5.66	pseudogene	
AT3G03620	5.47	3.72	MATE efflux family protein	
AT3G53040	5.46	3.71	late embryogenesis abundant protein, putative / LEA protein, putative	
AT5G04010	5.44	4.06	F-box family protein	
AT1G47980	5.44	4.65	unknown protein	
AT2G27940	5.40	4.20	RING/U-box superfamily protein	
AT3G03341	5.40	3.95	unknown protein	
AT2G36640	5.38	3.74	embryonic cell protein 63	
AT2G23640	5.38	3.57	Reticulan like protein B13	
AT4G21020	5.32	4.14	Late embryogenesis abundant protein (LEA) family protein	
AT4G36700	5.27	4.17	RmlC-like cupins superfamily protein	
AT2G18340	5.26	3.66	late embryogenesis abundant domain-containing protein / LEA domain-containing protein	
AT5G44310	5.23	4.00	Late embryogenesis abundant protein (LEA) family protein	
AT2G29380	5.18	3.13	highly ABA-induced PP2C gene 3	
AT5G65165	5.18	3.59	succinate dehydrogenase 2-3	
AT1G17810	5.11	3.43	beta-tonoplast intrinsic protein	
AT1G23070	5.09	3.74	Protein of unknown function (DUF300)	
AT1G14930	5.07	3.35	Polyketide cyclase/dehydrase and lipid transport superfamily protein	
AT1G16850	4.94	3.42	unknown protein	GO:0009651
AT5G49120	4.93	3.32	Protein of unknown function (DUF581)	
AT1G03120	4.91	3.22	responsive to abscisic acid 28	
AT3G18610	4.88	3.82	nucleolin like 2	
AT5G22545	4.86	4.33	unknown protein	
AT1G03790	4.84	3.12	Zinc finger C-x8-C-x5-C-x3-H type family protein	
AT1G01520	4.79	3.82	Homeodomain-like superfamily protein	
AT2G18050	4.79	3.80	histone H1-3	GO:0009414
AT1G22600	4.78	3.18	Late embryogenesis abundant protein (LEA) family protein	
AT5G06760	4.77	3.44	Late Embryogenesis Abundant 4-5	GO:0009414
AT1G04660	4.76	3.81	glycine-rich protein	
AT4G27530	4.76	3.25	unknown protein	
AT5G05220	4.73	4.00	unknown protein	
AT1G67855	4.67	3.97	unknown protein	
AT2G33280	4.65	4.32	Major facilitator superfamily protein	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT5G63350	4.65	3.39	unknown protein	
AT3G11050	4.63	3.08	ferritin 2	GO:0051235
				GO:0009737
AT1G67856	4.63	3.84	RING/U-box superfamily protein	
AT1G16730	4.57	2.93	unknown protein 6	
AT5G44260	4.55	2.42	Zinc finger C-x8-C-x5-C-x3-H type family protein	
AT5G51210	4.52	2.76	oleosin3	GO:0051235
AT1G24580	4.52	3.24	RING/U-box superfamily protein	
AT4G10020	4.51	3.37	hydroxysteroid dehydrogenase 5	
AT5G01670	4.50	2.56	NAD(P)-linked oxidoreductase superfamily protein	
AT2G02850	4.50	2.71	plantacyanin	
AT2G18180	4.48	4.52	Sec14p-like phosphatidylinositol transfer family protein	
AT2G21720	4.47	2.88	Plant protein of unknown function (DUF639)	
AT2G31980	4.45	2.70	PHYTOCYSTATIN 2	
AT1G04920	4.43	2.98	sucrose phosphate synthase 3F	
AT4G11910	4.42	3.05	unknown protein	
AT5G13210	4.39	3.30	Uncharacterised conserved protein UCP015417, vWA	
AT4G15396	4.35	4.27	cytochrome P450, family 702, subfamily A, polypeptide 6	
AT1G15330	4.29	3.30	Cystathionine beta-synthase (CBS) protein	
AT5G59390	4.20	3.74	XH/XS domain-containing protein	
AT3G02480	4.20	2.86	Late embryogenesis abundant protein (LEA) family protein	GO:0009414
AT1G67100	4.13	2.92	LOB domain-containing protein 40	
AT5G01520	4.12	2.97	RING/U-box superfamily protein	GO:0009737
				GO:0009651
AT2G35570	4.07	4.38	pseudogene	
AT2G38465	4.06	2.55	unknown protein	
AT2G18570	3.97	2.66	UDP-Glycosyltransferase superfamily protein	
AT5G04500	3.95	2.79	glycosyltransferase family protein 47	GO:0009737
				GO:0009651
AT5G60760	3.95	2.56	P-loop containing nucleoside triphosphate hydrolases superfamily protein	
AT5G57790	3.93	2.68	unknown protein	
AT4G01180	3.92	3.47	XH/XS domain-containing protein	
AT5G38780	3.91	2.80	S-adenosyl-L-methionine-dependent methyltransferases superfamily protein	
AT2G27380	3.89	4.17	extensin proline-rich 1	
AT5G59320	3.87	2.46	lipid transfer protein 3	GO:0009414
				GO:0009737
AT3G21380	3.80	3.56	Mannose-binding lectin superfamily protein	
AT4G02280	3.80	2.30	sucrose synthase 3	GO:0009414
AT2G15130	3.78	3.63	Plant basic secretory protein (BSP) family protein	
AT4G18650	3.76	2.54	transcription factor-related	
AT4G33467	3.74	3.34	unknown protein	
AT3G51750	3.72	2.19	unknown protein	
AT2G18190	3.71	3.13	P-loop containing nucleoside triphosphate hydrolases superfamily protein	
AT5G57550	3.70	3.35	xyloglucan endotransglucosylase/hydrolase 25	
AT5G53870	3.68	2.59	early nodulin-like protein 1	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT1G64110	3.63	2.71	P-loop containing nucleoside triphosphate hydrolases superfamily protein	
AT4G15390	3.61	2.30	HXXXD-type acyl-transferase family protein	
AT1G22340	3.59	2.86	UDP-glucosyl transferase 85A7	
AT2G04050	3.55	3.04	MATE efflux family protein	
AT3G22860	3.53	3.78	eukaryotic translation initiation factor 3 subunit C2	
AT1G77120	3.53	2.40	alcohol dehydrogenase 1	GO:0009414
				GO:0009737
				GO:0009651
AT5G55470	3.52	2.34	Na+/H+ (sodium hydrogen) exchanger 3	GO:0009651
AT5G55460	3.51	2.15	Bifunctional inhibitor/lipid-transfer protein/seed storage 2S albumin superfamily protein	
AT1G35910	3.46	2.62	Haloacid dehalogenase-like hydrolase (HAD) superfamily protein	GO:0009651
AT4G12680	3.46	2.29	unknown protein	
AT3G20710	3.46	2.07	F-box family protein	
AT4G19810	3.45	2.62	Glycosyl hydrolase family protein with chitinase insertion domain	GO:0009737
				GO:0009651
AT2G36270	3.42	2.17	Basic-leucine zipper (bZIP) transcription factor family protein	GO:0009414
				GO:0009737
				GO:0009651
AT4G18220	3.40	2.66	Drug/metabolite transporter superfamily protein	
AT3G27473	3.39	1.97	Cysteine/Histidine-rich C1 domain family protein	
AT4G24040	3.36	2.74	trehalase 1	
AT2G20800	3.35	2.03	NAD(P)H dehydrogenase B4	
AT1G21520	3.32	2.22	unknown protein	
AT5G60142	3.31	3.69	AP2/B3-like transcriptional factor family protein	
AT1G78780	3.22	2.00	pathogenesis-related family protein	
AT5G61740	3.17	3.11	ABC2 homolog 14	
AT5G07060	3.15	2.60	CCCH-type zinc fingerfamily protein with RNA-binding domain	
AT1G65370	3.15	2.83	TRAF-like family protein	
AT5G50770	3.12	2.58	hydroxysteroid dehydrogenase 6	
AT3G45730	3.01	1.99	unknown protein	
AT5G52310	3.00	2.21	low-temperature-responsive protein 78 (LTI78) / desiccation-responsive protein 29A (RD29A)	GO:0009414
				GO:0009737
				GO:0009651
AT4G10440	2.99	3.63	S-adenosyl-L-methionine-dependent methyltransferases superfamily protein	
AT1G08830	2.98	2.59	copper/zinc superoxide dismutase 1	GO:0009651
AT1G62710	2.96	1.89	beta vacuolar processing enzyme	
AT3G06435	2.95	2.45	Expressed protein	
AT4G12290	2.94	1.36	Copper amine oxidase family protein	
AT3G30120	2.92	2.11	pseudogene	
AT5G18220	2.92	2.23	O-Glycosyl hydrolases family 17 protein	
AT3G21600	2.90	1.36	Senescence/dehydration-associated protein-related	
AT1G01240	2.90	1.84	unknown protein	
AT1G19490	2.90	1.86	Basic-leucine zipper (bZIP) transcription factor family protein	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT1G07985	2.89	2.27	Expressed protein	
AT5G22110	2.89	2.67	DNA polymerase epsilon subunit B2	
AT5G58610	2.86	2.40	PHD finger transcription factor, putative	
AT1G62290	2.82	1.76	Saposin-like aspartyl protease family protein	
AT5G44417	2.82	2.35	pseudogene	
AT3G12203	2.80	2.18	serine carboxypeptidase-like 17	
AT1G14520	2.80	2.01	myo-inositol oxygenase 1	
AT4G23600	2.78	3.67	Tyrosine transaminase family protein	GO:0009737
				GO:0009651
AT3G30460	2.78	2.19	RING/U-box superfamily protein	
AT1G12520	2.77	1.45	copper chaperone for SOD1	
AT2G28190	2.77	1.31	copper/zinc superoxide dismutase 2	GO:0009651
AT1G01600	2.77	2.14	cytochrome P450, family 86, subfamily A, polypeptide 4	
AT1G79610	2.74	2.05	Na+/H+ antiporter 6	
AT1G01470	2.74	1.70	Late embryogenesis abundant protein	GO:0009414
AT5G02580	2.74	2.20	Plant protein 1589 of unknown function	
AT2G04070	2.73	2.37	MATE efflux family protein	
AT4G26590	2.72	1.71	oligopeptide transporter 5	
AT4G15910	2.70	1.39	drought-induced 21	GO:0009414
				GO:0009737
AT1G69260	2.70	1.91	ABI five binding protein	GO:0009737
AT5G47810	2.69	1.30	phosphofructokinase 2	
AT3G24780	2.69	2.12	Uncharacterised conserved protein UCP015417, vWA	
AT1G26800	2.68	1.76	RING/U-box superfamily protein	
AT1G10300	2.68	1.61	Nucleolar GTP-binding protein	
AT5G39850	2.66	1.57	Ribosomal protein S4	
AT3G15357	2.64	1.62	unknown protein	
AT1G05680	2.63	1.40	Uridine diphosphate glycosyltransferase 74E2	GO:0009414
				GO:0009737
				GO:0009651
