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Comparative genomics of seed dormancy using *Brachypodium distachyon* as a model for temperate cereals

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Abstract

Seed dormancy is a natural postponing mechanism to time the germination of seeds at the most suitable conditions. Previous studies have shown that phylogenies and environmental conditions shape the evolutionary trajectories of seed dormancy, making it an interesting subject for comparative genomics analysis between the dicot model plant *Arabidopsis thaliana* (Arabidopsis), the tropical cereal crop rice (*Oryza sativa*) and *Brachypodium distachyon* (Brachypodium), the monocot model plant for temperate grasses which include important cereal crops like wheat, barley and oat. We curated genes with known functions in seed dormancy and compared their evolutionary relationships between Arabidopsis, rice and Brachypodium (accession Bd21), highlighting conserved central hormonal pathways while also revealing gene loss and duplication events. The Brachypodium genome encodes conserved components of major pathways regulating seed dormancy induction, maintenance and release, most notably seed covering mediated dormancy imposition, plant hormones (ABA, GA, Auxin, Ethylene, Jasmonate, Brassinosteroids) metabolism and signalling, environmental signals (temperature, light and nutrient) perception and integration. Major seed dormancy genes, including *MFT*, *MKK3*, *Sdr4*, *AlaAT* and *DOG1,* show high homology between cereal species while lacking similar roles in Arabidopsis in some cases. Overall, our results indicate a conserved mechanism governing seed dormancy via the central hormonal pathways integrating diverse environmental cues through coordinated molecular components.

Keywords: Seed Dormancy, Pre-harvest sprouting, Comparative genomics, Phylogenetic analysis, Temperate Cereals, *Brachypodium distachyon*

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Introduction

Seed dormancy describes the inability of an intact viable seed to germinate under conditions otherwise favourable for germination [1]. This trait confers advantages to overcome harsh environmental conditions and retains seed viability, as revealed by the germination of long-lived seeds that survived extreme conditions [2].

A widely adopted classification system of seed dormancy includes five classes: physiological dormancy, morphological dormancy, morphophysiological dormancy, physical dormancy and combinational dormancy [3]. For the widely examined species like Arabidopsis and cereal crops, physiological dormancy is most relevant.

Central to the induction of seed dormancy is the phytohormone abscisic acid (ABA). Specifically, ABA synthesized by the zygote establishes seed dormancy during seed maturation [4]. Both metabolism and signalling of ABA are fundamental to the establishment, maintenance and release of seed dormancy. Molecular components involved in these processes have been extensively examined in Arabidopsis and

cereal crops. Other plant hormones, such as gibberellic acid (GA), auxin, ethylene, brassinosteroids (BRs) and jasmonates (JAs) act to coordinate or antagonize ABA to modulate seed dormancy. Besides internal regulators, external environmental cues strongly influence seed dormancy upon perception and integration into the hormonal pathways, be them temperature, light and nutrient availability.

Brachypodium has emerged as the model plant for temperate cereals to study multiple traits, including but not limited to flowering time, disease resistance and cell wall modifications. As an evolutionarily close relative to important grain crops like wheat and barley, Brachypodium with its many advantages provides opportunities to assist candidate identification of QTLs from other species and enable functional genetics of conserved mechanisms governing important biological processes [5]. However, its potential for seed dormancy and germination studies has not been fully exploited.

In this study, we conducted an extensive homology search and compared protein encoding genes with established or experimentally proven roles in seed dormancy and germination between Arabidopsis and cereal crops. Through analysis of these genes and their involvement in known pathways, we aim to elucidate the similarities and differences between Arabidopsis, rice and temperate cereals using Brachypodium as a model. Furthermore, phylogenetic analyses of gene families were conducted to study the evolutionary relationship of gene homologs and infer their functional roles.

Materials and Methods

Source of sequences

FASTA formatted files of published protein sequences were downloaded from Phytozome, UniProt, and Ensemble Plants. Versions of the reference genomes are: *Brachypodium distachyon* v3.0, *Arabidopsis thaliana* TAIR10.1, *Triticum aestivum* cv. Chinese Spring IWGSC, *Hordeum vulgare* subsp. Vulgare Morex V3, *Oryza sativa* subsp. Japonica IRGSP-1.0, *Zea mays* cv. B73 reference 5.0.

Homolog identification

For genes with known function in seed dormancy and germination identified in Arabidopsis and cereal crops, BLASTP search was conducted against Brachypodium protein sequences with an E value threshold of $1e^{-20}$. Reciprocal BLAST was performed against the Arabidopsis protein to confirm homology of the top ranked protein.

Database searches using profile HMMs

For proteins encoded by gene families, profile Hidden Markov Models (HMMs) were performed using the HMMER suite of programs. First, selected protein sequences were aligned using PRANK, the output file was used as input for the HMMBUILD program to build a profile HMM file. Next, the HMM file was searched against protein databases using the HMMSEARCH program, which produced a list of hits. Candidates in the list were manually refined based on information retrieved from the protein database, including but not limited to conserved domain, sequence similarity and literature. Proteins obviously belonged to different groups were removed based on E-value and database annotation.

Phylogenetic Analysis

The maximum likelihood and Bayesian phylogenetic analysis were performed using PhyML and MrBayes V3.2, respectively. Bootstrap values summarize 100 bootstrap replicates. For MrBayes, two runs were performed for 10000 generations using the General Time Reversible model and sampled every 1000 generations. After convergence indicated by split frequencies <0.02, the first 25% steps were removed as burn-in. Bootstrap values and posterior probability values were displayed at the phylogenetic tree nodes.

Results

Based on published literature, genes with experimentally proven roles in seed dormancy and germination were selected for analysis (**Supplementary Table 1**). Hormonal pathways and critical seed dormancy regulators were the focus of this study, instead of enumerating all genes and pathways. For simplicity, we prefixed gene or protein names with two letters to specify species: At for *Arabidopsis thaliana*, Bd for *Brachypodium distachyon*, Hv for *Hordeum vulgare* (barley), Os for *Oryza sativa* (rice), Ta for *Triticum aestivum* (bread wheat) and Zm for *Zea mays* (maize).

1. Plant hormonal pathways

1.1 ABA metabolism proteins

As an essential determinant of seed dormancy, ABA plays a central role in both the monocot and dicot species examined to date. In line with this, ABA metabolism and signalling genes have been identified and found to be universally present in both plant groups. Our phylogenetic analysis identified homologs of key ABA synthesis and catabolism genes in Brachypodium and temperate cereals (**Figure 1A**).

As the rate-limiting enzyme in the ABA biosynthesis pathway, 9-cis-epoxycarotenoid dioxygenase (NCED) encoding genes have been extensively characterized in model species and cereal crops. *NCEDs* belongs to the Carotenoid Cleavage Dioxygenases (CCD) gene family, which includes both *CCDs* and *NCEDs*. In Arabidopsis, five *NCEDs* were involved in ABA synthesis, among which *AtNCED6* and *AtNCED9* show seed-specific expression and play essential roles during seed development to set seed dormancy [6]. Through sequence similarity searches, *NCEDs* were also cloned in rice, barley and wheat [7-10]. Gene expression patterns of *NCED1* and *NCED2* in these species have been consistently associated with grain dormancy induction and release under diverse environmental conditions [11-14]. Like in Arabidopsis, five *NCEDs* have been reported in rice. The role of *OsNCED3* in regulating seed germination and pre-harvest sprouting has been confirmed by independent research [15, 16], while the rest of the genes were implicated in ABA-related processes [15, 17-19]. *BdNCED1 (Bradi4g01440)* and *BdNCED2 (Bradi 1g13760)* share the highest sequence similarity with *OsNCED5* and *OsNCED3* respectively, which have proven roles in grain dormancy and germination. Meanwhile, gene expression levels of *BdNCED1* and *BdNCED2* correlated well with Brachypodium seed dormancy status under imbibition conditions [11], which was further supported by a gene expression time course during grain development (**Supplementary Figure 1**). Heterologous expression of *OsNCED4* in Arabidopsis led to delayed seed germination [17], it is thus possible that *BdNCED5* may play similar roles in modulating Brachypodium grain dormancy and germination.

The Arabidopsis CYP707As encode ABA 8'-hydroxylases, key enzymes in ABA catabolism [20, 21]. Among the gene family, *AtCYP707A1* and *AtCYP707A2*, were shown to be indispensable for seed dormancy and germination control in Arabidopsis [22]. Homologs of CYP707A were identified in cereals and classified into two major clades (**Figure 1B**), clustering with *AtCYP707A4* and *AtCYP707A1 to AtCYP707A3*. Among them, ABA8'OH-1 and ABA8'OH-2 have been consistently associated with grain dormancy in wheat, barley and Brachypodium through gene expression analysis [10, 11, 23]. In wheat, a bread wheat mutant deficient in ABA 8'-hydroxylase gene displayed stronger germination inhibition under field conditions and has been deployed for PHS resistance [24, 25].

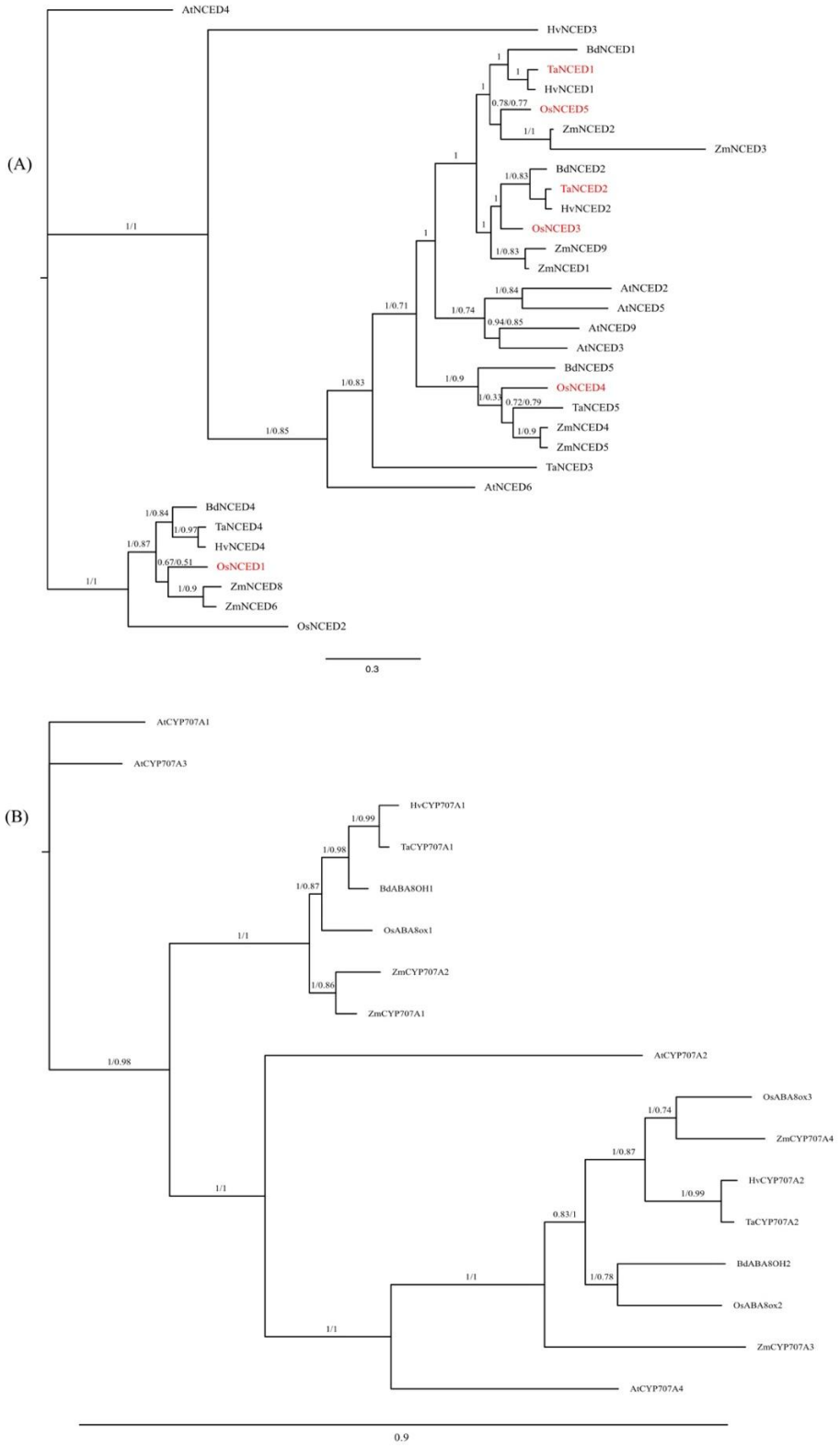

Figure 1, Maximum likelihood phylogeny of (A) NCED and CYP707A (B) proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.

1.2 ABA signalling proteins

Besides ABA metabolism, ABA signalling pathways integrate internal and external cues and trigger downstream effects through a group of PYR/PYL/RCAR receptors, type 2C protein phosphatases (PP2Cs) and SNF1-related protein kinase 2 proteins (SnRK2s). Arabidopsis ABA receptors can be grouped based on differential ABA inhibitions [26, 27]. A similar pattern was also supported by experimental evidence in Brachypodium [28, 29]. In group 1 and group 3 ABA receptors, Brachypodium and rice homologs cluster with corresponding Arabidopsis proteins (**Figure 2A**). While in group 2, four rice homologs are distant from Arabidopsis and Brachypodium proteins, indicating possible divergence between rice and Brachypodium [30].

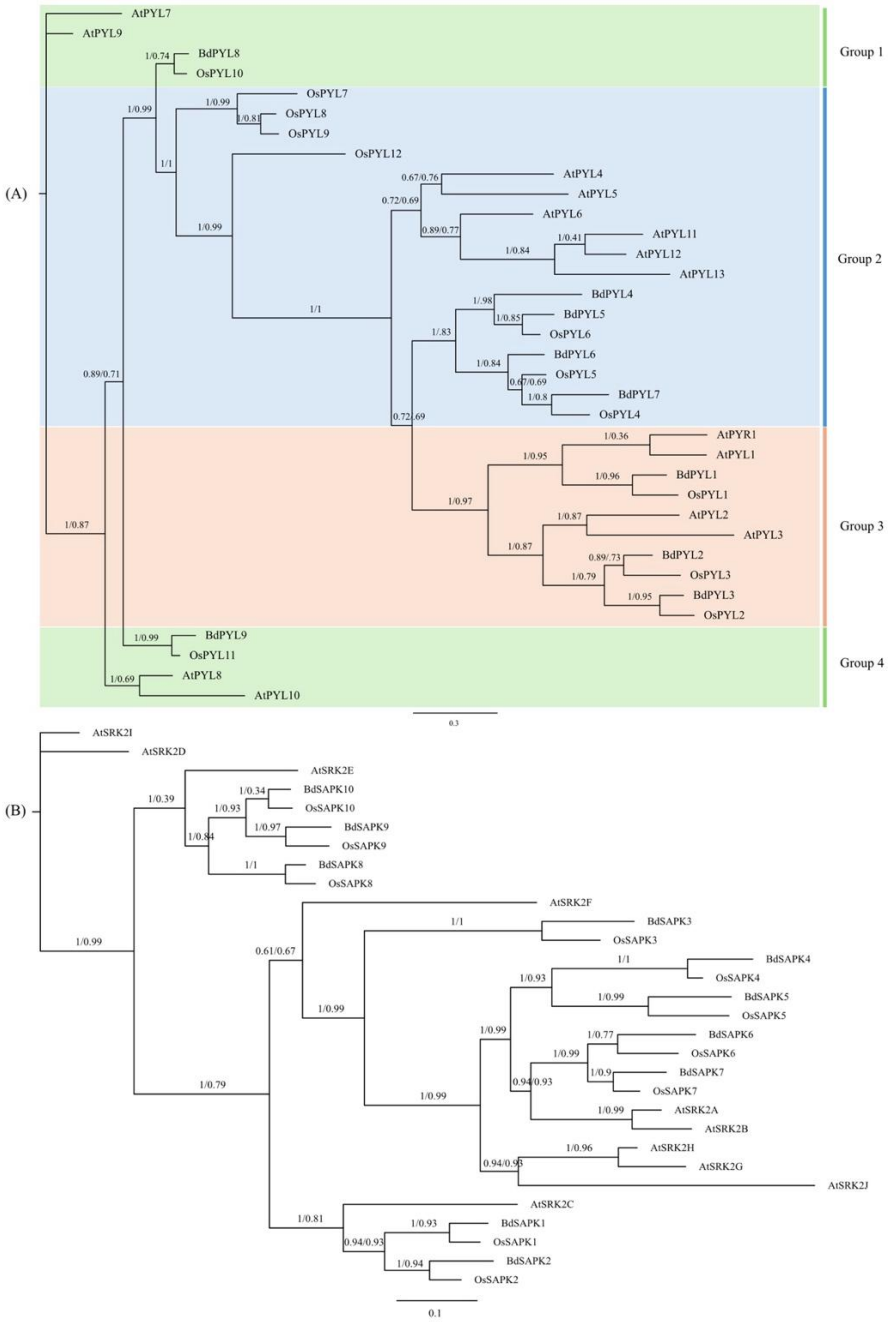

Figure 2, Maximum likelihood phylogeny of (A) PYR/RCAR/PYL ABA receptor and (B) SnRK proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.

Binding of ABA to its receptors releases PP2Cs from inhibiting SnRK2s, which phosphorylates downstream effectors leading to ABA related responses subsequently. The nine Arabidopsis PP2Cs can be classified into two subfamilies based on sequence similarities, namely ABA INSENSITIVE1 (ABI1) and ABA HYPERSENSITIVE GERMINATION1 (AHG1). The former group includes ABI1, ABI2, HYPERSENSITIVE TO ABA1 (HAB1) and HAB2, while the latter group consists of AHG1, AHG3/PROTEIN PHOSPHATASE 2CA (PP2CA), HIGHLY ABA-INDUCED PP2C GENE1 (HAI1), HAI2, and HAI3 [31]. Phylogenetic analysis clearly distinguished the two Arabidopsis PP2Cs subfamilies and showed the relationship to cereal homologs (**Figure 3**).

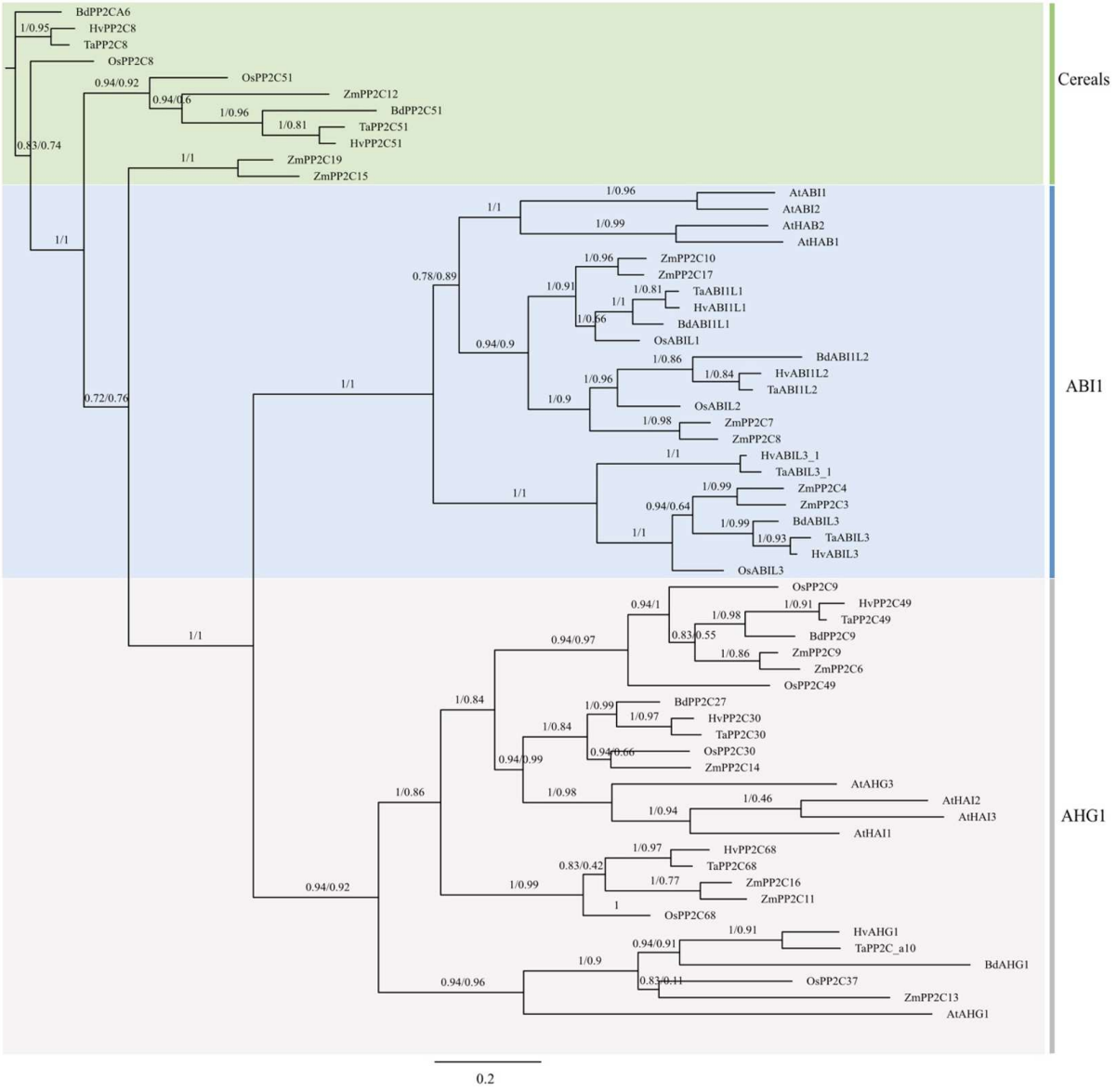

Figure 3, Maximum likelihood phylogeny of PP2C proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.

In the AHG1 group, several wheat homologs, including TaPP2C-a5, TaPP2C-a6 and TaPP2C-a10, have been shown to regulate seed dormancy and germination through interaction with core ABA signalling components TaPYLs and TaSnRK2s, but also with TaDOG1L proteins [32-34]. This indicates a highly conserved role of PP2Cs in ABA signalling perception and transduction among monocots and dicots, while also pointing to the usefulness of Brachypodium homologs in further investigation [35]. On top of the AHG1 and HAI groups, a single clade of cereals PP2Cs was also identified, which includes

BdPP2CA6 (Bradi2g45470) interacting with BdPYLs and BdSnRK2 to regulate salt tolerance in transgenic Arabidopsis [36], and a positive seed germination regulator OsPP2C51 [37].

Another core component of ABA signalling is composed of a group of plant-specific, Ser/Thr kinases called SNF1-related protein kinases 2 (SnRK2s). Both Arabidopsis, rice and Brachypodium genomes encode ten members of SnRK2s (**Figure 2B**), designated as SnRK2.1 to SnRK2.10 in Arabidopsis, and osmotic stress/ABA–activated protein kinases (SAPKs) SAPK1 to SAPK10 in rice and Brachypodium [38]. While in wheat and barley, SnRK2 homologs were revealed as ABA-induced protein kinases (PKABA) [39, 40].

Among these protein kinases, three Arabidopsis SnRK2s, SRK2D/SnRK2.2, SRK2E/SnRK2.6/OST1 and SRK2I/SnRK2.3, are essential for seed germination and dormancy control [41, 42]. Seed germination phenotypes have also been reported for OsSAPK8/9/10 and PKABA1 [43-45], indicating functional conservation of this subgroup of SnRK2s in seed dormancy and germination regulation. Concerning the conserved roles of SnRK2s in ABA signalling, investigation of Brachypodium homologs may provide further information on hormonal regulation of seed dormancy and germination in temperate cereals, as gene expression analysis already revealed their possible functionality in seed development and maturation (**Supplementary Figure 1**).

Arabidopsis seed development is regulated by a group of so-called LAFL network genes, which includes the B3 domain-containing transcription factors *ABSCISIC ACID INSENSITIVE3 (ABI3), FUSCA3 (FUS), LEAFY COTYLEDON2 (LEC2)*, and NF-YB family transcription factor encoding gene *LEC1* [46]. Coordination and interaction of these genes mediate the introduction and maintenance of seed dormancy. While genetic lesions in *lec1*, *lec2* and *fus3* led to defects in embryogenesis and maturation, *abi3* lesions yield green seeds with reduced reserves [47-49]. These genes have also been shown to be involved in seed dormancy and germination [50]. Furthermore, another two groups of transcription factors, namely VIVIPAROUS1/ABI3-LIKE1 (VAL1) and VAL2, and RELATED to ABSCISIC ACID INSENSITIVE3 /VIVIPAROUS1 (RAV), have also been implicated in seed dormancy and germination [51-53].

Homologs were identified in grasses for all these regulators, showing high levels of conservation among monocots and dicots (**Figure 4**). In the VAL3, VAL2, RAV1, ABI3 and FUS3 clades, a single protein exists in both Arabidopsis and grasses, while duplications were found in the LEC2 clade. No VAL1 homologs were identified in grasses. The involvement of ABI3/VP1 in seed dormancy has been documented in both Arabidopsis and cereals [54, 55]. Gene expression analysis in Arabidopsis suggested no correlation between LEC1, FUS3, ABI3 and seed dormancy [56], but opposite findings showing such association were reported in bread wheat [57]. During Brachypodium grain development and maturation, *BdLEC2.1 (Bradi5g26100)* and *BdFUS3 (Bradi2g48057)* expression levels peaked at the full-length grain stage, while *BdVP1 (Bradi2g58390)* was highly expressed in germinating and mature grain (**Supplementary Figure 1**). Further investigation into the Brachypodium homologs may help resolve this discrepancy and provide insights into the evolutionary relationship between the two plants groups.

1.3 Gibberellic acid (GA)

Besides ABA, other phytohormones, including Gibberellins, Ethylene, Brassinosteroids (BR) and Auxin among others, have long been known to act in seed dormancy and germination [58, 59].