AT1G24735	2.63	1.73	S-adenosyl-L-methionine-dependent methyltransferases superfamily protein	
AT5G61270	2.58	2.30	phytochrome-interacting factor7	
AT4G31520	2.52	1.92	SDA1 family protein	
AT4G04870	2.50	1.06	cardiolipin synthase	
AT5G22290	2.50	1.50	NAC domain containing protein 89	
AT5G45540	2.50	2.17	Protein of unknown function (DUF594)	
AT5G59670	2.49	2.14	Leucine-rich repeat protein kinase family protein	
AT5G66460	2.47	1.11	Glycosyl hydrolase superfamily protein	
AT3G01600	2.47	1.65	NAC domain containing protein 44	
AT4G22920	2.47	1.85	non-yellowing 1	
AT3G01345	2.45	2.72	Expressed protein	
AT4G00390	2.45	2.14	DNA-binding storekeeper protein-related transcriptional regulator	
AT4G22470	2.44	2.83	protease inhibitor/seed storage/lipid transfer protein (LTP) family protein	
AT5G66580	2.43	1.39	unknown protein	
AT4G23050	2.43	1.39	PAS domain-containing protein tyrosine kinase family protein	
AT5G53700	2.42	2.25	RNA-binding (RRM/RBD/RNP motifs) family protein	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT5G44980	2.41	1.76	F-box/RNI-like/FBD-like domains-containing protein	
AT5G06980	2.35	2.01	unknown protein	
AT1G08430	2.34	2.52	aluminum-activated malate transporter 1	
AT5G64080	2.34	1.03	Bifunctional inhibitor/lipid-transfer protein/seed storage 2S albumin superfamily protein	
AT4G22990	2.33	1.65	Major Facilitator Superfamily with SPX (SYG1/Pho81/XPR1) domain-containing protein	
AT1G13740	2.32	1.41	ABI five binding protein 2	GO:0009414
				GO:0009737
AT4G24480	2.30	1.42	Protein kinase superfamily protein	
AT2G43590	2.30	1.82	Chitinase family protein	
AT3G13090	2.28	2.15	multidrug resistance-associated protein 8	
AT5G07010	2.28	1.97	sulfotransferase 2A	
AT1G29940	2.26	2.20	nuclear RNA polymerase A2	
AT5G49990	2.26	1.04	Xanthine/uracil permease family protein	
AT4G32770	2.25	0.98	tocopherol cyclase, chloroplast / vitamin E deficient 1 (VTE1) / sucrose export defective 1 (SXD1)	
AT5G07360	2.23	0.89	Amidase family protein	
AT5G03570	2.22	1.93	iron regulated 2	
AT3G12320	2.22	1.59	unknown protein	
AT4G32290	2.21	1.17	Core-2/I-branching beta-1,6-N-acetylglucosaminyltransferase family protein	
AT5G24970	2.20	1.02	Protein kinase superfamily protein	
AT2G18193	2.20	1.59	P-loop containing nucleoside triphosphate hydrolases superfamily protein	
AT3G61630	2.19	1.70	cytokinin response factor 6	
AT2G19850	2.17	2.83	unknown protein	
AT4G35300	2.17	0.93	tonoplast monosaccharide transporter2	
AT4G17550	2.17	1.14	Major facilitator superfamily protein	
AT2G34655	2.17	2.10	unknown protein	
AT2G14100	2.16	1.86	cytochrome P450, family 705, subfamily A, polypeptide 13	
AT5G56100	2.15	1.82	glycine-rich protein / oleosin	GO:0051235
AT4G28240	2.14	1.61	Wound-responsive family protein	
AT1G71280	2.13	1.30	DEA(D/H)-box RNA helicase family protein	
AT3G28580	2.12	2.86	P-loop containing nucleoside triphosphate hydrolases superfamily protein	GO:0009737
AT5G64260	2.12	1.41	EXORDIUM like 2	
AT4G16563	2.12	1.53	Eukaryotic aspartyl protease family protein	
AT5G17800	2.09	1.44	myb domain protein 56	
AT4G01460	2.09	1.44	basic helix-loop-helix (bHLH) DNA-binding superfamily protein	
AT3G03310	2.08	1.13	lecithin:cholesterol acyltransferase 3	
AT5G06190	2.06	1.31	unknown protein	
AT4G27450	2.06	1.76	Aluminium induced protein with YGL and LRDR motifs	
AT1G07180	2.04	1.48	alternative NAD(P)H dehydrogenase 1	
AT3G09910	2.03	1.11	RAB GTPase homolog C2B	
AT4G19700	2.02	1.27	SBP (S-ribonuclease binding protein) family protein	
AT5G02200	2.02	2.01	far-red-elongated hypocotyl1-like	GO:0051235
AT3G50230	2.02	1.89	Leucine-rich repeat protein kinase family protein	
AT2G40010	2.01	1.35	Ribosomal protein L10 family protein	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT4G25170	1.99	1.64	Uncharacterised conserved protein (UCP012943)	
AT4G11350	1.97	1.26	Protein of unknown function (DUF604)	
AT4G04030	1.97	2.79	ovate family protein 9	
AT3G53210	1.96	1.46	nodulin MtN21 /EamA-like transporter family protein	
AT3G62090	1.95	1.16	phytochrome interacting factor 3-like 2	
AT1G08910	1.95	1.79	zinc ion binding;zinc ion binding	
AT1G34180	1.93	1.40	NAC domain containing protein 16	
AT3G27220	1.93	1.82	Galactose oxidase/kelch repeat superfamily protein	
AT3G23570	1.90	0.84	alpha/beta-Hydrolases superfamily protein	
AT1G68870	1.88	1.30	SOB five-like 2	
AT5G15120	1.87	1.72	Protein of unknown function (DUF1637)	
AT5G37500	1.87	1.43	gated outwardly-rectifying K+ channel	GO:0009414
				GO:0009737
AT5G57390	1.83	1.38	AINTEGUMENTA-like 5	
AT1G27680	1.83	0.82	ADPGLC-PPase large subunit	
AT5G05640	1.83	0.96	nucleoprotein-related	
AT2G43500	1.83	1.23	Plant regulator RWP-RK family protein	
AT3G15790	1.82	1.16	methyl-CPG-binding domain 11	
AT2G29090	1.81	1.47	cytochrome P450, family 707, subfamily A, polypeptide 2	
AT5G24280	1.81	1.17	gamma-irradiation and mitomycin c induced 1	
AT1G07080	1.80	0.88	Thioredoxin superfamily protein	
AT1G67960	1.78	1.78	unknown protein	GO:0051235
AT3G54730	1.77	2.51	unknown protein	
AT1G17960	1.75	1.44	Threonyl-tRNA synthetase	
AT5G60250	1.75	1.20	zinc finger (C3HC4-type RING finger) family protein	
AT3G10190	1.73	1.12	Calcium-binding EF-hand family protein	
AT5G08600	1.73	1.68	U3 ribonucleoprotein (Utp) family protein	
AT1G68020	1.72	0.97	UDP-Glycosyltransferase / trehalose-phosphatase family protein	
AT5G18210	1.72	1.30	NAD(P)-binding Rossmann-fold superfamily protein	
AT2G46270	1.71	1.35	G-box binding factor 3	GO:0009737
AT5G38200	1.71	1.41	Class I glutamine amidotransferase-like superfamily protein	
AT1G35530	1.68	1.64	DEAD/DEAH box RNA helicase family protein	
AT3G14595	1.67	0.83	Ribosomal protein L18ae family	
AT5G59570	1.67	1.10	Homeodomain-like superfamily protein	
AT3G10500	1.66	0.71	NAC domain containing protein 53	GO:0009414
AT3G02990	1.65	1.09	heat shock transcription factor A1E	
AT3G59580	1.65	0.94	Plant regulator RWP-RK family protein	
AT3G30214	1.63	1.20	pseudogene	
AT1G67120	1.62	1.04	ATPases;nucleotide binding;ATP binding;nucleoside-triphosphatases;transcription factor binding	
AT1G30040	1.62	1.62	gibberellin 2-oxidase	
AT4G31500	1.61	1.11	cytochrome P450, family 83, subfamily B, polypeptide 1	
AT1G68945	1.61	1.34	unknown protein	
AT5G59660	1.60	1.51	Leucine-rich repeat protein kinase family protein	
AT3G01490	1.59	1.32	Protein kinase superfamily protein	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT5G57240	1.59	1.05	OSBP(oxysterol binding protein)-related protein 4C	
AT4G31877	1.59	1.51	MIR156C; miRNA	
AT2G41070	1.55	1.06	Basic-leucine zipper (bZIP) transcription factor family protein	GO:0009737
AT1G65510	1.54	1.77	unknown protein	
AT1G18100	1.54	1.15	PEBP (phosphatidylethanolamine-binding protein) family protein	GO:0009737
AT5G51810	1.52	1.79	gibberellin 20 oxidase 2	
AT1G06720	1.52	1.12	P-loop containing nucleoside triphosphate hydrolases superfamily protein	
AT1G76170	1.50	1.26	2-thiocytidine tRNA biosynthesis protein, TtcA	
AT2G43510	1.49	1.02	trypsin inhibitor protein 1	
AT4G21326	1.47	1.58	subtilase 3.12	
AT5G25460	1.47	1.03	Protein of unknown function, DUF642	
AT1G18460	1.46	0.86	alpha/beta-Hydrolases superfamily protein	
AT5G56900	1.45	1.21	CwfJ-like family protein / zinc finger (CCCH-type) family protein	
AT5G15960	1.44	1.67	stress-responsive protein (KIN1) / stress-induced protein (KIN1)	GO:0009414
				GO:0009737
AT3G23470	1.44	1.42	Cyclopropane-fatty-acyl-phospholipid synthase	
AT3G06820	1.43	1.16	Mov34/MPN/PAD-1 family protein	
AT1G26680	1.41	1.21	transcriptional factor B3 family protein	
AT1G32583	1.41	1.47	unknown protein	
AT5G49300	1.41	0.97	GATA transcription factor 16	
AT3G16180	1.40	0.95	Major facilitator superfamily protein	
AT4G24900	1.39	1.25	unknown protein	
AT1G66760	1.36	1.40	MATE efflux family protein	
AT1G60060	1.34	1.21	Serine/threonine-protein kinase WNK (With No Lysine)-related	
AT5G65660	1.34	1.03	hydroxyproline-rich glycoprotein family protein	
AT2G44970	1.34	0.76	alpha/beta-Hydrolases superfamily protein	
AT3G27620	1.33	1.22	alternative oxidase 1C	
AT4G19960	1.33	1.25	K+ uptake permease 9	
AT4G00335	1.32	0.95	RING-H2 finger B1A	
AT3G48260	1.32	1.09	with no lysine (K) kinase 3	
AT2G36390	1.32	0.68	starch branching enzyme 2.1	
AT5G66730	1.32	0.69	C2H2-like zinc finger protein	
AT5G01740	1.30	1.65	Nuclear transport factor 2 (NTF2) family protein	
AT2G46420	1.30	0.96	Plant protein 1589 of unknown function	
AT4G38810	1.29	0.82	Calcium-binding EF-hand family protein	
AT1G15790	1.28	1.25	unknown protein	
AT4G04745	1.27	1.08	unknown protein	
AT3G53800	1.27	0.87	Fes1B	
AT4G21680	1.25	1.41	NITRATE TRANSPORTER 1.8	
AT1G21460	1.24	0.78	Nodulin MtN3 family protein	
AT5G50090	1.23	1.02	unknown protein	
AT1G62130	1.23	0.98	AAA-type ATPase family protein	
AT1G12420	1.23	0.98	ACT domain repeat 8	GO:0009737
AT5G65640	1.21	1.03	beta HLH protein 93	
AT5G22580	1.21	0.91	Stress responsive A/B Barrel Domain	
AT1G01990	1.20	0.75	unknown protein	
AT1G48540	1.19	0.80	Outer arm dynein light chain 1 protein	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT2G20570	1.19	1.38	GBF's pro-rich region-interacting factor 1	
AT2G34260	1.19	0.84	transducin family protein / WD-40 repeat family protein	
AT2G07680	1.19	0.84	multidrug resistance-associated protein 11	
AT4G16770	1.19	0.92	2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein	
AT4G36210	1.18	0.67	Protein of unknown function (DUF726)	
AT1G77320	1.18	1.07	transcription coactivators	
AT4G31000	1.17	1.39	Calmodulin-binding protein	
AT2G46730	1.15	1.01	pseudogene	
AT4G15260	1.15	1.00	UDP-Glycosyltransferase superfamily protein	
AT1G43670	1.15	0.82	Inositol monophosphatase family protein	GO:0009737
AT5G22500	1.14	1.13	fatty acid reductase 1	GO:0009651
AT4G18140	1.14	0.97	SCP1-like small phosphatase 4b	
AT3G18370	1.13	0.73	C2 domain-containing protein	
AT1G62360	1.11	1.13	KNOX/ELK homeobox transcription factor	
AT4G02430	1.11	0.94	RNA-binding (RRM/RBD/RNP motifs) family protein	
AT3G18980	1.09	0.70	EIN2 targeting protein1	
AT5G08430	1.09	0.84	SWIB/MDM2 domain;Plus-3;GYF	
AT3G10450	1.09	1.20	serine carboxypeptidase-like 7	
AT3G24450	1.08	1.34	Heavy metal transport/detoxification superfamily protein	
AT3G29270	1.08	0.87	RING/U-box superfamily protein	
AT1G26170	1.07	0.75	ARM repeat superfamily protein	
AT1G72770	1.06	0.81	homology to ABI1	
AT1G35320	1.06	0.74	unknown protein	
AT5G57050	1.05	0.99	Protein phosphatase 2C family protein	GO:0009414
				GO:0009737
AT3G16030	1.04	1.15	lectin protein kinase family protein	
AT1G54370	1.03	1.04	sodium hydrogen exchanger 5	
AT1G48840	1.03	0.65	Plant protein of unknown function (DUF639)	
AT1G21920	1.02	0.77	Histone H3 K4-specific methyltransferase SET7/9 family protein	
AT1G56220	1.02	0.87	Dormancy/auxin associated family protein	
AT4G30900	1.01	1.03	DNAse I-like superfamily protein	
AT5G43740	1.01	1.31	Disease resistance protein (CC-NBS-LRR class) family	
AT1G32230	1.01	0.84	WWE protein-protein interaction domain protein family	GO:0009414
				GO:0009651
AT5G09330	0.99	0.76	NAC domain containing protein 82	
AT2G35820	0.97	0.90	ureidoglycolate hydrolases	
AT1G11580	0.97	1.36	methylesterase PCR A	
AT5G38380	0.96	0.87	unknown protein	
AT1G52980	0.96	0.66	GTP-binding family protein	
AT5G50760	0.95	0.83	SAUR-like auxin-responsive protein family	
AT2G44270	0.94	0.79	repressor of lrx1	
AT5G58350	0.94	0.78	with no lysine (K) kinase 4	
AT3G61010	0.94	0.83	Ferritin/ribonucleotide reductase-like family protein	GO:0051235
AT1G23280	0.93	0.78	MAK16 protein-related	
AT4G23330	0.93	0.84	unknown protein	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT1G65920	0.92	0.96	Regulator of chromosome condensation (RCC1) family with FYVE zinc finger domain	
AT3G08030	0.92	0.87	Protein of unknown function, DUF642	
AT2G46450	0.91	0.96	cyclic nucleotide-gated channel 12	
AT5G49500	0.91	0.98	Signal recognition particle, SRP54 subunit protein	
AT5G51620	0.91	1.06	Uncharacterised protein family (UPF0172)	
AT2G45510	0.91	0.76	cytochrome P450, family 704, subfamily A, polypeptide 2	
AT5G18410	0.91	0.86	transcription activators	
AT5G67170	0.88	1.03	SEC-C motif-containing protein / OTU-like cysteine protease family protein	
AT3G51120	0.88	0.88	DNA binding;zinc ion binding;nucleic acid binding;nucleic acid binding	
AT5G01780	0.88	0.74	2-oxoglutarate-dependent dioxygenase family protein	
AT3G01820	0.88	0.72	P-loop containing nucleoside triphosphate hydrolases superfamily protein	
AT2G42170	0.87	0.77	Actin family protein	
AT5G14120	0.87	0.84	Major facilitator superfamily protein	
AT2G01100	0.86	0.75	unknown protein	
AT2G42330	0.86	0.82	GC-rich sequence DNA-binding factor-like protein with Tuftelin interacting domain	
AT5G66610	0.85	0.92	DA1-related protein 7	
AT5G42370	0.85	0.84	Calcineurin-like metallo-phosphoesterase superfamily protein	
AT3G55520	0.85	0.65	FKBP-like peptidyl-prolyl cis-trans isomerase family protein	
AT2G48100	0.84	0.67	Exonuclease family protein	
AT5G61520	0.84	0.86	Major facilitator superfamily protein	
AT1G06630	0.82	0.63	F-box/RNI-like superfamily protein	
AT5G03140	0.82	0.90	Concanavalin A-like lectin protein kinase family protein	
AT2G43970	0.81	0.65	RNA-binding protein	
AT1G49360	0.81	0.73	F-box family protein	
AT3G20100	0.81	0.97	cytochrome P450, family 705, subfamily A, polypeptide 19	
AT4G38270	0.80	0.65	galacturonosyltransferase 3	
AT3G53180	0.80	0.94	glutamate-ammonia ligases;catalytics;glutamate-ammonia ligases	GO:0009737
AT5G41370	0.80	0.75	homolog of xeroderma pigmentosum complementation group B 1	
AT2G39570	0.77	0.89	ACT domain-containing protein	
AT1G13710	0.77	0.80	cytochrome P450, family 78, subfamily A, polypeptide 5	
AT1G79950	0.75	0.72	RAD3-like DNA-binding helicase protein	
AT4G36980	0.75	0.70	unknown protein	
AT1G11280	0.74	0.55	S-locus lectin protein kinase family protein	
AT3G32940	0.74	0.74	RNA-binding KH domain-containing protein	
AT5G06560	0.74	0.76	Protein of unknown function, DUF593	
AT1G21050	0.74	0.89	Protein of unknown function, DUF617	
AT4G38240	0.74	0.68	alpha-1,3-mannosyl-glycoprotein beta-1,2-N-acetylglucosaminyltransferase, putative	
AT4G28570	0.73	0.70	Long-chain fatty alcohol dehydrogenase family protein	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT3G54670	0.72	0.68	Structural maintenance of chromosomes (SMC) family protein	
AT1G69690	0.71	1.07	TCP family transcription factor	
AT2G36080	0.71	0.89	AP2/B3-like transcriptional factor family protein	
AT5G19310	0.71	0.68	Homeotic gene regulator	
AT3G14230	0.68	0.69	related to AP2 2	
AT3G50670	0.68	0.62	U1 small nuclear ribonucleoprotein-70K	
AT4G36690	0.67	0.55	U2 snRNP auxilliary factor, large subunit, splicing factor	
AT5G08370	0.66	0.96	alpha-galactosidase 2	
AT2G43330	0.66	0.73	inositol transporter 1	
AT1G26270	0.65	0.87	Phosphatidylinositol 3- and 4-kinase family protein	
AT3G04520	0.64	0.73	threonine aldolase 2	
AT4G21910	0.63	0.86	MATE efflux family protein	
AT3G61700	0.62	0.78	Plant protein 1589 of unknown function	
AT1G24100	0.62	0.58	UDP-glucosyl transferase 74B1	
AT4G11450	0.60	0.64	Protein of unknown function (DUF3527)	
AT4G37550	0.57	0.58	Acetamidase/Formamidase family protein	
AT5G19330	0.56	0.52	ARM repeat protein interacting with ABF2	GO:0009737
				GO:0009651

Supplementary Data Set 2.

Gene Ontology (GO) analysis of upregulated genes in *drol1* mutants

ontology	number in reference	number in list	expected	fold enrichment	p-value
lipid storage (GO:0019915)	28	6	0.42	14.26	2.69e-2
↳maintenance of location (GO:0051235)	70	10	1.05	9.51	8.32e-4
response to abscisic acid (GO:0009737)	482	33	7.24	4.56	6.31e-9
↳response to lipid (GO:0033993)	652	38	9.80	3.88	1.28e-8
↳response to organic substance (GO:0010033)	1639	49	24.63	1.99	2.50e-2
↳response to chemical (GO:0042221)	2600	72	39.07	1.84	2.07e-3
↳response to stimulus (GO:0050896)	5373	125	80.74	1.55	7.34e-4
↳response to hormone (GO:0009725)	1197	43	17.99	2.39	1.01e-3
↳response to endogenous stimulus (GO:0009719)	1216	43	18.27	2.35	1.26e-3
↳response to alcohol (GO:0097305)	486	33	7.30	4.52	7.78e-9
↳response to oxygen-containing compound (GO:1901700)	1459	54	21.93	2.46	6.19e-6
response to water deprivation (GO:0009414)	347	23	5.21	4.41	2.60e-5
↳response to stress (GO:0006950)	3014	83	45.29	1.83	2.36e-4
↳response to water (GO:0009415)	355	23	5.33	4.31	3.88e-5
↳response to acid chemical (GO:0001101)	369	23	5.55	4.15	7.59e-5
↳response to abiotic stimulus (GO:0009628)	2072	66	31.14	2.12	3.30e-5
response to salt stress (GO:0009651)	432	21	6.49	3.23	1.36e-2
↳response to osmotic stress (GO:0006970)	510	25	7.66	3.26	1.47e-3

Supplementary Data Set 3.