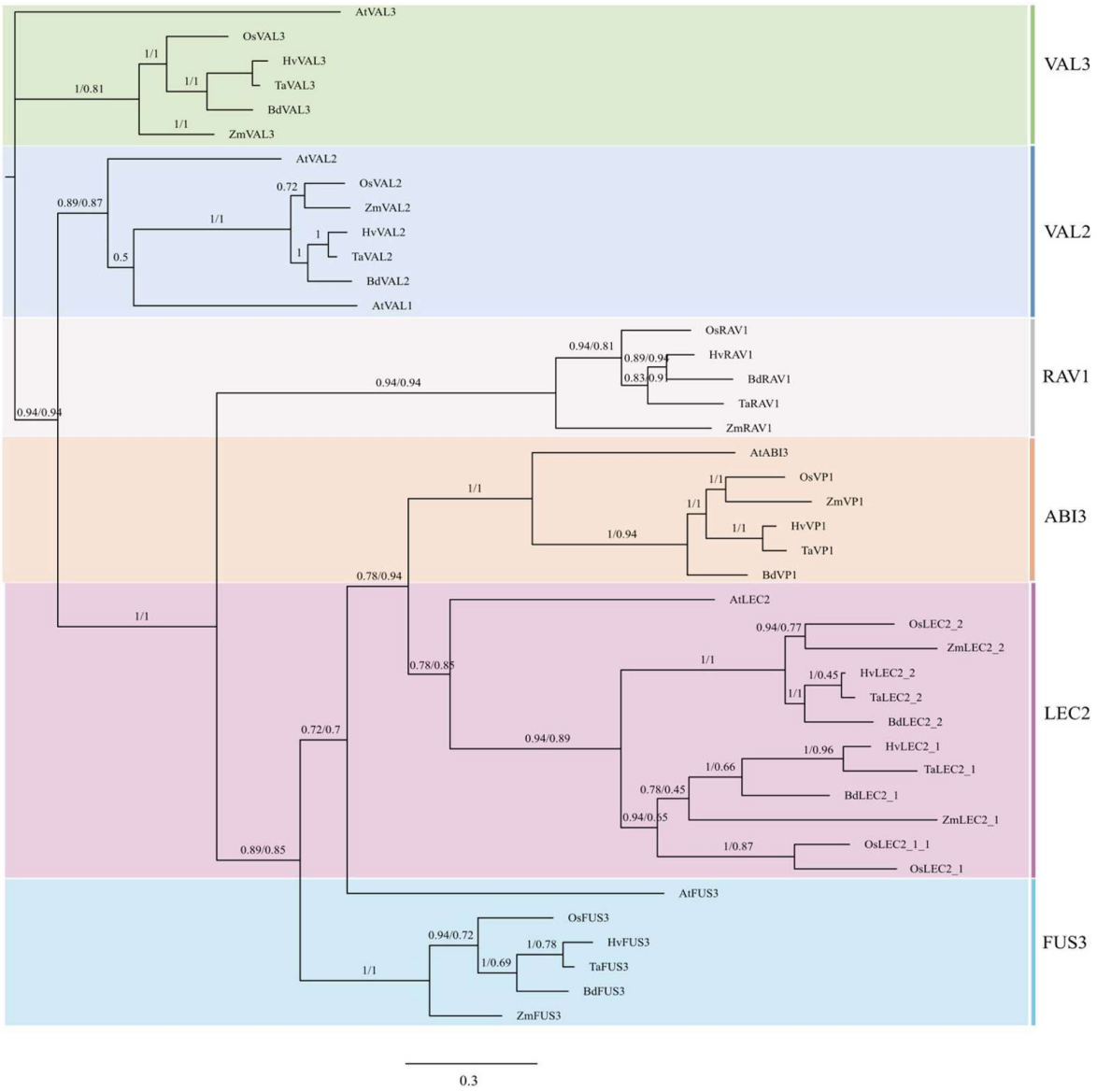

Figure 4, Maximum likelihood phylogeny of proteins encoded by LAFL genes showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.

Metabolism of GA is determined by key enzymes including Gibberellin 20-oxidases (GA20oxs) and Gibberellin 3-oxidases (GA3oxs) which are rate-limiting biosynthetic components, and Gibberellin 2-oxidases (GA2ox) playing major catabolic roles. In Arabidopsis, the above three enzymes were encoded by gene family, with nine in the GA2ox family, five members in the GA20ox family and four in the GA3ox family. Expression of these genes has been implicated in seed dormancy and germination in both Arabidopsis and cereals, including wheat, barley, rice and sorghum [60-63].

We looked for homologs of Arabidopsis GA2ox enzymes in the Brachypodium and rice genomes, corresponding to twelve members in the former and eleven in the latter (**Figure 5**). Possible gene duplication in the monocots could explain this difference, as evident in the monocots GA2ox5, GA2ox6 and GA2ox9 enzymes. For AtGA2ox1-4 and AtGA2ox6, Brachypodium and rice homologs group together with Arabidopsis enzymes, indicating conserved relationship. Interestingly, Brachypodium maintains an extra GA2ox8, which is a paralog derived from possible tandem duplication.

The Brachypodium genome encodes five GA20ox enzymes like Arabidopsis, while rice has four members with no GA20ox5 homolog identified. *OsGA20ox2* has been identified as the candidate gene for a major seed dormancy locus *Seed Dormancy1-2 (qSD1-2),* which regulates the development of endosperm-imposed dormancy in rice [63]. In the GA3ox family, two homologs were identified in both Brachypodium and rice, in contrast to the four members in Arabidopsis.

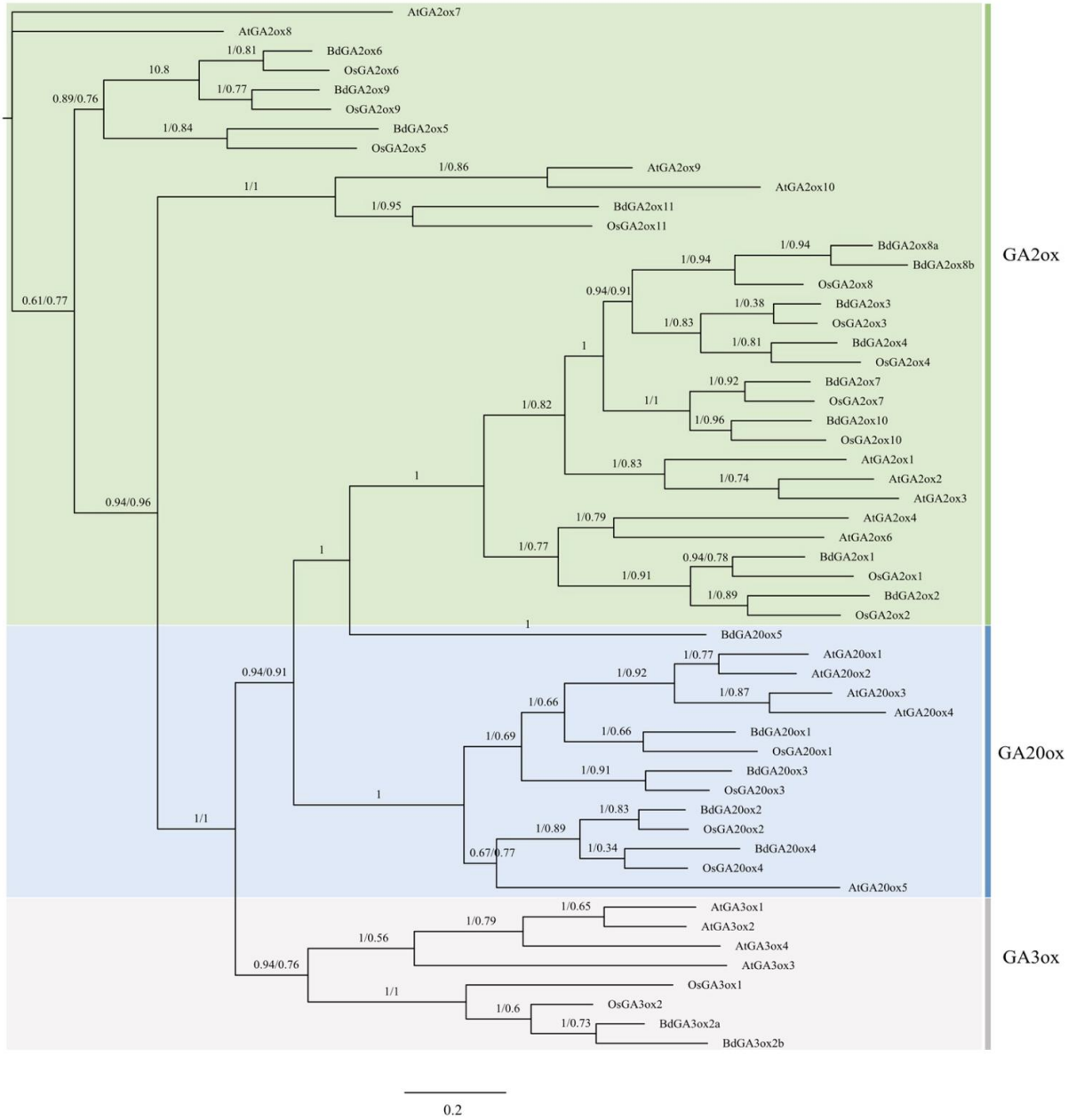

Figure 5, Maximum likelihood phylogeny of GA metabolism proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.

Besides GA metabolism, GA signalling integrates internal and external cues into the central hormonal mechanism and thus contributes to diverse plant growth and development aspects. DELLA proteins are key components in this process and function as germination repressors. In Arabidopsis, five DELLA proteins were revealed, namely GAI, RGA, RGL1, RGL2, and RGL3. The rice core DELLA protein was designated SLENDER RICE 1 (SLR1), which clusters in the same clade of barley Slender1 (SLN1), wheat Reduced height-1 (Rht-1), maize Dwarf plant8 (D8) and Dwarf plant9 (D9) proteins (**Figure 6**). Two other clades, SLR1-LIKE1 (SLRL1) and SLRL2, consisting of proteins specific to grasses were

also revealed. Brachypodium homologs were identified in all three clades. During Brachypodium grain germination, *BdSLR1 (Bradi1g11090), BdGA200x2 (Bradi2g57027)* and *BdGA20ox5 (Bradi1g56240)* were highly expressed, implying their involvement in grain germination (**Supplementary Figure 2**).

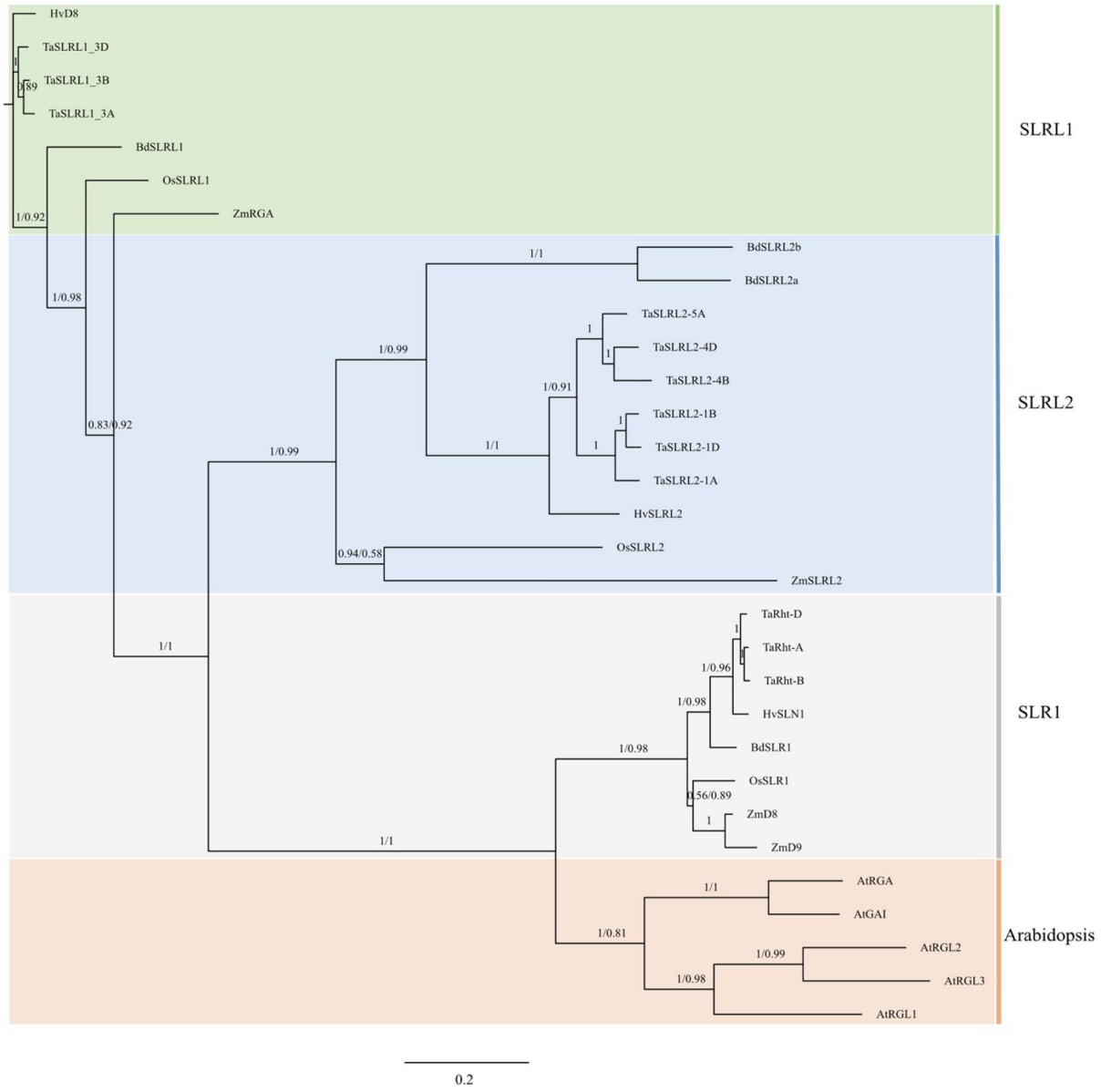

Figure 6, Maximum likelihood phylogeny of DELLA proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.

In Arabidopsis, loss of function of four DELLA genes led to GA- and light-independent germination [64]. Although no non-germinating GA-deficient mutant in cereals has been reported, DELLA proteins have been shown to induce the expression of reserve mobilisation enzymes upon seed germination, which was best studied in the barley aleurone cells [45, 65]. Functional characterization of BdSLR1 and BdSLRL1 (Bradi2g45117) revealed their conserved roles in GA-mediated growth regulation [66].

Upon GA perception by the GID1 hormone receptor and binding to DELLA, an F-box protein SLEEPY1 specifically targets the GA-GID1-DELLA complex, which subsequently leads to ubiquitination and 26S proteasome-mediated destruction and thus relieving the repression of DELLA [67]. In Arabidopsis, SLEEPY1 (SLY1) has been proved responsible for this process while another homologous protein SNEEZY1 (SNE) also contributes [68, 69]. The rice protein corresponding to

SLY1 was identified as gibberellin-insensitive dwarf2 (GID2), which specifically interacts with phosphorylated SLR1 and regulates the GA-dependent degradation of SLR1 in rice [70, 71]. The wheat GID2 homologous genes have also been characterized to play similar roles in an E3 ubiquitin-ligase SCF complex [72]. Homologous proteins are identified in Brachypodium, which correspond to GID2 and SNE respectively (**Supplementary Figure 3A**). Interestingly, in the GID2 clade, two homologs exist in wheat, barley and maize, in contrast to Brachypodium and rice with single proteins identified.

1.4 Auxin

Auxin coordinates ABA to promote seed dormancy and inhibit germination. Auxin biosynthesized by the YUCCA family proteins can be transported by the PIN family and AUX/LAX proteins, which trigger downstream effect through the AUXIN RESPONSE FACTOR (ARF) and AUX/IAA family proteins [73].

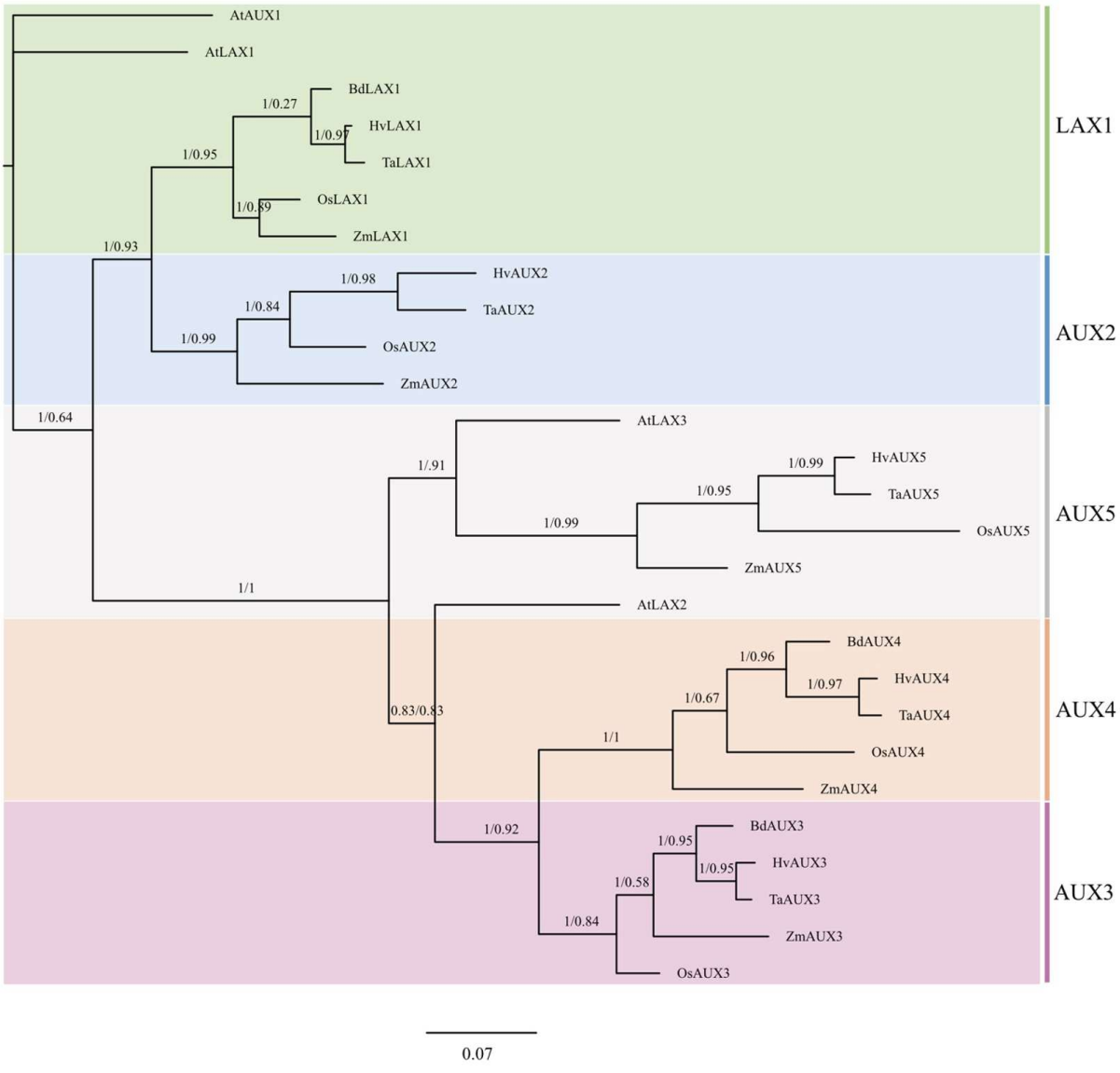

Figure 7, Maximum likelihood phylogeny of LAX and AUX proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.

The Arabidopsis AUX/LAX family contains four members, namely AUX1 and LAX1-3 [74]. Homologs of the four proteins were identified in grass species, but species-specific distinctions were revealed in the phylogeny (**Figure 7**). In the cereal AUX2 and AUX5 clades, no Brachypodium

homologous protein was identified, indicating possible gene loss at least in the Bd21 accession. Furthermore, in contrast to a single AtLAX2 protein, two homologous proteins were identified in the grass species grouped into AUX3 and AUX4 clades, possibly due to duplication events that led to such expansion in grasses. *BdAUX1/LAX1 (Bradi2g55340)*, *BdAUX3 (Bradi1g68350)* and *BdAUX4 (Bradi3g21090)* were expressed at the highest levels in germinating grains, which strongly suggest their participation in this process (**Supplementary Figure 4**).

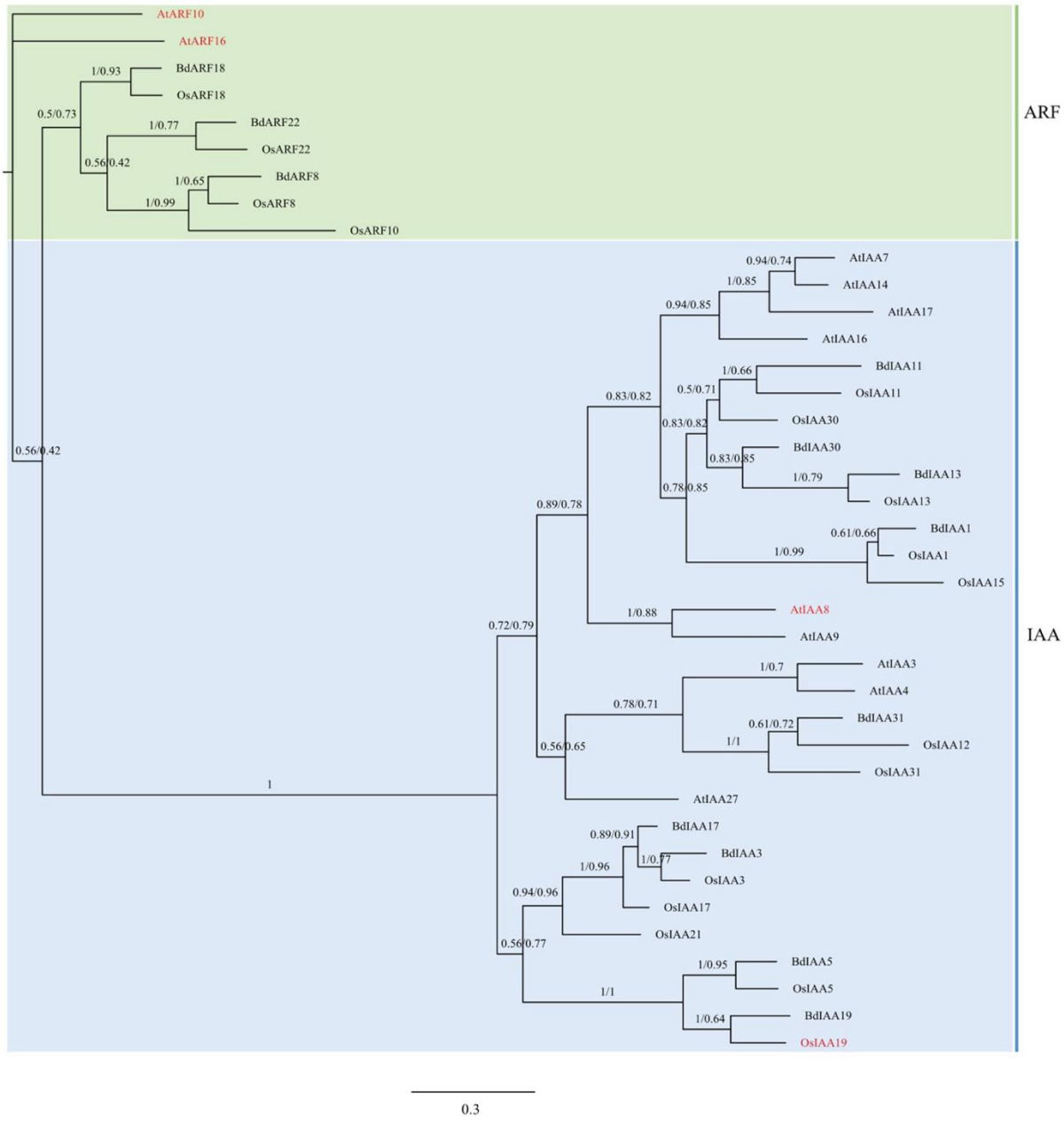

Figure 8, Maximum likelihood phylogeny of IAA and ARF proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.

Functional analysis showed that AtAUX1 plays important roles in the regulation of seed germination [75]. Epigenetic modification of AtAUX1 through SWI-INDEPENDENT3 (SIN3)-LIKE1 (SNL1) and SNL2 controls Arabidopsis seed germination speed [76]. In rice, OsAUX1 has been proved necessary not only for the long coleoptile trait under submergence conditions, but also for root hair elongation in response to low external phosphate [77, 78]. In Brachypodium, functional characterisation of BdAUX1/LAX1 uncovered fundamentally different wiring of root auxin transport in Brachypodium

and Arabidopsis during developmental processes [79]. Considering the contrasting seed germination conditions between tropical and temperate cereals, and distinct developmental phenotypes of AUX1 mutants in monocots and dicots, it is highly possible that AUX1 also participates in seed dormancy and germination in temperate cereals but plays different roles. Further investigation down this line could reveal novel insights into auxin regulation of seed germination in this plant group.

In Arabidopsis, auxin contributes to seed dormancy via the ABA signalling pathway, which involves interactions between ARFs, notably ARF10 and ARF16, and ABI3 [80, 81]. During seed germination, auxin participates in jasmonate-mediated ABA signalling through interactions between ARF10/16 and JASMONATE ZIM-DOMAIN (JAZ) proteins on the one hand, and physical interaction with ABI5 on the other hand [82]. ARF16 also physically interacts with a PHD finger protein GERMOSTATIN RESISTANCE LOCUS 1 (GSR1) to modulate seed dormancy and germination [83]. The auxin signalling repressor IAA8 promotes seed germination through down-regulation of ABI3 in Arabidopsis [84].

Homologs of AtARF10 and AtARF16 were identified in rice and Brachypodium, including four members in rice and three in Brachypodium (**Figure 8**). In rice, OsARF9 modulates ABA-mediated inhibition of seed germination through translational repression of OsABI3 [85]. Wheat grain dormancy induction, maintenance and alleviation by after-ripening also involves ARFs [86, 87]. The importance of ARFs in grain dormancy and germination control was also observed in barley, where three putative ARFs encoding genes were differentially expressed between wildtype and transgenic plants over-expressing *miR393* [88].

In the IAA group, homologs were also identified for both Brachypodium and rice. Among rice IAAs identified, OsIAA19 has been shown to promote seed germination [89]. In Brachypodium, homologs of *AtIAA3/4/27* and *AtIAA7/14/16/17* were up-regulated upon exogenous IAA treatment [90], indicating they are functional in mediating hormone signalling and possibly play roles in plant growth and developmental processes like seed dormancy and germination. In wheat, indoleacetic acid (IAA) was shown to complement the role of ABA in grain germination [91]. A natural allelic variation of *TaIAA10-6A* was revealed to confer pre-harvest sprouting resistance through GWAS analysis [92].