Downregulated genes in *drol1* seedlings at 3 DAG

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT4G12550	-7.12	-3.81	Auxin-Induced in Root cultures 1	
AT3G24230	-7.05	-3.05	Pectate lyase family protein	
AT5G23990	-6.75	-6.73	ferric reduction oxidase 5	
AT3G29630	-6.14	-6.12	UDP-Glycosyltransferase superfamily protein	
AT2G47880	-6.10	-4.11	Glutaredoxin family protein	
AT5G23980	-6.10	-5.25	ferric reduction oxidase 4	
AT1G52770	-5.90	-3.06	Phototropic-responsive NPH3 family protein	
AT1G05650	-5.42	-2.43	Pectin lyase-like superfamily protein	
AT2G35075	-5.09	-3.06	unknown protein	
AT5G10230	-5.05	-3.33	annexin 7	
AT3G53980	-5.03	-2.89	Bifunctional inhibitor/lipid-transfer protein/seed storage 2S albumin superfamily protein	
AT4G18510	-4.95	-2.25	CLAVATA3/ESR-related 2	
AT5G10180	-4.93	-2.89	slufate transporter 2;1	
AT5G15290	-4.88	-1.44	Uncharacterised protein family (UPF0497)	
AT3G25820	-4.87	-2.61	terpene synthase-like sequence-1,8-cineole	
AT1G71692	-4.86	-2.68	AGAMOUS-like 12	
AT1G06830	-4.75	-2.32	Glutaredoxin family protein	
AT1G71200	-4.72	-2.27	basic helix-loop-helix (bHLH) DNA-binding superfamily protein	
AT2G18800	-4.69	-3.22	xyloglucan endotransglucosylase/hydrolase 21	
AT1G30840	-4.62	-2.19	purine permease 4	
AT1G22150	-4.52	-3.20	sulfate transporter 1;3	
AT4G25010	-4.48	-2.99	Nodulin MtN3 family protein	
AT4G25100	-4.46	-1.59	Fe superoxide dismutase 1	
AT3G46900	-4.42	-4.06	copper transporter 2	
AT5G47450	-4.40	-3.30	tonoplast intrinsic protein 2;3	
AT5G56080	-4.37	-2.60	nicotianamine synthase 2	
AT1G23130	-4.29	-2.91	Polyketide cyclase/dehydrase and lipid transport superfamily protein	
AT3G11430	-4.23	-2.78	glycerol-3-phosphate acyltransferase 5	
AT3G59930	-4.14	-3.61	unknown protein	
AT1G17300	-4.06	-2.04	unknown protein	
AT5G66815	-4.05	-1.60	unknown protein	
AT1G73410	-4.02	-2.66	myb domain protein 54	
AT5G33355	-4.01	-4.49	Defensin-like (DEFL) family protein	
AT5G46890	-4.00	-2.10	Bifunctional inhibitor/lipid-transfer protein/seed storage 2S albumin superfamily protein	
AT3G09220	-3.78	-3.34	laccase 7	
AT5G23190	-3.72	-2.33	cytochrome P450, family 86, subfamily B, polypeptide 1	
AT3G19710	-3.71	-1.76	branched-chain aminotransferase4	
AT5G50800	-3.70	-2.17	Nodulin MtN3 family protein	
AT3G45680	-3.69	-1.80	Major facilitator superfamily protein	
AT1G03445	-3.67	-2.54	Serine/threonine protein phosphatase family protein	
AT4G30110	-3.59	-1.32	heavy metal atpase 2	
AT4G15300	-3.55	-1.89	cytochrome P450, family 702, subfamily A, polypeptide 2	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT4G33550	-3.51	-1.50	Bifunctional inhibitor/lipid-transfer protein/seed storage 2S albumin superfamily protein	
AT5G46240	-3.48	-2.16	potassium channel in Arabidopsis thaliana 1	
AT5G09520	-3.47	-3.19	hydroxyproline-rich glycoprotein family protein	
AT2G48130	-3.41	-1.50	Bifunctional inhibitor/lipid-transfer protein/seed storage 2S albumin superfamily protein	
AT4G15290	-3.41	-2.56	Cellulose synthase family protein	GO:1903047
				GO:0000910
AT4G12545	-3.40	-1.87	Bifunctional inhibitor/lipid-transfer protein/seed storage 2S albumin superfamily protein	
AT4G16270	-3.39	-2.54	Peroxidase superfamily protein	
AT3G16280	-3.38	-1.28	Integrase-type DNA-binding superfamily protein	
AT2G27550	-3.38	-2.27	centroradialis	
AT3G57510	-3.33	-5.02	Pectin lyase-like superfamily protein	
AT1G19900	-3.33	-2.98	glyoxal oxidase-related protein	
AT3G56240	-3.31	-1.77	copper chaperone	
AT5G23660	-3.31	-1.21	homolog of Medicago truncatula MTN3	
AT3G22880	-3.30	-2.60	DNA repair (Rad51) family protein	
AT3G14210	-3.29	-2.94	epithiospecifier modifier 1	
AT3G63110	-3.28	-1.43	isopentenyltransferase 3	
AT2G18328	-3.27	-2.38	RAD-like 4	
AT5G09220	-3.26	-1.84	amino acid permease 2	
AT4G28780	-3.22	-2.53	GDSL-like Lipase/Acylhydrolase superfamily protein	
AT4G21445	-3.21	-1.74	unknown protein	
AT3G16800	-3.17	-1.24	Protein phosphatase 2C family protein	GO:0007017
AT1G01390	-3.17	-1.89	UDP-Glycosyltransferase superfamily protein	
AT2G05910	-3.11	-3.32	Protein of unknown function (DUF567)	
AT3G16660	-3.11	-2.35	Pollen Ole e 1 allergen and extensin family protein	
AT1G78995	-3.09	-1.86	unknown protein	
AT2G37870	-3.08	-2.26	Bifunctional inhibitor/lipid-transfer protein/seed storage 2S albumin superfamily protein	
AT3G50610	-3.05	-2.05	unknown protein	
AT4G14020	-3.04	-1.15	Rapid alkalinization factor (RALF) family protein	
AT4G20240	-3.04	-1.55	cytochrome P450, family 71, subfamily A, polypeptide 27	
AT4G17030	-3.03	-2.30	expansin-like B1	
AT2G32620	-3.02	-2.47	cellulose synthase-like B	GO:1903047
				GO:0000910
AT2G33790	-3.02	-1.43	arabinogalactan protein 30	
AT3G04960	-3.00	-4.28	Domain of unknown function (DUF3444)	
AT2G16760	-2.98	-2.08	Calcium-dependent phosphotriesterase superfamily protein	
AT1G32780	-2.97	-1.79	GroES-like zinc-binding dehydrogenase family protein	
AT3G28070	-2.96	-1.60	nodulin MtN21 /EamA-like transporter family protein	
AT4G08300	-2.91	-4.21	nodulin MtN21 /EamA-like transporter family protein	
AT3G13610	-2.89	-1.83	2-oxoglutarate (2OG) and Fe(II)-dependent oxygenase superfamily protein	
AT2G41730	-2.88	-2.16	unknown protein	
AT5G09530	-2.83	-2.27	hydroxyproline-rich glycoprotein family protein	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT4G18290	-2.83	-1.58	potassium channel in Arabidopsis thaliana 2	
AT5G05960	-2.81	-1.51	Bifunctional inhibitor/lipid-transfer protein/seed storage 2S albumin superfamily protein	
AT5G63850	-2.80	-1.34	amino acid permease 4	
AT5G15530	-2.77	-0.89	biotin carboxyl carrier protein 2	
AT2G35770	-2.75	-1.51	serine carboxypeptidase-like 28	
AT3G05600	-2.66	-1.47	alpha/beta-Hydrolases superfamily protein	
AT3G53950	-2.65	-1.46	glyoxal oxidase-related protein	
AT1G67195	-2.65	-1.62	MIR414 (MICRORNA 414)	
AT4G09350	-2.64	-1.15	Chaperone DnaJ-domain superfamily protein	
ATCG00050	-2.63	-2.24	ribosomal protein S16	
AT4G39710	-2.62	-1.43	FK506-binding protein 16-2	
AT1G21540	-2.60	-1.76	AMP-dependent synthetase and ligase family protein	
AT5G24655	-2.59	-3.47	response to low sulfur 4	
AT3G10340	-2.58	-1.26	phenylalanine ammonia-lyase 4	
AT5G04970	-2.57	-1.93	Plant invertase/pectin methylesterase inhibitor superfamily	
AT3G56620	-2.57	-1.46	nodulin MtN21 /EamA-like transporter family protein	
AT1G07050	-2.54	-1.61	CCT motif family protein	
AT2G47370	-2.54	-1.28	Calcium-dependent phosphotriesterase superfamily protein	
AT1G57790	-2.54	-1.26	F-box family protein	
AT5G27290	-2.53	-1.73	unknown protein	
AT5G40690	-2.53	-1.71	unknown protein	
AT2G20590	-2.53	-1.10	Reticulon family protein	
AT1G67035	-2.51	-1.53	unknown protein	
AT4G33666	-2.46	-2.05	unknown protein	
AT4G24265	-2.46	-1.55	unknown protein	
AT3G06840	-2.45	-1.21	unknown protein	
AT1G22590	-2.44	-2.06	AGAMOUS-like 87	
AT1G18140	-2.43	-1.31	laccase 1	
AT5G48430	-2.43	-2.87	Eukaryotic aspartyl protease family protein	
AT5G59520	-2.43	-1.48	ZRT/IRT-like protein 2	
AT1G61450	-2.42	-1.59	unknown protein	
AT1G07400	-2.39	-1.80	HSP20-like chaperones superfamily protein	
AT3G02900	-2.36	-1.03	unknown protein	
AT1G49130	-2.33	-2.53	B-box type zinc finger protein with CCT domain	
AT5G05940	-2.31	-1.23	ROP guanine nucleotide exchange factor 5	
AT4G17240	-2.31	-1.35	unknown protein	
AT5G01420	-2.30	-1.28	Glutaredoxin family protein	
AT2G37750	-2.30	-1.93	unknown protein	
AT1G20030	-2.30	-1.37	Pathogenesis-related thaumatin superfamily protein	
AT3G12750	-2.28	-1.25	zinc transporter 1 precursor	
AT5G01910	-2.28	-0.99	unknown protein	
AT4G15140	-2.27	-1.28	unknown protein	
AT1G08160	-2.26	-1.15	Late embryogenesis abundant (LEA) hydroxyproline-rich glycoprotein family	
AT5G25090	-2.26	-1.23	early nodulin-like protein 13	
AT4G28430	-2.25	-1.27	Reticulon family protein	
AT2G42110	-2.25	-1.30	unknown protein	
AT4G36610	-2.23	-2.24	alpha/beta-Hydrolases superfamily protein	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT4G00880	-2.23	-1.50	SAUR-like auxin-responsive protein family	
AT4G03100	-2.22	-1.25	Rho GTPase activating protein with PAK-box/P21-Rho-binding domain	
AT5G52640	-2.21	-1.94	heat shock protein 90.1	
AT5G10625	-2.20	-1.49	unknown protein	
AT3G10840	-2.20	-1.39	alpha/beta-Hydrolases superfamily protein	
AT5G51600	-2.19	-1.23	Microtubule associated protein (MAP65/ASE1) family protein	GO:0000910
				GO:0007017
AT1G18370	-2.19	-1.17	ATP binding microtubule motor family protein	GO:0000910
AT5G36120	-2.19	-1.22	cofactor assembly, complex C (B6F)	
AT1G44110	-2.18	-1.20	Cyclin A1;1	GO:1903047
				GO:0044772
AT4G15830	-2.18	-1.33	ARM repeat superfamily protein	GO:0007017
AT4G26220	-2.17	-1.52	S-adenosyl-L-methionine-dependent methyltransferases superfamily protein	
AT3G26050	-2.17	-0.97	TPX2 (targeting protein for Xklp2) protein family	
AT1G05440	-2.17	-1.34	C-8 sterol isomerases	
AT3G08920	-2.16	-1.02	Rhodanese/Cell cycle control phosphatase superfamily protein	
AT2G26760	-2.15	-1.31	Cyclin B1;4	GO:1903047
				GO:0044772
AT4G12900	-2.14	-1.72	Gamma interferon responsive lysosomal thiol (GILT) reductase family protein	
AT1G31335	-2.13	-1.49	unknown protein	
AT1G23790	-2.12	-1.06	Plant protein of unknown function (DUF936)	