1.5 Ethylene

Opposite to Auxin, ethylene promotes seed germination and counteracts ABA effects [58]. Ethylene can be perceived by a group of five members, namely ETHYLENE RESPONSE1 (ETR1), ETR2, ETHYLENE RESPONSE SENSOR1 (ERS1), ERS2, and ETHYLENE INSENSITIVE4 (EIN4). This signal perception was integrated by the central signalling factor ETHYLENE INSENSITIVE 2 (EIN2), which triggers downstream effects on plant growth and development [93]. In rice, similar components have been reported but named differently, which include the five receptors (OsERS1, OsERS2, OsETR2, OsETR3, OsETR4) and the central signalling factor OsEIN2 [94]. Homologs of these proteins were identified in grasses and followed the nomenclature of rice proteins (**Figure 9, Supplementary Figure 3B**). In the ETR2, ETR3 and ERS2 clades, both plant groups maintain a single protein, indicating high level of conservation. However, in the ETR4 and ERS1 clade, two homologous proteins were identified in wheat and barley, possibly derived from gene duplication.

The importance of ethylene in Arabidopsis seed dormancy and germination has been extensively characterized and summarized [95-97]. The Arabidopsis *etr1-2* gain-of-function mutation enhanced seed dormancy, influenced moist-chilling and germination through hormonal metabolic pathways, including ABA, auxin, cytokinin and GA [98]. On the contrary, *etr1-6*, *etr1-7* and *rdo3* (*reduced dormancy 3*, allelic to *ETR1*) loss-of-function mutations reduced seed dormancy but increased ethylene sensitivity, indicating the positive role of ETR1 in the establishment of seed dormancy [99]. Sub-

functionalization of Arabidopsis ethylene receptors in seed dormancy and germination control was observed, in that *ETR1* and *EIN4* loss-of-function mutations reduced dormancy, *ETR2* loss-of-function increased seed dormancy, while loss of either ERS1 or ERS2 had no measurable effect on germination [100].

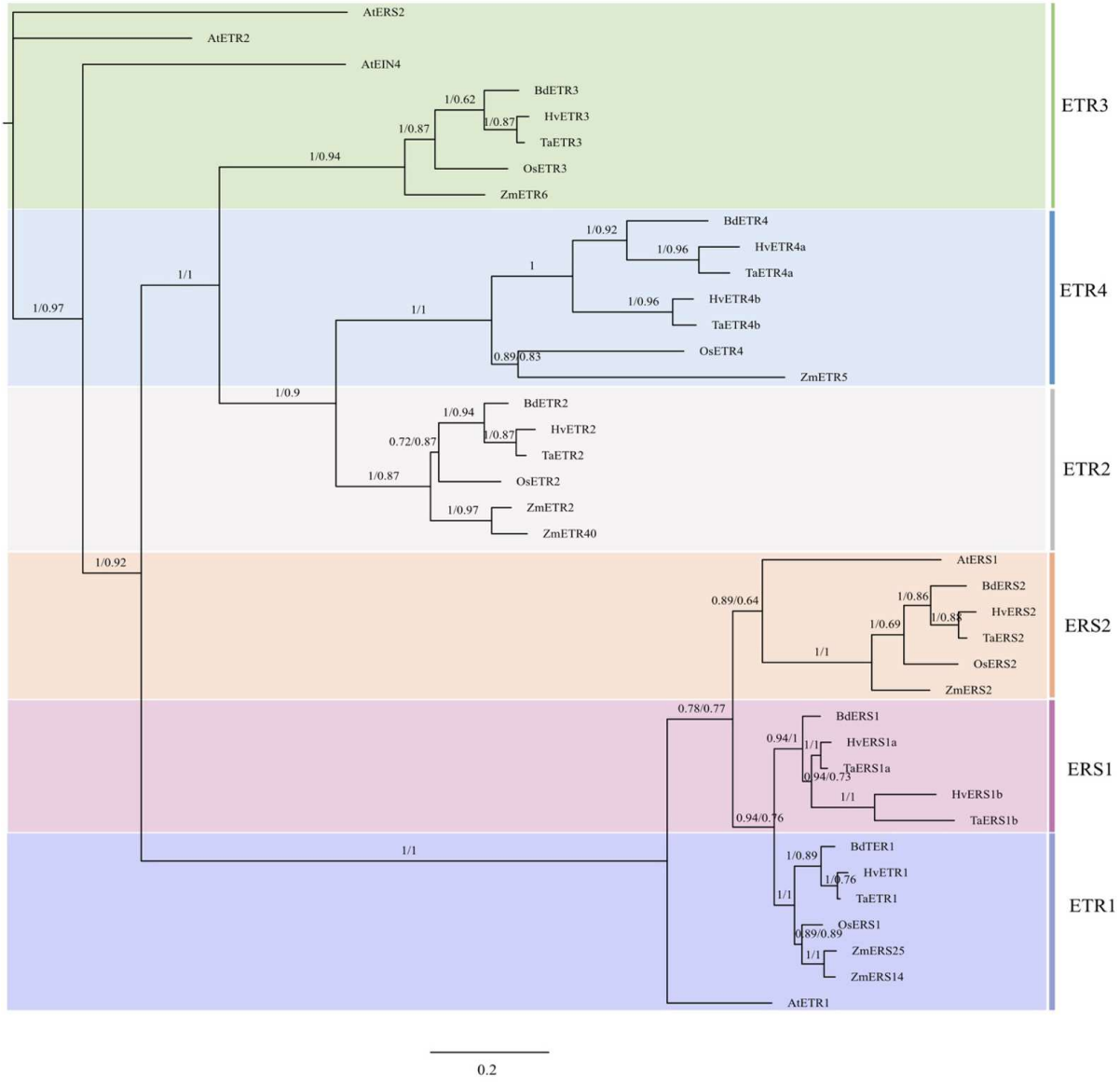

Figure 9, Maximum likelihood phylogeny of ETR and ERS proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.

Functional characterisation of grass ethylene receptors during seed dormancy and germination remains largely unexplored, however, it has been shown that overexpression of *TaETR1-1* enhanced seed dormancy and ethylene insensitivity in wheat [101], like that of Arabidopsis *AtETR1*. As the most similar homolog to both Arabidopsis and wheat ETR1, *BdETR1 (Bradi1g11540)* expression fluctuates in the grain development regime and peaks before flowering (**Supplementary Figure 4**), it is thus possible that this gene plays a role in setting seed dormancy.

1.6 Brassinosteroids (BRs)

BRs are a class of steroid hormones essential for normal growth and development in plants. BR perception by the cell-surface receptor BRI1 triggers the kinase activity of BRI1. This inhibits the kinase activity of BRASSINOSTEROID INSENSITIVE2 (BIN2, also called GSK3-like kinase) leading to

dephosphorylation and accumulation of BZR1 and BRINSENSITIVE1 (BRI1)-EMS-SUPPRESSOR1 (BES1/BZR2) proteins in the nucleus, which modulate plant growth and development response and feedback regulation of BR biosynthesis [102].

The role of BRs in seed germination has been repeated in tobacco, Arabidopsis and rice [103-105], which involves hormonal interactions with GA and ABA. In Arabidopsis, BRs antagonize ABA through ABI5, which interacts with BIN2 and can be hindered by BES1, while BRI1 engages in seed dormancy release by cold stratification [106-108]. In rice, BRs promote seed germination through BZR1 to modulates reserve mobilisation, while also orchestrating the effect of GA [103, 109]. Brachypodium homologs of BRI1, BIN2 and BZR grouped together with rice proteins, indicating high conservation levels between these two species (**Supplementary Figure 5**).

1.6 Jasmonate (JA)

JA has been shown to function synergistically with ABA to delay seed germination through ABA signalling pathways in Arabidopsis [110], which involves repressed transcription of ABI3 and ABI5 by the JA signalling repressor JASMONATE ZIM-DOMAIN (JAZ) proteins through direct interaction (**Supplementary Figure 6**). Homologs of Arabidopsis JAZ proteins with proven roles in seed germination were identified in Brachypodium and rice. Among them, OsJAZ5 (Os04g0395800) was proposed as the candidate gene of a QTL that positively regulates seed germination in rice [111]. However, the effect of JA on seed dormancy and germination varies between plant groups, as it was shown to inhibit germination in Arabidopsis but release dormancy in wheat [112, 113]. Further investigation focusing on Brachypodium JAZ homologs may provide insights into this intricacy.

2. DELAY OF GERMINATION 1 (DOG1)

2.1 Conservation of DOG1 family proteins in seed dormancy

DELAY OF GERMINATION 1 (DOG1) has been identified as a major regulator of seed dormancy in Arabidopsis [114]. Besides *DOG1*, the Arabidopsis genome encodes five *DOG1-like* genes, designated as *DOG1L1* to *DOG1L5* [31]. BLAST search identified homologs of *DOG1L* genes in rice and temperate grasses (**Figure 10A**). Phylogenetic analysis shows distinct clustering of Arabidopsis and grass *DOG1* genes. Consistent with published results, *AtDOG1, AtDOGL1, AtDOGL2,* and *AtDOGL3* forms a single clade, while *AtDOGL4* and *AtDOGL5* were distributed within the grass clades [115].

AtDOGL4 was clustered in the grass *DOG1L3* clade. In rice, *OsDOG1L3* has been proposed as a candidate gene responsible for a seed dormancy QTL *qSd-1-1* [116]. Interestingly, the maize homologs have been previously identified as *Response to ABA and Salt 1 (RAS1)*, a negative regulator of salt tolerance during seed germination by enhancing ABA sensitivity, implying the involvement of *DOG1L* genes in ABA signalling [117].

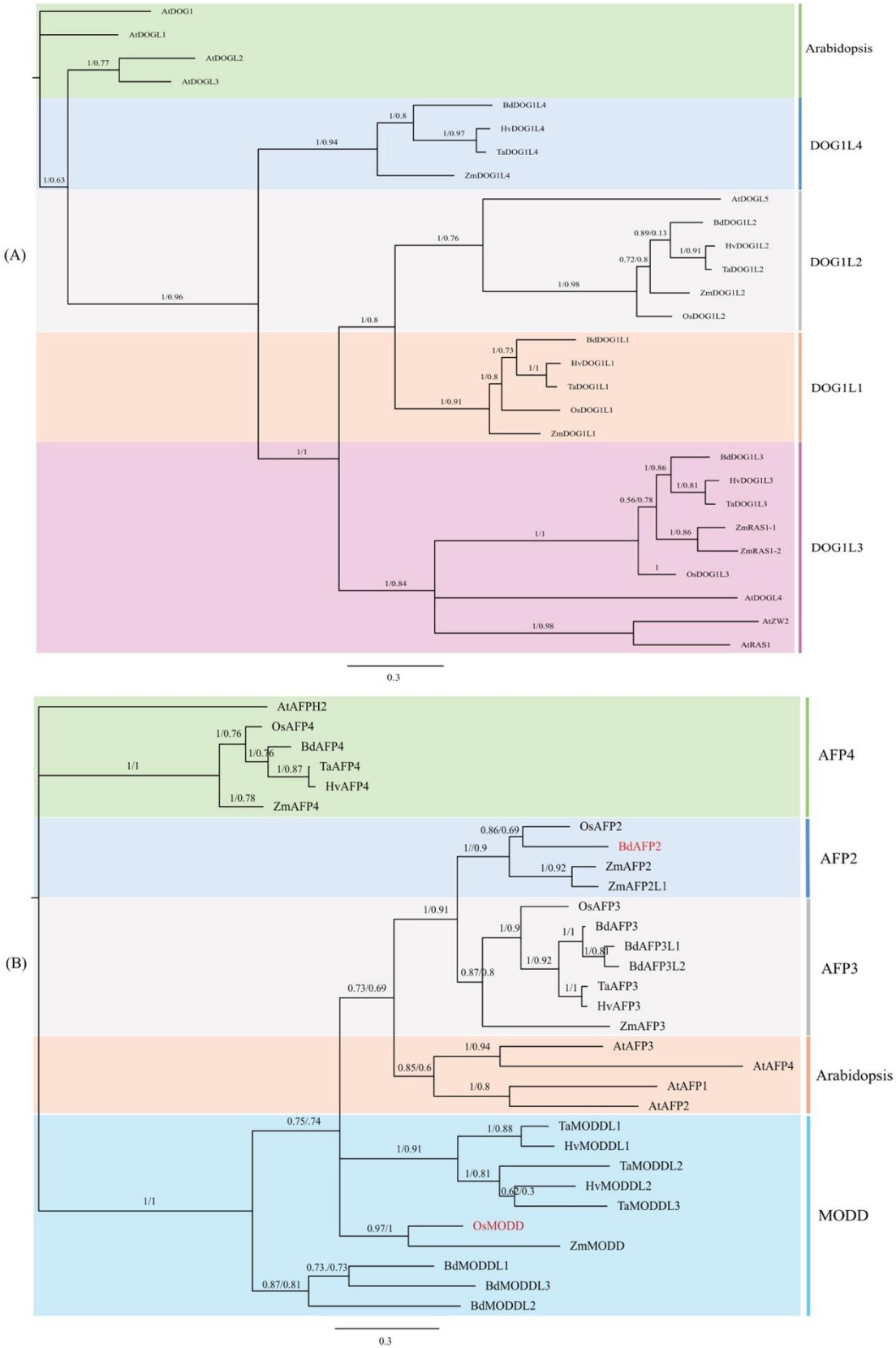

Figure 10, Maximum likelihood phylogeny of (A) DOG1 proteins and (B) AFP proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.

The grass *DOG1L4* clade contains homologs from Brachypodium, barley, wheat and maize. Ectopic expression showed possible conservation of Triticeae *DOG1L* genes in seed dormancy regulation [118, 119]. Physical interactions between wheat *DOG1L* genes and ABA signalling components revealed the wider framework in which DOG1 functions to regulate seed dormancy [32, 120, 121]. No rice *DOG1L4* gene was found.