AT4G16880	-2.11	-1.76	Leucine-rich repeat (LRR) family protein	
AT5G02490	-2.10	-1.36	Heat shock protein 70 (Hsp 70) family protein	
AT2G21640	-2.10	-1.66	unknown protein	
AT2G39080	-2.09	-1.14	NAD(P)-binding Rossmann-fold superfamily protein	
AT3G13450	-2.09	-1.31	Transketolase family protein	
AT5G52860	-2.07	-1.63	ABC-2 type transporter family protein	
AT4G32830	-2.07	-1.32	ataurora1	GO:1903047
				GO:0007017
AT1G02730	-2.06	-1.04	cellulose synthase-like D5	GO:1903047
				GO:0000910
AT1G53520	-2.05	-1.54	Chalcone-flavanone isomerase family protein	
AT3G15550	-2.05	-1.06	unknown protein	
AT3G55660	-2.05	-1.19	ROP (rho of plants) guanine nucleotide exchange factor 6	
AT1G20930	-2.04	-1.12	cyclin-dependent kinase B2;2	GO:1903047
				GO:0044772
AT5G55180	-2.04	-0.98	O-Glycosyl hydrolases family 17 protein	
AT3G27925	-2.03	-1.19	DegP protease 1	
AT3G02120	-2.03	-1.32	hydroxyproline-rich glycoprotein family protein	
AT5G24380	-2.02	-1.20	YELLOW STRIPE like 2	
AT5G16250	-2.02	-1.18	unknown protein	
AT2G28620	-2.02	-1.23	P-loop containing nucleoside triphosphate hydrolases superfamily protein	GO:0000910
AT4G39800	-2.02	-1.25	myo-inositol-1-phosphate synthase 1	
AT3G52110	-2.02	-0.99	unknown protein	
AT5G36710	-2.01	-1.41	unknown protein	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT5G36800	-2.01	-1.41	unknown protein	
AT4G35620	-2.01	-0.94	Cyclin B2;2	GO:1903047
				GO:0044772
AT1G49870	-2.01	-0.97	unknown protein	
AT3G51930	-2.00	-1.00	Transducin/WD40 repeat-like superfamily protein	
AT3G09580	-2.00	-1.04	FAD/NAD(P)-binding oxidoreductase family protein	
AT4G23800	-2.00	-1.03	HMG (high mobility group) box protein	
AT4G02800	-2.00	-1.13	unknown protein	
AT2G47920	-1.98	-1.29	Kinase interacting (KIP1-like) family protein	
AT3G05625	-1.98	-1.17	Tetratricopeptide repeat (TPR)-like superfamily protein	
AT1G60000	-1.97	-1.21	RNA-binding (RRM/RBD/RNP motifs) family protein	
AT5G51440	-1.97	-1.52	HSP20-like chaperones superfamily protein	
AT5G55520	-1.97	-1.01	unknown protein	GO:0007017
AT5G15510	-1.96	-1.05	TPX2 (targeting protein for Xklp2) protein family	
AT1G32170	-1.96	-0.93	xyloglucan endotransglucosylase/hydrolase 30	
AT4G17000	-1.96	-1.14	unknown protein	
AT1G53140	-1.96	-1.19	Dynamin related protein 5A	GO:0000910
AT3G18010	-1.96	-1.01	WUSCHEL related homeobox 1	
AT5G13840	-1.95	-0.86	FIZZY-related 3	
AT1G11850	-1.95	-1.69	unknown protein	
AT3G05330	-1.95	-0.87	cyclin family	GO:1903047
				GO:0000910
AT1G55370	-1.95	-1.04	NDH-dependent cyclic electron flow 5	
ATCG01040	-1.94	-1.88	Cytochrome C assembly protein	
AT3G10310	-1.93	-1.16	P-loop nucleoside triphosphate hydrolases superfamily protein with CH (Calponin Homology) domain	
AT5G53490	-1.93	-1.07	Tetratricopeptide repeat (TPR)-like superfamily protein	
AT5G56120	-1.93	-1.26	unknown protein	
AT5G60520	-1.93	-1.43	Late embryogenesis abundant (LEA) protein-related	
AT1G04760	-1.93	-1.40	vesicle-associated membrane protein 726	
AT1G72250	-1.92	-1.14	Di-glucose binding protein with Kinesin motor domain	
AT2G47015	-1.92	-1.35	MIR408; miRNA	
AT5G58240	-1.92	-1.65	FRAGILE HISTIDINE TRIAD	
AT5G45700	-1.92	-1.26	Haloacid dehalogenase-like hydrolase (HAD) superfamily protein	
AT1G08560	-1.91	-1.00	syntaxin of plants 111	
AT2G16270	-1.91	-1.04	unknown protein	
AT4G31840	-1.90	-1.13	early nodulin-like protein 15	
AT2G16586	-1.90	-1.31	unknown protein	
AT4G38070	-1.90	-1.13	basic helix-loop-helix (bHLH) DNA-binding superfamily protein	
AT2G33400	-1.89	-1.15	unknown protein	
AT2G34190	-1.89	-0.91	Xanthine/uracil permease family protein	
AT3G12870	-1.89	-1.25	unknown protein	
AT4G21820	-1.89	-1.12	binding;calmodulin binding	
AT1G61580	-1.89	-1.78	R-protein L3 B	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT2G25060	-1.89	-1.18	early nodulin-like protein 14	
AT1G16070	-1.88	-0.97	tubby like protein 8	
AT3G02640	-1.87	-1.18	unknown protein	
AT1G68540	-1.87	-1.01	NAD(P)-binding Rossmann-fold superfamily protein	
AT1G50490	-1.86	-1.21	ubiquitin-conjugating enzyme 20	
AT5G06150	-1.86	-1.08	Cyclin family protein	GO:1903047
				GO:0044772
AT1G03780	-1.86	-0.87	targeting protein for XKLP2	GO:0007017
AT2G46630	-1.85	-1.36	unknown protein	
AT5G42720	-1.85	-1.05	Glycosyl hydrolase family 17 protein	
AT5G48310	-1.85	-0.87	unknown protein	
AT2G19690	-1.85	-1.38	phospholipase A2-beta	
AT5G42330	-1.84	-0.89	unknown protein	
AT3G51280	-1.83	-1.09	Tetratricopeptide repeat (TPR)-like superfamily protein	
AT1G78430	-1.83	-0.96	ROP interactive partner 2	
AT2G28605	-1.83	-0.99	Photosystem II reaction center PsbP family protein	
AT1G75640	-1.83	-1.15	Leucine-rich receptor-like protein kinase family protein	
AT4G23500	-1.83	-1.20	Pectin lyase-like superfamily protein	
AT3G60370	-1.83	-0.98	FKBP-like peptidyl-prolyl cis-trans isomerase family protein	
AT4G05190	-1.82	-1.03	kinesin 5	GO:0007017
AT2G36145	-1.82	-0.97	unknown protein	
AT5G17160	-1.82	-0.88	unknown protein	
AT4G34950	-1.82	-1.30	Major facilitator superfamily protein	
AT5G66230	-1.81	-1.07	Chalcone-flavanone isomerase family protein	
AT3G51080	-1.81	-0.99	GATA transcription factor 6	
AT3G11090	-1.81	-1.63	LOB domain-containing protein 21	
AT3G23670	-1.81	-1.19	phragmoplast-associated kinesin-related protein, putative	GO:1903047
				GO:0000910
				GO:0007017
AT5G38300	-1.80	-1.03	unknown protein	
AT5G40500	-1.79	-1.26	unknown protein	
AT1G35420	-1.79	-0.98	alpha/beta-Hydrolases superfamily protein	
AT1G11220	-1.77	-1.03	Protein of unknown function (DUF761)	
AT2G05760	-1.76	-1.16	Xanthine/uracil permease family protein	
AT5G05510	-1.76	-1.06	Mad3/BUB1 homology region 1	GO:1903047
AT3G23760	-1.76	-0.89	unknown protein	
AT3G20150	-1.76	-0.94	Kinesin motor family protein	GO:0007017
AT3G11520	-1.76	-1.09	CYCLIN B1;3	GO:1903047
				GO:0044772
AT2G33560	-1.75	-0.83	BUB1-related (BUB1: budding uninhibited by benzymidazol 1)	GO:1903047
AT1G73630	-1.75	-1.58	EF hand calcium-binding protein family	
AT5G42070	-1.75	-1.01	unknown protein	
AT4G33270	-1.74	-0.96	Transducin family protein / WD-40 repeat family protein	
AT3G15650	-1.74	-1.74	alpha/beta-Hydrolases superfamily protein	
AT5G18660	-1.74	-1.05	NAD(P)-binding Rossmann-fold superfamily protein	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT3G13470	-1.74	-1.01	TCP-1/cpn60 chaperonin family protein	
AT3G58650	-1.72	-0.94	unknown protein	GO:1903047
				GO:0000910
				GO:0007017
AT4G21270	-1.72	-0.95	kinesin 1	GO:0007017
AT3G23890	-1.72	-1.01	topoisomerase II	GO:1903047
AT4G24120	-1.72	-1.20	YELLOW STRIPE like 1	
AT1G75280	-1.71	-0.95	NmrA-like negative transcriptional regulator family protein	
AT3G12685	-1.71	-1.10	Acid phosphatase/vanadium-dependent haloperoxidase-related protein	
AT3G25980	-1.71	-1.24	DNA-binding HORMA family protein	GO:1903047
AT3G57160	-1.71	-1.16	unknown protein	
AT5G18700	-1.70	-1.02	Protein kinase family protein with ARM repeat domain	GO:1903047
				GO:0000910
AT5G60930	-1.69	-1.03	P-loop containing nucleoside triphosphate hydrolases superfamily protein	GO:1903047
				GO:0007017
AT1G16630	-1.69	-1.03	unknown protein	
AT4G30140	-1.69	-1.74	GDSL-like Lipase/Acylhydrolase superfamily protein	
AT1G60600	-1.69	-0.97	UbiA prenyltransferase family protein	
AT2G32765	-1.68	-1.15	small ubiquitinrelated modifier 5	
AT2G22610	-1.68	-0.92	Di-glucose binding protein with Kinesin motor domain	
AT1G43560	-1.68	-1.01	thioredoxin Y2	
AT3G50070	-1.68	-1.42	CYCLIN D3;3	GO:1903047
				GO:0044772
AT1G20090	-1.67	-0.91	RHO-related protein from plants 2	GO:0007017
AT4G05520	-1.66	-0.76	EPS15 homology domain 2	
AT4G14330	-1.66	-1.00	P-loop containing nucleoside triphosphate hydrolases superfamily protein	GO:0007017
AT1G72670	-1.66	-0.82	IQ-domain 8	
AT5G07860	-1.65	-0.77	HXXXD-type acyl-transferase family protein	
AT1G34355	-1.65	-1.28	forkhead-associated (FHA) domain-containing protein	
AT5G67270	-1.65	-0.99	end binding protein 1C	GO:0007017
AT1G76450	-1.65	-0.84	Photosystem II reaction center PsbP family protein	
AT3G44050	-1.64	-0.92	P-loop containing nucleoside triphosphate hydrolases superfamily protein	GO:0000910
				GO:0007017
AT3G57430	-1.64	-1.17	Tetratricopeptide repeat (TPR)-like superfamily protein	
AT1G29530	-1.64	-0.81	unknown protein	
AT5G21482	-1.63	-0.88	cytokinin oxidase 7	
AT4G14490	-1.63	-0.96	SMAD/FHA domain-containing protein	
AT4G28230	-1.63	-0.84	unknown protein	
AT1G63100	-1.63	-1.05	GRAS family transcription factor	
AT4G24175	-1.62	-1.12	unknown protein	
AT3G58200	-1.62	-1.53	TRAF-like family protein	
AT2G37420	-1.61	-0.87	ATP binding microtubule motor family protein	
AT4G11070	-1.61	-1.24	WRKY family transcription factor	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT2G23530	-1.60	-1.06	Zinc-finger domain of monoamine-oxidase A repressor R1	
AT4G13370	-1.60	-1.19	Plant protein of unknown function (DUF936)	
AT2G45450	-1.60	-1.38	protein binding	
AT2G16700	-1.60	-1.23	actin depolymerizing factor 5	
AT2G43945	-1.60	-0.79	unknown protein	
AT2G26180	-1.59	-1.08	IQ-domain 6	
AT1G67780	-1.58	-0.89	Zinc-finger domain of monoamine-oxidase A repressor R1 protein	
AT4G32590	-1.57	-0.99	2Fe-2S ferredoxin-like superfamily protein	
AT5G43380	-1.57	-1.14	type one serine/threonine protein phosphatase 6	
AT5G11950	-1.57	-0.91	Putative lysine decarboxylase family protein	
AT1G30120	-1.57	-0.72	pyruvate dehydrogenase E1 beta	
AT3G51290	-1.57	-1.09	Protein of unknown function (DUF630) ;Protein of unknown function (DUF632)	
AT5G22300	-1.56	-1.10	nitrilase 4	
AT2G01660	-1.56	-1.11	plasmodesmata-located protein 6	
AT3G15360	-1.56	-0.88	thioredoxin M-type 4	
AT4G14870	-1.55	-0.81	secE/sec61-gamma protein transport protein	GO:0009657
AT1G73650	-1.55	-0.88	Protein of unknown function (DUF1295)	
AT1G76540	-1.55	-0.86	cyclin-dependent kinase B2;1	GO:1903047
				GO:0044772
AT5G40960	-1.55	-1.67	Protein of unknown function (DUF 3339)	
AT3G47290	-1.55	-0.74	phosphatidylinositol-speciwc phospholipase C8	
AT4G11820	-1.54	-0.80	hydroxymethylglutaryl-CoA synthase / HMG-CoA synthase / 3-hydroxy-3-methylglutaryl coenzyme A synthase	
AT3G44020	-1.54	-0.87	thylakoid lumenal P17.1 protein	
AT2G36885	-1.54	-0.78	unknown protein	
AT1G68590	-1.53	-0.85	Ribosomal protein PSRP-3/Ycf65	GO:0009657
AT2G21370	-1.53	-0.70	xylulose kinase-1	
AT5G27550	-1.53	-0.93	P-loop containing nucleoside triphosphate hydrolases superfamily protein	GO:0007017
AT4G01883	-1.52	-0.78	Polyketide cyclase / dehydrase and lipid transport protein	
AT1G29520	-1.52	-1.30	AWPM-19-like family protein	
AT5G22090	-1.52	-1.23	Protein of unknown function (DUF3049)	
AT2G38620	-1.52	-0.96	cyclin-dependent kinase B1;2	GO:1903047
				GO:0044772
AT1G10780	-1.52	-0.82	F-box/RNI-like superfamily protein	
AT1G26760	-1.51	-0.93	SET domain protein 35	
AT3G60510	-1.50	-0.79	ATP-dependent caseinolytic (Clp) protease/crotonase family protein	
AT3G22760	-1.50	-1.10	Tesmin/TSO1-like CXC domain-containing protein	
AT5G60200	-1.49	-0.73	TARGET OF MONOPTEROS 6	
AT1G25510	-1.49	-0.78	Eukaryotic aspartyl protease family protein	
AT1G68585	-1.49	-1.27	unknown protein	
AT3G14190	-1.48	-1.16	unknown protein	
AT4G37490	-1.47	-0.90	CYCLIN B1;1	GO:1903047
				GO:0044772
AT1G29390	-1.46	-0.85	cold regulated 314 thylakoid membrane 2	
AT5G57170	-1.46	-0.85	Tautomerase/MIF superfamily protein	
AT2G18230	-1.46	-0.76	pyrophosphorylase 2	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT3G03130	-1.45	-0.95	unknown protein	
AT1G55140	-1.45	-1.03	Ribonuclease III family protein	
AT3G18870	-1.45	-0.84	Mitochondrial transcription termination factor family protein	GO:0009657
AT4G34510	-1.44	-1.62	3-ketoacyl-CoA synthase 17	
AT1G50240	-1.42	-1.01	Protein kinase family protein with ARM repeat domain	GO:0000910
AT5G22140	-1.42	-1.55	FAD/NAD(P)-binding oxidoreductase family protein	
AT2G20635	-1.42	-1.10	ATP binding;protein kinases;protein serine/threonine kinases	GO:1903047
AT5G11510	-1.42	-0.95	myb domain protein 3r-4	
AT1G75170	-1.41	-0.93	Sec14p-like phosphatidylinositol transfer family protein	
AT2G24440	-1.41	-1.46	selenium binding	
AT2G16850	-1.41	-0.73	plasma membrane intrinsic protein 2;8	
AT2G29550	-1.41	-1.03	tubulin beta-7 chain	GO:0007017
AT4G34730	-1.40	-1.01	ribosome-binding factor A family protein	
AT4G11100	-1.39	-0.72	unknown protein	
AT1G76680	-1.38	-0.89	12-oxophytodienoate reductase 1	
AT2G43030	-1.38	-0.91	Ribosomal protein L3 family protein	
AT5G19730	-1.37	-1.07	Pectin lyase-like superfamily protein	
AT4G29360	-1.37	-0.89	O-Glycosyl hydrolases family 17 protein	
AT3G09150	-1.35	-0.73	phytochromobilin:ferredoxin oxidoreductase, chloroplast / phytochromobilin synthase (HY2)	
AT2G47910	-1.35	-0.97	chlororespiratory reduction 6	
AT1G13270	-1.34	-0.92	methionine aminopeptidase 1B	
AT1G16330	-1.33	-0.94	cyclin b3;1	
AT1G32070	-1.33	-0.77	nuclear shuttle interacting	
AT3G26900	-1.33	-0.86	shikimate kinase like 1	GO:0009657
AT1G73530	-1.33	-0.89	RNA-binding (RRM/RBD/RNP motifs) family protein	
AT4G03210	-1.32	-0.98	xyloglucan endotransglucosylase/hydrolase 9	
AT5G47110	-1.32	-0.91	Chlorophyll A-B binding family protein	
AT5G12110	-1.32	-1.13	Glutathione S-transferase, C-terminal-like;Translation elongation factor EF1B/ribosomal protein S6	
AT1G36390	-1.32	-0.70	Co-chaperone GrpE family protein	
AT3G27160	-1.32	-0.75	Ribosomal protein S21 family protein	
AT4G19840	-1.32	-0.97	phloem protein 2-A1	
AT1G50900	-1.31	-0.85	Ankyrin repeat family protein	GO:0009657
AT1G07610	-1.31	-1.32	metallothionein 1C	
AT5G24314	-1.31	-0.86	plastid transcriptionally active7	
AT4G14010	-1.30	-1.06	ralf-like 32	
AT5G37010	-1.30	-0.91	unknown protein	
AT3G27830	-1.30	-1.05	ribosomal protein L12-A	
AT2G29180	-1.30	-0.84	unknown protein	
AT1G20060	-1.30	-0.89	ATP binding microtubule motor family protein	
AT5G66550	-1.30	-0.72	Maf-like protein	
AT3G04650	-1.29	-0.75	FAD/NAD(P)-binding oxidoreductase family protein	
AT3G51740	-1.29	-0.79	inflorescence meristem receptor-like kinase 2	
AT1G54575	-1.29	-1.16	unknown protein	
AT1G15570	-1.28	-0.73	CYCLIN A2;3	GO:1903047
				GO:0044772

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT5G63100	-1.28	-0.90	S-adenosyl-L-methionine-dependent methyltransferases superfamily protein	
AT3G51720	-1.27	-0.78	Plant protein of unknown function (DUF827)	GO:0009657
AT1G63610	-1.27	-0.75	unknown protein	
AT5G42146	-1.27	-1.59	unknown protein	
AT5G27390	-1.27	-0.77	Mog1/PsbP/DUF1795-like photosystem II reaction center PsbP family protein	
AT4G25370	-1.27	-0.92	Double Clp-N motif protein	
AT4G33520	-1.27	-1.12	P-type ATP-ase 1	
AT5G16140	-1.27	-0.98	Peptidyl-tRNA hydrolase family protein	
AT3G04760	-1.26	-0.99	Pentatricopeptide repeat (PPR-like) superfamily protein	
AT2G27290	-1.26	-1.13	Protein of unknown function (DUF1279)	
AT5G23580	-1.26	-0.80	calmodulin-like domain protein kinase 9	
AT1G73760	-1.25	-0.67	RING/U-box superfamily protein	
AT3G06110	-1.25	-1.03	MAPK phosphatase 2	
AT1G44920	-1.25	-0.80	unknown protein	
AT5G64620	-1.25	-0.93	cell wall / vacuolar inhibitor of fructosidase 2	
AT1G45170	-1.24	-0.57	unknown protein	
AT2G21385	-1.24	-0.76	unknown protein	
AT4G01310	-1.24	-0.67	Ribosomal L5P family protein	
AT3G47650	-1.24	-0.71	DnaJ/Hsp40 cysteine-rich domain superfamily protein	
AT5G10160	-1.24	-0.89	Thioesterase superfamily protein	
AT3G06030	-1.23	-0.79	NPK1-related protein kinase 3	GO:0007017
AT5G35220	-1.23	-0.71	Peptidase M50 family protein	GO:0009657
AT2G34460	-1.23	-0.84	NAD(P)-binding Rossmann-fold superfamily protein	
AT3G03680	-1.23	-0.94	C2 calcium/lipid-binding plant phosphoribosyltransferase family protein	
AT3G15110	-1.22	-0.93	unknown protein	
AT3G27850	-1.22	-0.99	ribosomal protein L12-C	
AT3G44890	-1.21	-0.62	ribosomal protein L9	
AT4G27600	-1.21	-0.87	pfkB-like carbohydrate kinase family protein	
AT4G37040	-1.21	-0.71	methionine aminopeptidase 1D	
AT3G63160	-1.21	-1.32	unknown protein	
AT3G25480	-1.21	-0.85	Rhodanese/Cell cycle control phosphatase superfamily protein	
AT3G01410	-1.21	-1.08	Polynucleotidyl transferase, ribonuclease H-like superfamily protein	
AT4G11175	-1.20	-0.67	Nucleic acid-binding, OB-fold-like protein	
AT1G67040	-1.20	-0.82	unknown protein	
AT1G48350	-1.20	-0.84	Ribosomal L18p/L5e family protein	
AT1G75350	-1.19	-0.82	Ribosomal protein L31	
AT2G26840	-1.19	-0.93	unknown protein	GO:0009657
AT1G76690	-1.19	-0.92	12-oxophytodienoate reductase 2	
AT1G69700	-1.19	-0.97	HVA22 homologue C	
AT3G44880	-1.18	-0.86	Pheophorbide a oxygenase family protein with Rieske [2Fe-2S] domain	
AT1G78380	-1.18	-0.92	glutathione S-transferase TAU 19	
AT5G14660	-1.18	-0.69	peptide deformylase 1B	
AT3G12930	-1.18	-0.83	Lojap-related protein	
AT3G15570	-1.18	-0.87	Phototropic-responsive NPH3 family protein	
AT1G44800	-1.18	-1.13	nodulin MtN21 /EamA-like transporter family protein	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT3G45050	-1.18	-0.87	unknown protein	
AT3G54710	-1.18	-0.90	homolog of yeast CDT1 B homolog of yeast CDT1 B	GO:0009657
AT4G08290	-1.17	-1.57	nodulin MtN21 /EamA-like transporter family protein	
AT5G28500	-1.17	-0.72	unknown protein	
AT5G13510	-1.17	-0.76	Ribosomal protein L10 family protein	
AT3G47860	-1.17	-0.77	chloroplastic lipocalin	
AT4G35730	-1.16	-0.92	Regulator of Vps4 activity in the MVB pathway protein	
AT4G13615	-1.15	-0.92	Uncharacterised protein family SERF	
AT5G23910	-1.15	-0.90	ATP binding microtubule motor family protein	GO:0007017
AT1G70690	-1.15	-1.25	Receptor-like protein kinase-related family protein	
AT1G67830	-1.15	-0.78	alpha-fucosidase 1	
AT5G51110	-1.14	-0.80	Transcriptional coactivator/pterin dehydratase	
AT3G08010	-1.14	-0.64	RNA binding	GO:0009657
AT5G11450	-1.14	-0.75	Mog1/PsbP/DUF1795-like photosystem II reaction center PsbP family protein	
AT1G35680	-1.13	-0.69	Ribosomal protein L21	GO:0009657
AT3G60900	-1.13	-1.09	FASCICLIN-like arabinogalactan-protein 10	
AT1G29070	-1.13	-0.95	Ribosomal protein L34	
AT3G25410	-1.13	-0.61	Sodium Bile acid symporter family	
AT2G34860	-1.12	-0.70	DnaJ/Hsp40 cysteine-rich domain superfamily protein	GO:0009657
AT5G05200	-1.12	-0.78	Protein kinase superfamily protein	
AT4G20760	-1.12	-0.79	NAD(P)-binding Rossmann-fold superfamily protein	
AT3G24590	-1.11	-0.82	plastidic type i signal peptidase 1	GO:0009657
AT2G25880	-1.11	-0.93	ataurora2	GO:1903047
				GO:0007017
AT2G41950	-1.11	-0.93	unknown protein	
AT5G14320	-1.11	-0.85	Ribosomal protein S13/S18 family	