In Arabidopsis, DOG1 requires the ABA signalling components PP2C phosphatases ABA-HYPERSENSITIVE GERMINATION 1 (AHG1) and AHG3 to control seed dormancy. Mutational analysis identified functional DOG1 residues necessary for the interaction between DOG1 and AHG1. The P178L mutation, which contains an amino acid substitution, abolished the interaction with AHG1, which underscores its role for proper DOG1 function. Among DOGL homologs from grasses, DOGL3 and DOGL4 clades contain the same proline residue, DOGL1 clade contains lysine, while DOGL2 clade lacks this residue and its bordering fragment. In wheat, a protein phosphatase TaPP2C-a10 has been shown to interact with TaDOG1L1 and TaDOG1L4, like that of AtAHG1.

2.2 AFPs emerge as a converging point of ABA and DOG1

AFP was initially characterised as a novel negative regulator of ABA signalling [122]. In another yeast-two-hybrid screen for ABI5 interacting proteins, a small highly conserved plant-specific protein family consisting of four members were identified and designated as AFP one to four [123]. During Arabidopsis seed germination, AFP promotes ABI5 protein degradation by targeting ABI5 for ubiquitin-mediated degradation in nuclear bodies. AFP was later found to regulate stress response in germinating Arabidopsis seeds and seedlings. Mutations in AFP1 or AFP2 result in increased sensitivity to ABA and salt while *afp4* mutants are mildly ABA-resistant. Under stress conditions, *afp* mutants show reduced germination or seedling growth [123].

Phylogenetic analysis clusters monocot AFP homologs into four groups, namely the MODD group, AFP1 group, AFP3 group and AFP4 group (**Figure 10B**). AtAFP4 clusters in the same clade of the monocot AFP4 homologs. AtAFP1, AtAFP2, and AtAFP3 cluster separately from AtAFP4 and monocot homologs.

In the MODD group, a single gene copy was identified in rice and maize genome, two copies were identified in barley, three gene copies were detected in the Brachypodium and wheat genomes. The rice MODD gene was first reported as *MEDIATOR OF OSBZIP46 DEACTIVATION AND DEGRADATION*, which mediates deactivation and degradation of OsbZIP46 to negatively regulate ABA signalling and drought resistance [124]. Recently, MODD was shown to be the encoding gene for the Seed Dormancy 3.1 (SDR3.1) QTL from a GWAS study of rice seed dormancy [125]. SDR3.1 physically interacts with ABI5 and represses its transcriptional activation, thus negatively regulates ABA signalling. Natural variations of SDR3.1 were associated with differences in seed dormancy.

In the AFP2 clade, while homologs were detected in rice, Brachypodium, and maize genomes, no homologs were detected for wheat and barley. The Brachypodium gene, *BdAFP2 (Bradi1g59982)*, was shown to be ABA-responsive in a transcriptome analysis [90].

In the AFP3 clade, a single gene copy was retrieved for rice, maize, barley and three copies for Brachypodium and wheat. Three wheat homologs, TaAFP-2A, TaAFP-2D and TaAFP-2D, were shown to be expressed in multiple tissues including flag leaves, roots, and seedling leaves, which is different from AtAFPs. On the other hand, TaAFP-2A and TaAFP-2D responded to ABA, salt stress and dehydration conditions, in line with previous findings in Arabidopsis [126]. On top of gene expression and stress response, a 4-bp deletion in the 5'-UTR of TaAFP-2B was found to be associated with seed dormancy, indicating its conserved role in seed dormancy [127, 128]. The presence of three gene copies

on different Brachypodium chromosomes suggests possible gene duplication. One Brachypodium homolog, *BdAFP3 (Bradi1g22180)* was found to be ABA-responsive in the same transcriptome analysis as that of *BdAFP2* [90]. During grain development, no expression was detected for *BdAFP3L2 (Bradi3g07965)*, in contrast to *BdAFP3L1 (Bradi2g42280)* which was expressed at high levels in pre-anthesis ovaries and full-length grain (**Supplementary Figure 1**), indicating that *BdAFP3L2* may be a pseudogene.

3. Covering tissue mediated dormancy

The link between seed colour and seed dormancy has been observed in multiple species. Most notably the *transparent testa (tt)* mutants in Arabidopsis, and the red grains in rice, wheat and barley. Colourisation of seed covering tissue occurs through the biochemical modification of seed coat composition, with strong influence from the seed maturation environment. Red coloured grains accumulate phlobaphenes or anthocyanins in the pericarp. Regulation of phlobaphene synthesis is exerted by R2R3-MYB transcriptional factors, as encoded by the *P1* gene in maize and *Yellow seed1* in sorghum, whereas regulation of anthocyanin synthesis is controlled by transcriptional complexes consisting of R2R3-MYB, basic-helix-loop-helix (bHLH), and WD-repeat (WDR) proteins (MBW complex) [129].

Homologs of proteins conferring covering tissue mediated dormancy were identified in Brachypodium and other grass species (**Supplementary Figure 7A**). In the *TT8* clade, homologs in grasses were identified, including the rice *red coleoptiles* (*Rc*) locus [130]. The red gain colour of wheat and barley has been attributed to MYB10 transcription factors, homologous to the Arabidopsis *TT2* locus [131-133]. GWAS analysis in wheat revealed that *TaMYB10-D* confers pre-harvest sprouting resistance by regulating NCED in ABA biosynthesis pathway [134, 135]. In the MYB7 clade, natural variation at the *TaMYB7-A1* locus has been associated with PHS resistance in a GWAS study [136].

4. Epigenetic regulation

Seed dormancy is established during seed development and is tightly regulated at both genetic and epigenetic levels. Epigenetic mechanisms have been implicated in the interactions between endosperm and embryo, and the inheritance of maternal environmental memory by the progeny.

4.1 Chromatin remodelling

Chromosome organization as influenced by chromatin remodelling strongly affecting its accessibility, which may lead to gene activation or inactivation. Specific modifications of the histone proteins have been associated with transcriptional silencing, most notably histone methylation of lysine 27 (H3K27me) and H3K9me, which can be deposited by histone mark writers like Polycomb Repressive Complex 2 (PRC2) and removed by histone mark erasers such as Jumonji (JMJ)-domain containing proteins [137].

In plants, core PRC2 components consist of Enhancer of Zeste (E(z)), Suppressor of Zeste (12) (Su(z)12), and Extra Sex Combs (ESC) proteins, which include EZ/SET1 and CURLY LEAF (CLF)/SWINGER (SWN), EMBRYONIC FLOWER (EMF) and FERTILIZATION-INDEPENDENT ENDOSPERM (FIE) respectively. Our phylogenetic analysis identified homologs of these proteins in Brachypodium, rice and other grasses (**Figure 11A**).

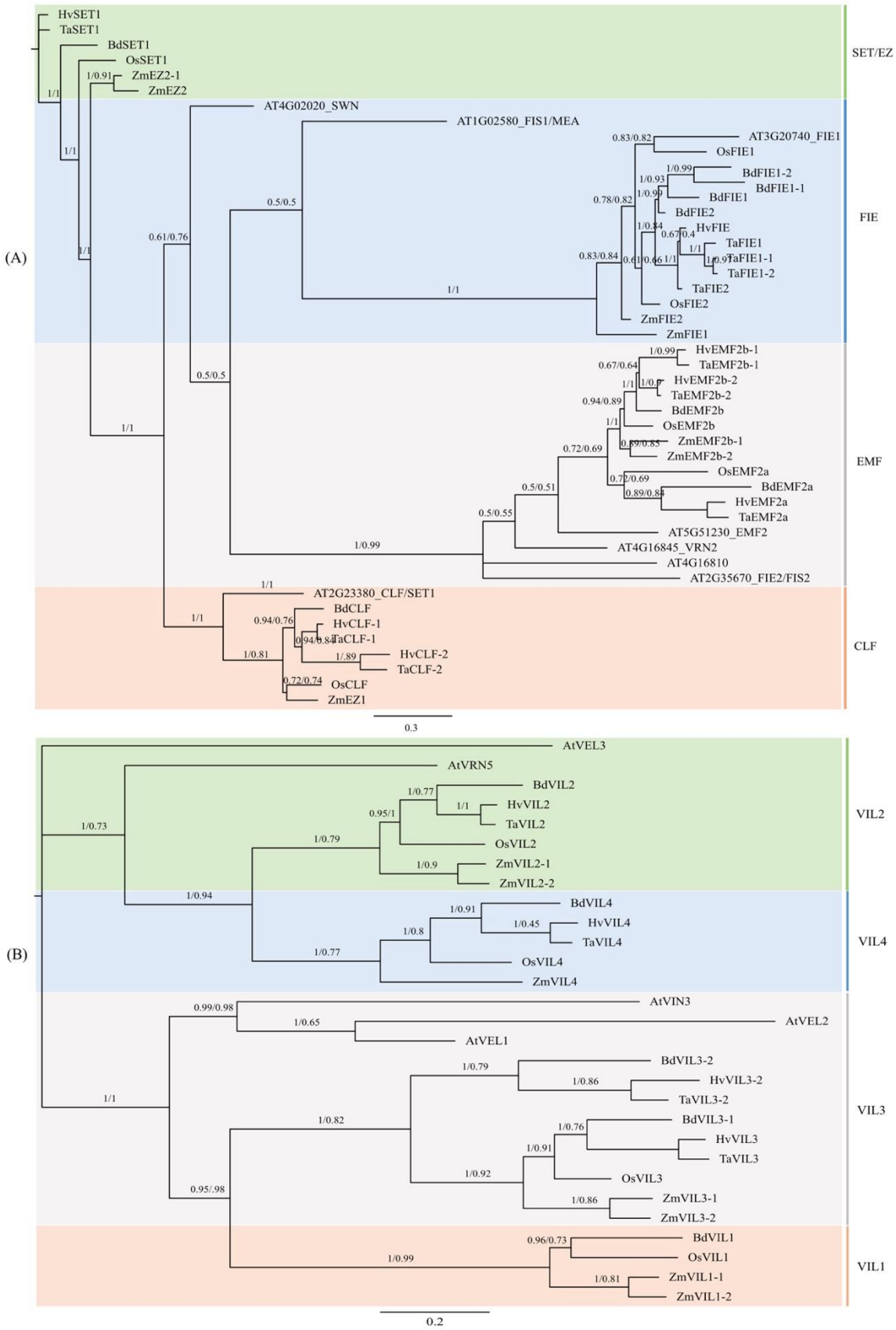

Figure 11, Maximum likelihood phylogeny of (A) PRC2 proteins and (B) VIN3 proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.

In the EZ/SET1 clade, grasses contain a single protein. In the FIE clade, two homologs were identified in the rice and maize genomes, while Brachypodium and wheat have two additional FIE1 proteins, possibly due to gene duplication. A single FIE protein was identified in barley. The maternally expressed *OsFIE1* gene has been implicated in rice seed development and dormancy [138, 139]. Expression levels of the three Brachypodium *FIE1* genes, *BdFIE1 (Bradi3g17417)*, *BdFIE1-1 (Bradi3g14510), BdFIE1-2 (Bradi2g07820),* peaked at the full-length grain stage, while *BdFIE2 (Bradi3g14520)* was expressed at high levels in the pre-anthesis ovaries (**Supplementary Figure 8**). Such expression pattern strongly suggests their possible roles in regulating seed development and dormancy, as has been shown in rice [140, 141]. The barley *HvFIE* gene was found to be induced by exogenously applied ABA, implying a possible association with ABA-mediated processes such as seed development and dormancy [142]. Further investigation into the Brachypodium *FIE* genes with respect to seed development and dormancy in the lens of epigenetics may provide evidence to consolidate the evolutionary relationship of these proteins among monocots and dicots.

In the EMF clade, grass homologs were distinguished by two sub-groups, designated as EMF2a and EMF2b, in contrast to a single EMF2 protein in Arabidopsis. In rice, the maternally expressed *OsEMF2a* plays essential role in endosperm cellularization and imprinting [143], while *OsEMF2b* controls seed dormancy by regulating the expression of *OsVP1* [144]. *BdEMF2a (Bradi4g11608)* was expressed at the highest level in full-length grains, in contrast to *BdEMF2b (Bradi3g03106)* whose expression peaked in germinating grains (**Supplementary Figure 8**). Such expression profiles indicate possible functional diversification of the two genes in regulating grain development and possibly dormancy, which needs to be further tested by experimental approaches.

No Arabidopsis VRN2 homologs were identified in Brachypodium, as has been shown previously [145].

Besides PRC2 proteins, homologs of JMJ-domain containing proteins were also identified in Brachypodium and rice (**Figure 12A**). Previous study in Arabidopsis links histone arginine demethylases AtJMJ20 and AtJMJ22 with increased seed germination when induced by light in a phytochrome B dependent manner [146]. Similarly, the H3K27 demethylase RELATIVE OF EARLY FLOWERING 6 (REF6) was also proved to be a positive regulator of light-promoted seed germination in Arabidopsis. Mechanistically, during seed development, REF6 directly binds to *CYP707A1* and *CYP707A3* leading to increased gene expression and ABA catabolism [147]. Upon seed imbibition, REF6 activates hormone-related and expansin-coding genes that are important for germination through H3K27me3 depletion [148]. Such activation has been shown to take place mostly at maternal expressed gene alleles marked by H3K27me3 alone, but not by H3K27me3, H3K9me2, and CHG methylation [149]. A single homolog of AtJMJ20 and AtJMJ22 is present in Brachypodium (Bradi2g40677 and Bradi4g16020) and rice, among which *Bradi4g16020* was highly expressed in germinating grains (**Supplementary Figure 8**). Two REF6 homologs were identified in Brachypodium and rice, which indicates possible gene duplication considering the single AtREF6. *BdREF6-2 (Bradi2g58130)* was highly expressed in germinating grains and this expression peaked in pre-anthesis ovaries, while *BdREF6-1 (Bradi4g39130)* expression initiated later but peaked at the same stage as *BdREF6-2*. Thus, BdREF6 may play important roles in coordinating grain development and dormancy possibly through histone modification as AtREF6.