AT5G55820	-1.11	-0.74	unknown protein	
AT2G24090	-1.11	-0.79	Ribosomal protein L35	
AT5G55270	-1.11	-1.27	Protein of unknown function (DUF295)	
AT5G46800	-1.10	-0.77	Mitochondrial substrate carrier family protein	
AT3G04790	-1.10	-0.92	Ribose 5-phosphate isomerase, type A protein	
AT2G37660	-1.10	-0.66	NAD(P)-binding Rossmann-fold superfamily protein	
AT5G44040	-1.09	-0.66	unknown protein	
AT2G30390	-1.09	-0.70	ferrochelatase 2	
AT1G80370	-1.09	-0.73	Cyclin A2;4	GO:1903047
				GO:0044772
AT5G47190	-1.08	-0.61	Ribosomal protein L19 family protein	
AT2G29500	-1.08	-0.88	HSP20-like chaperones superfamily protein	
AT5G24850	-1.08	-0.73	cryptochrome 3	
AT1G32990	-1.07	-0.75	plastid ribosomal protein l11	
AT4G23550	-1.07	-1.20	WRKY family transcription factor	
AT1G74970	-1.07	-0.67	ribosomal protein S9	
AT4G28640	-1.07	-0.85	indole-3-acetic acid inducible 11	
AT3G52150	-1.06	-0.91	RNA-binding (RRM/RBD/RNP motifs) family protein	
AT1G33040	-1.06	-0.77	nascent polypeptide-associated complex subunit alpha-like protein 5	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT5G38290	-1.06	-0.85	Peptidyl-tRNA hydrolase family protein	
AT5G59890	-1.06	-0.60	actin depolymerizing factor 4	
AT5G20720	-1.05	-0.77	chaperonin 20	
AT2G30695	-1.05	-0.61	unknown protein	
AT5G40160	-1.05	-0.57	Ankyrin repeat family protein	
AT1G03680	-1.05	-0.79	thioredoxin M-type 1	
AT4G36810	-1.04	-0.83	geranylgeranyl pyrophosphate synthase 1	
AT1G77060	-1.03	-0.62	Phosphoenolpyruvate carboxylase family protein	
AT1G18550	-1.03	-0.77	ATP binding microtubule motor family protein	GO:0007017
AT5G55710	-1.03	-0.83	unknown protein	
AT3G19590	-1.03	-0.75	Transducin/WD40 repeat-like superfamily protein	GO:1903047
AT4G13550	-1.03	-0.78	triglyceride lipases;triglyceride lipases	
AT1G64510	-1.02	-0.65	Translation elongation factor EF1B/ribosomal protein S6 family protein	
AT2G26550	-1.02	-0.67	heme oxygenase 2	
AT3G28460	-1.02	-0.85	methyltransferases	
AT1G75820	-1.01	-0.79	Leucine-rich receptor-like protein kinase family protein	
AT3G06483	-1.01	-0.66	pyruvate dehydrogenase kinase	
AT2G21130	-1.00	-1.15	Cyclophilin-like peptidyl-prolyl cis-trans isomerase family protein	
AT1G73885	-1.00	-0.73	unknown protein	
AT5G52440	-1.00	-0.62	Bacterial sec-independent translocation protein mttA/Hcf106	
AT3G15190	-1.00	-0.87	chloroplast 30S ribosomal protein S20, putative	
AT1G07320	-1.00	-0.71	ribosomal protein L4	
AT2G39290	-0.99	-0.81	phosphatidylglycerolphosphate synthase 1	GO:0009657
AT1G11790	-0.99	-0.56	arogenate dehydratase 1	
AT5G12130	-0.99	-0.69	integral membrane TerC family protein	GO:0009657
AT2G05990	-0.99	-0.88	NAD(P)-binding Rossmann-fold superfamily protein	
AT3G61310	-0.98	-0.73	AT hook motif DNA-binding family protein	
AT4G26860	-0.98	-0.69	Predicted pyridoxal phosphate-dependent enzyme, YBL036C type	
AT3G06730	-0.98	-0.85	Thioredoxin z	GO:0009657
AT4G02990	-0.98	-0.87	Mitochondrial transcription termination factor family protein	
AT2G26930	-0.98	-0.61	4-(cytidine 5'-phospho)-2-C-methyl-D-erithritol kinase	
AT5G63310	-0.98	-0.81	nucleoside diphosphate kinase 2	
AT3G49260	-0.98	-0.68	IQ-domain 21	
AT5G65220	-0.97	-0.84	Ribosomal L29 family protein	
AT3G20060	-0.97	-0.68	ubiquitin-conjugating enzyme19	
AT1G66670	-0.97	-0.87	CLP protease proteolytic subunit 3	
AT3G51140	-0.96	-0.80	Protein of unknown function (DUF3353)	
AT2G22230	-0.96	-0.76	Thioesterase superfamily protein	
AT1G16445	-0.96	-0.82	S-adenosyl-L-methionine-dependent methyltransferases superfamily protein	
AT2G44650	-0.96	-0.70	chloroplast chaperonin 10	
AT2G28800	-0.96	-0.62	63 kDa inner membrane family protein	GO:0009657
AT5G14910	-0.96	-0.65	Heavy metal transport/detoxification superfamily protein	
AT3G06950	-0.95	-0.76	Pseudouridine synthase family protein	
AT5G30510	-0.95	-0.72	ribosomal protein S1	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT1G21440	-0.95	-0.85	Phosphoenolpyruvate carboxylase family protein	
AT4G17560	-0.95	-0.77	Ribosomal protein L19 family protein	
AT4G33400	-0.94	-0.81	Vacuolar import/degradation, Vid27-related protein	
AT4G03150	-0.94	-1.07	unknown protein	
AT2G45770	-0.94	-0.67	signal recognition particle receptor protein, chloroplast (FTSY)	GO:0009657
AT1G49510	-0.94	-0.57	embryo defective 1273	GO:0009657
AT3G52155	-0.93	-0.69	Phosphoglycerate mutase family protein	
AT4G24770	-0.93	-0.63	31-kDa RNA binding protein	
AT2G27680	-0.92	-0.69	NAD(P)-linked oxidoreductase superfamily protein	
AT5G48470	-0.92	-0.70	unknown protein	GO:0009657
AT5G54180	-0.92	-0.67	plastid transcriptionally active 15	GO:0009657
AT3G18420	-0.91	-0.94	Protein prenylyltransferase superfamily protein	GO:0009657
AT1G21350	-0.91	-0.68	Thioredoxin superfamily protein	
AT5G58250	-0.91	-0.66	unknown protein	
AT2G18290	-0.91	-0.69	anaphase promoting complex 10	
AT2G04530	-0.91	-0.74	Metallo-hydrolase/oxidoreductase superfamily protein	
AT3G20930	-0.90	-0.59	RNA-binding (RRM/RBD/RNP motifs) family protein	
AT3G29185	-0.89	-0.65	Domain of unknown function (DUF3598)	GO:0009657
AT1G10522	-0.89	-0.63	unknown protein	
AT3G58570	-0.89	-0.69	P-loop containing nucleoside triphosphate hydrolases superfamily protein	
AT4G33470	-0.89	-0.84	histone deacetylase 14	
AT1G67660	-0.89	-0.67	Restriction endonuclease, type II-like superfamily protein	
AT3G13120	-0.89	-0.58	Ribosomal protein S10p/S20e family protein	
AT1G32220	-0.89	-0.84	NAD(P)-binding Rossmann-fold superfamily protein	
AT3G09980	-0.89	-0.62	Family of unknown function (DUF662)	
AT4G24610	-0.89	-0.70	unknown protein	
AT2G26670	-0.89	-0.63	Plant haem oxygenase (decyclizing) family protein	
AT2G24060	-0.88	-0.56	Translation initiation factor 3 protein	GO:0009657
AT2G01110	-0.88	-0.78	Sec-independent periplasmic protein translocase	GO:0009657
AT1G35780	-0.88	-0.65	unknown protein	
AT1G02560	-0.88	-0.65	nuclear encoded CLP protease 5	
AT2G07170	-0.88	-0.69	ARM repeat superfamily protein	
AT2G43360	-0.87	-0.71	Radical SAM superfamily protein	
AT1G67820	-0.87	-1.08	Protein phosphatase 2C family protein	
AT3G43210	-0.87	-0.63	ATP binding microtubule motor family protein	GO:0000910
				GO:0007017
AT4G15420	-0.87	-0.62	Ubiquitin fusion degradation UFD1 family protein	
AT5G17870	-0.86	-0.79	plastid-specific 50S ribosomal protein 6	
AT5G54290	-0.86	-0.75	cytochrome c biogenesis protein family	
AT3G04550	-0.86	-0.62	unknown protein	
AT3G53850	-0.86	-1.16	Uncharacterised protein family (UPF0497)	
AT4G20960	-0.86	-0.53	Cytidine/deoxycytidylate deaminase family protein	
AT2G45300	-0.85	-0.60	RNA 3'-terminal phosphate cyclase/enolpyruvate transferase, alpha/beta	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT1G15960	-0.85	-0.62	NRAMP metal ion transporter 6	
AT2G44870	-0.85	-0.66	unknown protein	
AT3G27330	-0.85	-0.82	zinc finger (C3HC4-type RING finger) family protein	
AT4G28310	-0.85	-0.80	unknown protein	
AT4G01940	-0.84	-0.66	NFU domain protein 1	GO:0009657
AT2G42770	-0.84	-0.74	Peroxisomal membrane 22 kDa (Mpv17/PMP22) family protein	
AT3G29230	-0.84	-0.71	Tetratricopeptide repeat (TPR)-like superfamily protein	
AT1G33810	-0.84	-0.93	unknown protein	
AT3G09440	-0.84	-0.74	Heat shock protein 70 (Hsp 70) family protein	
AT5G52540	-0.83	-0.97	Protein of unknown function (DUF819)	
AT5G55540	-0.83	-0.68	tornado 1	
AT5G50250	-0.82	-0.55	chloroplast RNA-binding protein 31B	
AT5G46290	-0.82	-0.72	3-ketoacyl-acyl carrier protein synthase I	
AT1G01970	-0.82	-0.79	Tetratricopeptide repeat (TPR)-like superfamily protein	
AT2G38270	-0.81	-0.64	CAX-interacting protein 2	
AT5G64150	-0.81	-0.77	RNA methyltransferase family protein	
AT3G10970	-0.81	-0.58	Haloacid dehalogenase-like hydrolase (HAD) superfamily protein	
AT3G63410	-0.80	-0.78	S-adenosyl-L-methionine-dependent methyltransferases superfamily protein	
AT4G01935	-0.80	-0.71	unknown protein	
AT1G01080	-0.80	-0.53	RNA-binding (RRM/RBD/RNP motifs) family protein	
AT3G15030	-0.80	-0.91	TCP family transcription factor 4	
AT1G07790	-0.79	-0.73	Histone superfamily protein	
AT4G29400	-0.79	-0.77	Protein of unknown function (DUF3531)	
AT1G28140	-0.79	-0.78	unknown protein	
AT4G26370	-0.79	-0.64	antitermination NusB domain-containing protein	
AT1G79080	-0.78	-0.71	Pentatricopeptide repeat (PPR) superfamily protein	
AT1G10830	-0.78	-0.68	15-cis-zeta-carotene isomerase	
AT1G27385	-0.78	-0.76	unknown protein	
AT2G02740	-0.78	-0.83	ssDNA-binding transcriptional regulator	
AT5G24650	-0.78	-0.68	Mitochondrial import inner membrane translocase subunit Tim17/Tim22/Tim23 family protein	
AT5G05740	-0.78	-0.59	ethylene-dependent gravitropism-deficient and yellow-green-like 2	
AT1G48450	-0.78	-0.58	Protein of unknown function (DUF760)	
AT2G02500	-0.78	-0.67	Nucleotide-diphospho-sugar transferases superfamily protein	
AT1G17850	-0.78	-0.53	Rhodanese/Cell cycle control phosphatase superfamily protein	
AT1G14410	-0.77	-0.81	ssDNA-binding transcriptional regulator	
AT3G46100	-0.77	-0.58	Histidyl-tRNA synthetase 1	
AT2G43630	-0.77	-0.53	unknown protein	
AT5G26940	-0.77	-0.61	Polynucleotidyl transferase, ribonuclease H-like superfamily protein	
AT5G59500	-0.77	-0.97	protein C-terminal S-isoprenylcysteine carboxyl O-methyltransferases	
AT5G52110	-0.76	-0.78	Protein of unknown function (DUF2930)	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT4G34265	-0.76	-0.63	unknown protein	
AT2G21860	-0.76	-0.83	violaxanthin de-epoxidase-related	
AT2G42070	-0.76	-0.76	nudix hydrolase homolog 23	
AT4G25130	-0.75	-0.64	peptide met sulfoxide reductase 4	
AT2G43235	-0.75	-0.59	unknown protein	
AT1G04940	-0.75	-0.75	translocon at the inner envelope membrane of chloroplasts 20	
AT2G20690	-0.75	-0.64	lumazine-binding family protein	
AT5G02370	-0.75	-0.96	ATP binding microtubule motor family protein	GO:0007017
AT3G61610	-0.75	-0.75	Galactose mutarotase-like superfamily protein	
AT1G12050	-0.74	-0.57	fumarylacetoacetase, putative	
AT1G11750	-0.74	-0.61	CLP protease proteolytic subunit 6	GO:0009657
AT3G47350	-0.73	-0.88	hydroxysteroid dehydrogenase 2	
AT4G16060	-0.73	-0.66	unknown protein	
AT2G43710	-0.73	-0.55	Plant stearoyl-acyl-carrier-protein desaturase family protein	
AT3G52880	-0.73	-0.53	monodehydroascorbate reductase 1	
AT1G68260	-0.73	-0.79	Thioesterase superfamily protein	
AT5G20060	-0.73	-0.59	alpha/beta-Hydrolases superfamily protein	
AT5G02380	-0.72	-0.97	metallothionein 2B	
AT1G76130	-0.72	-1.14	alpha-amylase-like 2	
AT5G44560	-0.72	-0.69	SNF7 family protein	
AT1G47740	-0.72	-0.51	PPPDE putative thiol peptidase family protein	
AT2G40760	-0.72	-0.67	Rhodanese/Cell cycle control phosphatase superfamily protein	
AT2G34590	-0.71	-0.52	Transketolase family protein	
AT1G23040	-0.71	-0.87	hydroxyproline-rich glycoprotein family protein	
AT2G37220	-0.71	-0.59	RNA-binding (RRM/RBD/RNP motifs) family protein	
AT2G42130	-0.71	-0.70	Plastid-lipid associated protein PAP / fibrillin family protein	
AT5G58560	-0.71	-0.52	Phosphatidate cytidylyltransferase family protein	
AT5G39980	-0.71	-0.60	Tetratricopeptide repeat (TPR)-like superfamily protein	GO:0009657
AT2G47840	-0.70	-0.89	Uncharacterised conserved protein ycf60	
AT3G13740	-0.70	-0.59	Ribonuclease III family protein	
AT5G23310	-0.69	-0.71	Fe superoxide dismutase 3	
AT2G21250	-0.69	-0.58	NAD(P)-linked oxidoreductase superfamily protein	
AT4G38220	-0.69	-0.57	Peptidase M20/M25/M40 family protein	
AT3G14110	-0.69	-0.55	Tetratricopeptide repeat (TPR)-like superfamily protein	
AT4G33670	-0.69	-0.70	NAD(P)-linked oxidoreductase superfamily protein	
AT4G17040	-0.69	-0.62	CLP protease R subunit 4	
AT5G20000	-0.69	-0.73	AAA-type ATPase family protein	
AT4G12060	-0.68	-0.62	Double Clp-N motif protein	
AT3G60210	-0.67	-0.69	GroES-like family protein	
AT5G57930	-0.66	-0.58	Arabidopsis thaliana protein of unknown function (DUF794)	
AT3G44620	-0.66	-0.52	protein tyrosine phosphatases;protein tyrosine phosphatases	
AT3G25860	-0.65	-0.57	2-oxoacid dehydrogenases acyltransferase family protein	
AT2G47590	-0.65	-0.61	photolyase/blue-light receptor 2	

Gene ID	logFC		Gene function	GO ID
	drol1-1	*drol1-2*		
AT1G17650	-0.65	-0.51	glyoxylate reductase 2	
AT5G56910	-0.64	-0.63	Proteinase inhibitor I25, cystatin, conserved region	
AT3G48040	-0.64	-0.70	RHO-related protein from plants 10	
AT2G35390	-0.63	-0.71	Phosphoribosyltransferase family protein	
AT3G15680	-0.63	-0.70	Ran BP2/NZF zinc finger-like superfamily protein	
AT2G20270	-0.63	-0.81	Thioredoxin superfamily protein	
AT5G48230	-0.61	-0.64	acetoacetyl-CoA thiolase 2	
AT5G14460	-0.61	-0.61	Pseudouridine synthase family protein	
AT1G50910	-0.59	-0.69	unknown protein	
AT5G13120	-0.59	-0.61	cyclophilin 20-2	
AT1G19800	-0.59	-0.65	trigalactosyldiacylglycerol 1	
AT1G30110	-0.58	-0.65	nudix hydrolase homolog 25	
AT4G34290	-0.58	-0.52	SWIB/MDM2 domain superfamily protein	
AT5G33320	-0.57	-0.71	Glucose-6-phosphate/phosphate translocator-related	
AT4G26500	-0.57	-0.64	chloroplast sulfur E	
AT2G44050	-0.56	-0.54	6,7-dimethyl-8-ribityllumazine synthase / DMRL synthase / lumazine synthase / riboflavin synthase	
AT5G08540	-0.56	-0.61	unknown protein	
AT1G06190	-0.55	-0.49	Rho termination factor	
AT1G79550	-0.54	-0.64	phosphoglycerate kinase	
AT2G45340	-0.53	-0.60	Leucine-rich repeat protein kinase family protein	
AT1G06730	-0.53	-0.56	pfkB-like carbohydrate kinase family protein	
AT4G28210	-0.53	-0.72	embryo defective 1923	
AT1G32500	-0.53	-0.79	non-intrinsic ABC protein 6	GO:0009657
AT5G45390	-0.52	-0.71	CLP protease P4	GO:0009657
AT3G20390	-0.50	-0.58	endoribonuclease L-PSP family protein	
AT5G24400	-0.50	-0.54	NagB/RpiA/CoA transferase-like superfamily protein	
AT5G23040	-0.50	-0.56	Protein of unknown function (DUF3353)	GO:0009657
AT3G54660	-0.49	-0.63	glutathione reductase	
AT4G39470	-0.49	-0.60	Tetratricopeptide repeat (TPR)-like superfamily protein	
AT5G40580	-0.48	-0.59	20S proteasome beta subunit PBB2	
AT3G13180	-0.48	-0.55	NOL1/NOP2/sun family protein / antitermination NusB domain-containing protein	
AT1G78620	-0.46	-0.53	Protein of unknown function DUF92, transmembrane	
AT1G48860	-0.45	-0.49	RNA 3'-terminal phosphate cyclase/enolpyruvate transferase, alpha/beta	
AT5G19370	-0.44	-0.56	rhodanese-like domain-containing protein / PPIC-type PPIASE domain-containing protein	

Supplementary Data Set 4.

GO analysis of upregulated genes in *drol1* mutants

ontology	number in reference	number in list	expected	fold enrichment	p-value
mitotic spindle assembly checkpoint (GO:0007094)	10	5	0.24	21.19	4.45e-2
➥mitotic spindle checkpoint (GO:0071174)	10	5	0.24	21.19	4.45e-2
➥spindle checkpoint (GO:0031577)	10	5	0.24	21.19	4.45e-2
➥cellular process (GO:0009987)	11472	329	270.73	1.22	1.71e-2
➥regulation of cell cycle (GO:0051726)	240	26	5.66	4.59	2.04e-6
➥regulation of mitotic cell cycle (GO:0007346)	103	14	2.43	5.76	1.51e-3
➥mitotic cell cycle process (GO:1903047)	187	28	4.41	6.34	4.25e-10
➥mitotic cell cycle (GO:0000278)	230	30	5.43	5.53	1.44e-9
➥cell cycle (GO:0007049)	441	44	10.41	4.23	3.59e-11
➥cell cycle process (GO:0022402)	404	43	9.53	4.51	9.20e-12
➥negative regulation of mitotic metaphase/anaphase transition (GO:0045841)	10	5	0.24	21.19	4.45e-2
➥negative regulation of metaphase/anaphase transition of cell cycle (GO:1902100)	10	5	0.24	21.19	4.45e-2
➥regulation of cell cycle phase transition (GO:1901987)	53	12	1.25	9.59	7.54e-5
➥regulation of cell cycle process (GO:0010564)	122	17	2.88	5.90	6.74e-5
➥regulation of metaphase/anaphase transition of cell cycle (GO:1902099)	22	7	0.52	13.48	9.42e-3
➥regulation of sister chromatid segregation (GO:0033045)	34	8	0.80	9.97	1.27e-2
➥regulation of chromosome segregation (GO:0051983)	36	8	0.85	9.42	1.82e-2
➥negative regulation of mitotic sister chromatid separation (GO:2000816)	10	5	0.24	21.19	4.45e-2
➥regulation of mitotic sister chromatid separation (GO:0010965)	23	7	0.54	12.90	1.20e-2
➥regulation of chromosome separation (GO:1905818)	23	7	0.54	12.90	1.20e-2
➥regulation of mitotic sister chromatid segregation (GO:0033047)	29	7	0.68	10.23	4.38e-2
➥negative regulation of chromosome separation (GO:1905819)	10	5	0.24	21.19	4.45e-2
➥negative regulation of chromosome segregation (GO:0051985)	10	5	0.24	21.19	4.45e-2
➥negative regulation of mitotic sister chromatid segregation (GO:0033048)	10	5	0.24	21.19	4.45e-2
➥negative regulation of sister chromatid segregation (GO:0033046)	10	5	0.24	21.19	4.45e-2

ontology	number in reference	number in list	expected	fold enrichment	p-value
regulation of mitotic metaphase/anaphase transition (GO:0030071)	22	7	0.52	13.48	9.42e-3
regulation of mitotic cell cycle phase transition (GO:1901990)	51	12	1.20	9.97	5.21e-5
spindle assembly checkpoint (GO:0071173)	10	5	0.24	21.19	4.45e-2
chloroplast rRNA processing (GO:1901259)	19	7	0.45	15.61	4.22e-3
cellular component biogenesis (GO:0044085)	1272	56	30.02	1.87	3.85e-2
cellular component organization or biogenesis (GO:0071840)	2724	109	64.28	1.70	2.76e-4
microtubule-based movement (GO:0007018)	31	11	0.73	15.04	5.63e-6
microtubule-based process (GO:0007017)	186	24	4.39	5.47	3.77e-7
movement of cell or subcellular component (GO:0006928)	56	11	1.32	8.32	1.00e-3
thylakoid membrane organization (GO:0010027)	46	12	1.09	11.05	1.93e-5
plastid membrane organization (GO:0009668)	53	12	1.25	9.59	7.54e-5
plastid organization (GO:0009657)	297	31	7.01	4.42	1.11e-7
cellular component organization (GO:0016043)	2320	94	54.75	1.72	1.51e-3
mitotic cell cycle phase transition (GO:0044772)	48	12	1.13	10.59	2.91e-5
cell cycle phase transition (GO:0044770)	49	12	1.16	10.38	3.55e-5
cytokinesis by cell plate formation (GO:0000911)	65	11	1.53	7.17	3.71e-3
cytokinesis (GO:0000910)	98	14	2.31	6.05	8.79e-4
cell division (GO:0051301)	205	17	4.84	3.51	4.88e-2
microtubule cytoskeleton organization (GO:0000226)	150	16	3.54	4.52	4.57e-3
chloroplast organization (GO:0009658)	231	20	5.45	3.67	4.93e-3
translation (GO:0006412)	495	30	11.68	2.57	1.66e-2
peptide biosynthetic process (GO:0043043)	499	30	11.78	2.55	3.02e-2
peptide metabolic process (GO:0006518)	566	33	13.36	2.47	1.45e-2
cellular amide metabolic process (GO:0043603)	703	39	16.59	2.35	6.63e-3
amide biosynthetic process (GO:0043604)	572	35	13.50	2.59	2.29e-3
cellular nitrogen compound biosynthetic process (GO:0044271)	1199	54	28.30	1.91	3.21e-2
cellular component assembly (GO:0022607)	795	40	18.76	2.13	4.75e-2

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