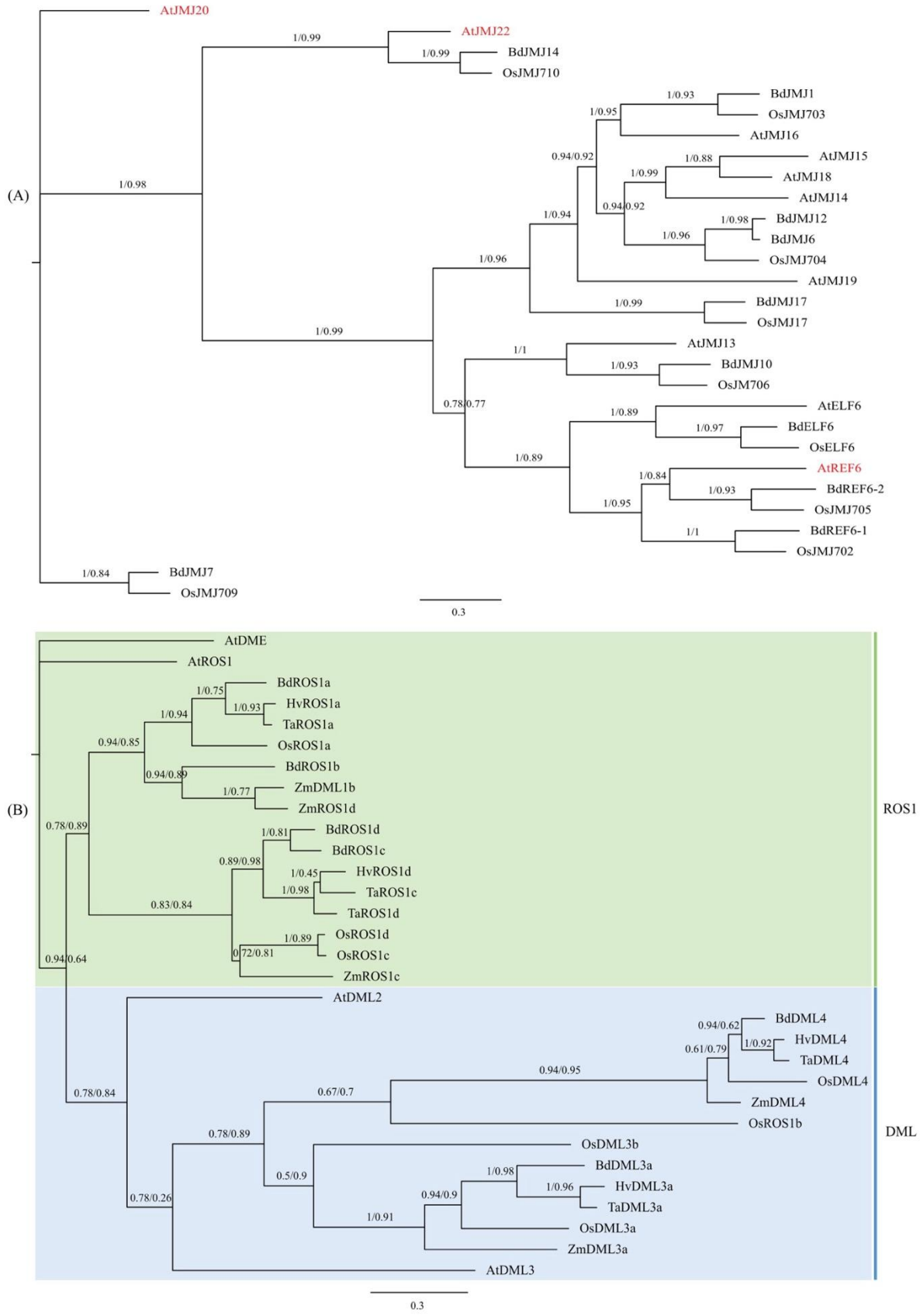

Figure 12, Maximum likelihood phylogeny of (A) JMJ-domain containing proteins and (B) ROS1 and DML proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.

Furthermore, VERNALIZATION5/VIN3-LIKE 3 (VEL3) has been shown to control progeny dormancy by establishing an epigenetic state under low seed maturation temperature in Arabidopsis [150], which involves deacetylation and H3K27me3 mark deposition in the central cell. VERNALIZATION INSENSITIVE 3 (VIN3) could associate with polycomb group proteins, leading to a polycomb-like protein complex (PRC) which promotes Arabidopsis flowering by cold temperature, so-called vernalization [151]. Genes in the Arabidopsis vernalization flowering pathway, notably *FLOWERING LOCUS C (FLC)*, *VERNALIZATION2 (VRN2)* and *VIN3,* have been shown to influence seed germination [152]. Importantly, ABA negatively regulates the Polycomb-mediated H3K27me3 through VIL1. Genetic evidence showed that *vil1* mutants exhibit hypersensitivity to ABA during early seed germination and enhanced drought tolerance [153]. Furthermore, VIL1 has also been proved necessary for light-dependent chromatin remodelling triggered by Phytochrome B [154].

VIN3 family proteins can be grouped into four sub-families, namely VERNALIZATION INSENSITIVE 3-LIKE 1 (VIL1) to VIL4 (**Figure 11B**). Although no vernalization is required for rice to flower, homologs were identified in all sub-families. In the VIL3 clade, two paralogs were found in Brachypodium, wheat and barley, indicating possible segmental duplication. No wheat and barley homologs were found in the VIL1 clade, possibly due to gene loss. OsVIL2 and OsVIL3 have been implicated in promoting rice flowering time by depositing H3K27me3 repressive marks at major flowering time gene *Heading date 1* (ortholog of Arabidopsis *CONSTANS*) and *Heading date 3a* (similar to the Arabidopsis *FLOWERING LOCUS T*) [155, 156]. In temperate cereals, three VIL proteins from diploid wheat (*Triticum monococcum L.*), TmVIL1, TmVIL2, and TmVIL3, retained a similar structure and transcriptional regulation as Arabidopsis VIN3/VIL homologs [157, 158]. In Brachypodium, BdVIL4 regulates flowering time and branching in ambient temperature dependent way [159], indicating functional conservation with other VIL homologs.

4.2 DNA methylation

In Arabidopsis, DNA demethylation is mediated by the DEMETER family DNA glycosylases, which includes three DEMETER-LIKE (DML) proteins REPRESSOR OF SILENCING1 (ROS1), DML2, and DML3 [160]. Among these proteins, ROS1 has been shown to play roles in seed development and seed dormancy displaying parent-of-origin characteristics [161], which involves imprinting of *DOG1-LIKE 4 (DOGL4)* in the endosperm in the latter case.

Homologs of ROS1, DML3 and DML4 were identified in monocot species, but not for DML2 (**Figure 12B**). In comparison to Arabidopsis, they contain an expanded ROS1 family, possibly due to gene duplication after the split of Arabidopsis and grasses.

5. Environmental regulation

5.1 Photoreceptors integrate light and temperature cues to regulate seed dormancy and germination

Light signals can be perceived by specific photoreceptors, be them phytochromes (PHY) for red and far-red light or cryptochromes (CRY) for blue light (**Supplementary Figure 9**). Arabidopsis contains five PHYs (PHYA-PHYE), in contrast to three members present in grasses. In Brachypodium, an additional BdPHY (Bradi1g10510) was identified, but the absence of detectable gene expression across germination and development stages suggests it may be a pseudogene (**Supplementary Figure 10**).

Mutation of these phytochromes led to increased seed dormancy, indicating their involvement in setting primary seed dormancy. During seed development, PHYs are synthesized in their inactive red-light absorbing form, which can be switched to the active far-red light absorbing form and vice versa. Upon seed imbibition, PHYs perceive light signals and interact with PIFs, which triggers downstream effects on genes involved in hormonal metabolism and cell wall modification to promote seed germination. In

domesticated cereal crops, no evidence of red/far-red involvement in grain germination has been reported, but observations in Brachypodium and weedy rice indicate possible participation of phytochromes [11, 162].

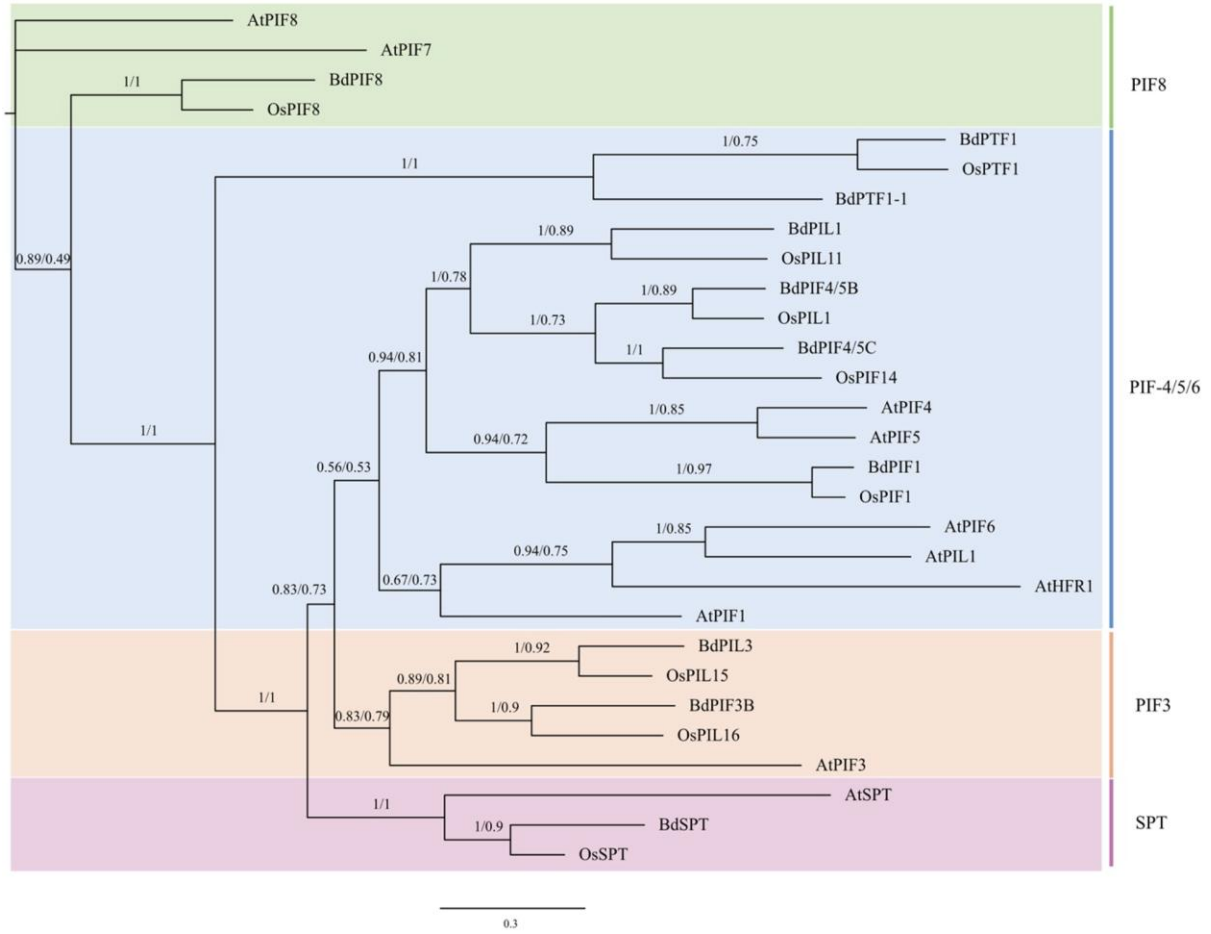

Figure 13, Maximum likelihood phylogeny of PIF and SPT proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.

The inhibitory effect of blue light on germination has been shown in temperate cereals including Brachypodium, wheat and barley, while an opposite role was revealed in Arabidopsis. In the CRY1 clade, two proteins were identified for grasses instead of one protein for Arabidopsis, which indicates possible gene duplication preceding the divergence between grasses and Arabidopsis. In the CRY2 clade, a single protein is present for all analysed species. Extensive research in barley using RNAi mutant lines revealed that blue light receptor CRY1 was responsible for this inhibition through CYP707A [12, 163]. However, expression of the wheat *CRY1a* and *CRY2* in Arabidopsis resulted in reduced germination in the presence of ABA compared to wildtype when imbibed under white light / dark conditions, raising the possibility that both CRYs may be involved in blue light inhibited grain germination [164]. Mutants deficient in rice *CRY1a* and *CRY1b* proved their indispensable roles for inactivation of GA through *GA2ox* genes under blue light in seedling [165]. Considering the critical contribution of GA, it is possible that CRY1 inhibits rice seed germination through a similar pathway, thus pointing to a conserved mechanism which maintains grain dormancy and inhibits germination through CRY1 in grasses.

Phytochromes and cryptochromes interact with PHYTOCHROME INTERACTING FACTORs (PIFs) [166, 167]. As basic helix-loop-helix transcription factors, PIF and its homologs were identified as groups in a gene family (**Figure 13**). In Arabidopsis, PIF1, PIF6, HFR1 and SPT have been implicated

in seed dormancy, germination and thermoinhibition [168-172]. Mechanistically, these factors interact with phytochrome pathway components to integrate diverse environmental cues including temperature and light, thus modulating downstream hormonal signalling or metabolism responses [173].

In Brachypodium, mutant characterization of BdPIL1 and BdPIL3 reveals their roles in light-mediated flowering time and growth control, indicating functional conservation and further implication in light-regulated processes like germination [174]. Meanwhile, based on gene expression and ectopic expression analysis, BdPIF4/5C produced the most pronounced hypocotyl elongation phenotype [175]. These observations provide important information about the roles played by BdPIFs in plant growth and development; further investigation will be required to reveal the function of other members and their involvement in seed dormancy and germination control.

5.2 Flowering time genes sense temperature to modulate seed dormancy and germination

5.2.1 *FLOWERING LOCUS C (FLC)*

As the central flowering repressor in Arabidopsis, FLOWERING LOCUS C (FLC) also regulates the germination timing of Arabidopsis [176, 177]. This regulation involves additional genes like *FLOWERING LOCUS T, SUPRESSOR of CONSTANS 1* in the flowering time pathway, and acts on the ABA catabolic pathway and GA biosynthetic pathway to modulate seed germination.

FLC genes have already been revealed in monocot species, including Brachypodium, wheat and barley [178], which can also be seen in our phylogenetic analysis (**Figure 14A**). Functional characterization indicates these genes function as flowering repressors and respond to vernalisation treatment, like that of *AtFLC* [178, 179]. Possible involvement of monocot *FLC* genes in seed dormancy and germination may reveal functional conservation, which could only be tested by experimental characterization.

5.2.2 *FLOWERING LOCUS T (FT)*

Phylogenetic analysis identified FT family proteins in Brachypodium and rice (**Supplementary Figure 7B**). Among them, the phosphatidylethanolamine-binding protein MOTHER-OF-FT-AND-TFL1 (MFT) was identified as a promoter of germination in Arabidopsis and responsible for pre-harvest sprouting resistance in wheat [180, 181]. By interacting with ABA and GA pathways, AtMFT forms a negative feedback loop through DELLA and ABI proteins. In contrast, under far-red light conditions AtMFT was found to repress germination through a transcription factor SPATULA (SPT) via the PIF1/SOM/ABI5/DELLA pathway. Research in cereals has revealed the significant contribution of *MFT* genes in seed dormancy and germination control in both rice, wheat and barley [182-184]. MFT homologs exist in both Arabidopsis and grass species (**Figure 14B**), among which the two rice proteins OsMFT1 and OsMFT2 have been extensively examined. However, a mechanistic understanding of seed dormancy and germination regulation by MFT is still lacking in temperate cereals. Considering the close homology, exploration of *BdMFT2* (Bradi2g01020) may provide analogous insights (**Supplementary Figure 7B**), as gene expression suggests a similar pattern as that of *TaMFT* and hence it could possibly function as a positive regulator of seed dormancy [180].

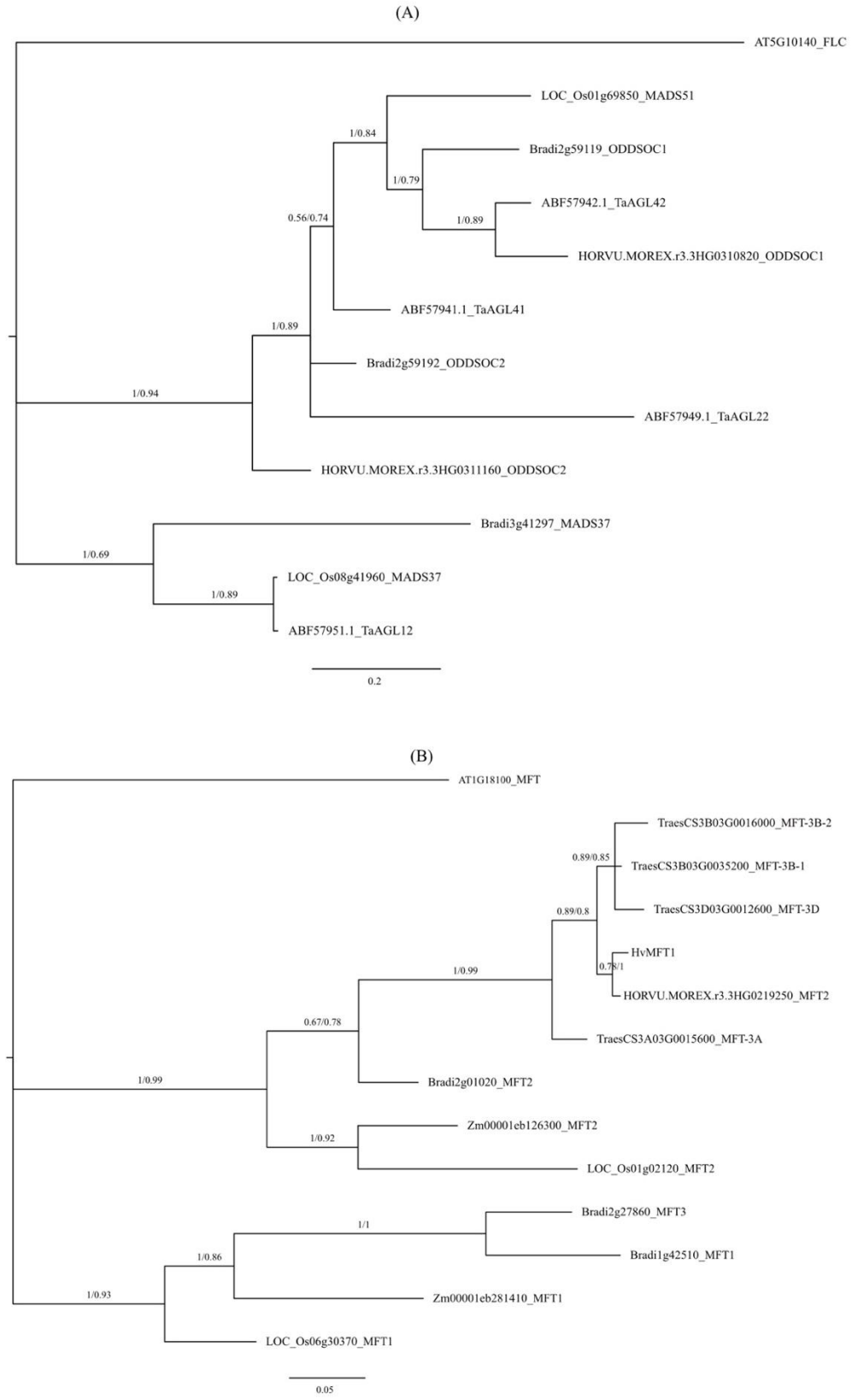

Figure 14, Maximum likelihood phylogeny of FLC (A) and MFT (B) proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.

5.3 Reactive oxygen species (ROS)

Reactive oxygen species (ROS) have been implicated in seed dormancy and germination via the ABA signalling pathway [185]. ROS are produced by plant-specific NADPH oxidases (NOX), also called respiratory burst oxidase homologs (RBOHs). Arabidopsis *rbohd* and *rbohf* mutants display impaired seed germination inhibition by ABA. Further evidence suggests that AtRBOHB plays roles in seed dry after-ripening and thermoinhibition, possibly through ABA signalling or post-translational protein modifications [186, 187]. Research in cereals also links ROS with seed dormancy induction and release through mechanism spanning ABA signalling, DNA methylation and protein phosphorylation [43, 188, 189].

Homologs of RBOH/NOX proteins are identified in Brachypodium and rice (**Figure 15A**). In the RBOHB clade, two Brachypodium and rice proteins exist instead of one Arabidopsis protein, indicating possible gene duplication. OsRBOHB has been proved to potentiate an ABA response upon phosphorylation by the Ca^{2+}/calmodulin-dependent protein kinase OsDMI3 [43]. In the RBOHD clade, one Brachypodium protein was identified, but no rice homolog was found. In the RBOHH/J, RBOHF/I and RBOHE clades, two proteins were found for Brachypodium and rice each.

5.4 Nitrogen

The effect of nitrogen on seed dormancy has been widely documented, mostly in its simple inorganic forms such as nitric oxide, nitrate and nitrite [190, 191]. Evidence in Arabidopsis and other species reveal that nitrogen promotes seed germination through relieving seed dormancy or eliminating the effects of environmental conditions that inhibit germination [192]. In Arabidopsis, NIN-like protein 8 (NLP8) has been proved to be a master regulator of nitrate-promoted seed germination, which counteracts ABA through interacting with ABI3 and ABI5 [193]. Phylogenetic analysis identified NLP protein homologs in Brachypodium and rice (**Figure 15B**). Arabidopsis proteins form separate groups, while Brachypodium and rice homologs cluster together, indicating close homology between the two grass species.

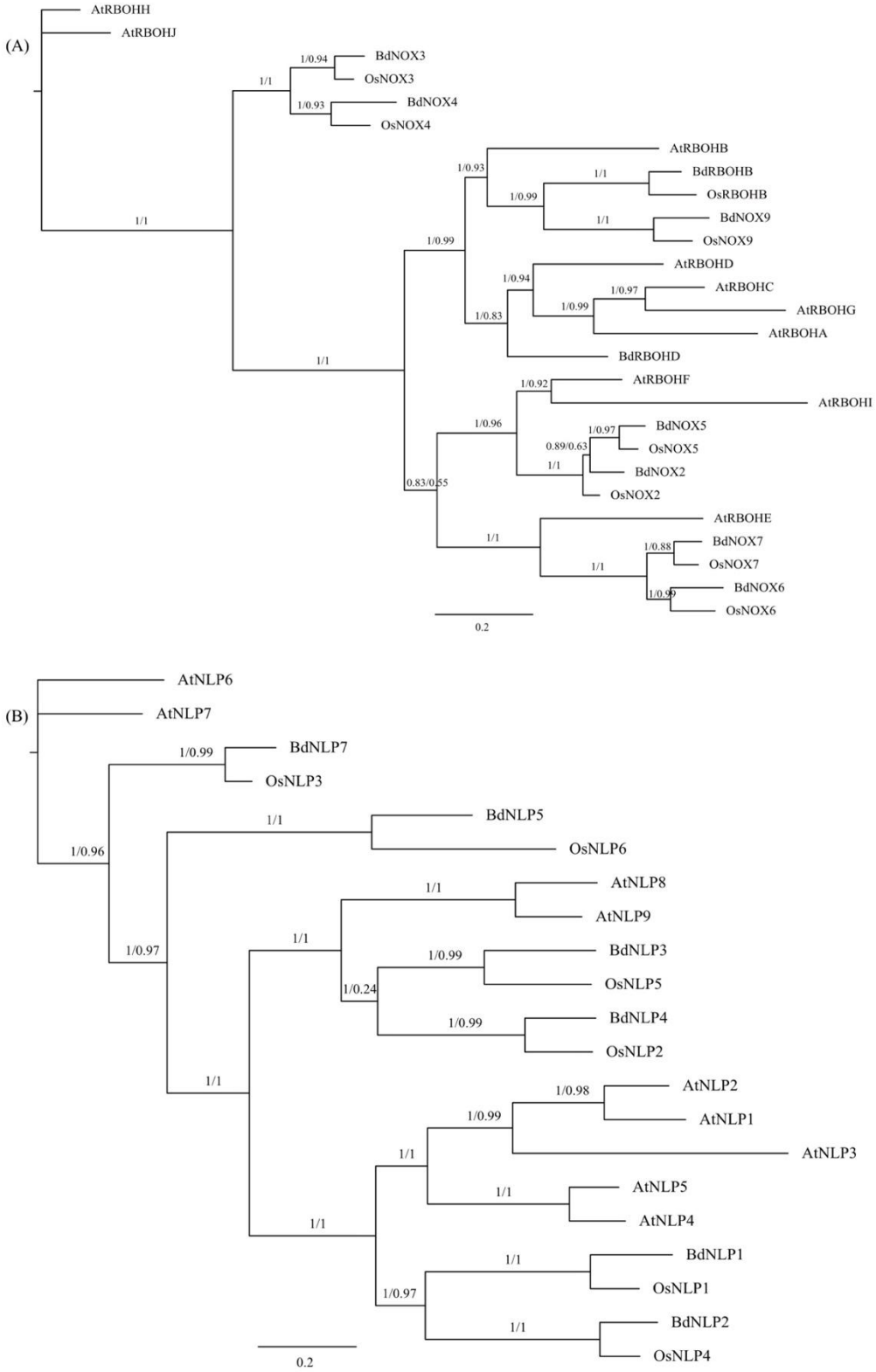

Figure 15, Maximum likelihood phylogeny of RBOH (A) and NLP(B) proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.

6. Other regulators of seed dormancy and germination

6.1 *Quantitative seed dormancy 1 (Qsd1)*

Qsd1, which encodes an alanine aminotransferase (AlaAT), is the causal gene of a critical QTL controlling barley seed dormancy [194]. The role of wheat homolog *TaQsd1* in seed dormancy has also been confirmed via induced mutations [195]. In our phylogenetic analysis, five Qsd clades were identified, namely *Qsd1* to *Qsd5* **(Supplementary Figure 11)**. In each clade, homologs were identified for all grasses analysed, indicating high conservation among these species. However, except in wheat and barley, no other *Qsd* gene has been implicated in seed dormancy. Meanwhile, the functional mechanism through which *Qsd1* regulates seed dormancy has remained elusive since its cloning a decade ago, due in part to the difficulties of working directly with crops harbouring large and complex genomes. The recently emerged link between alanine aminotransferase and hypoxia sensitivity offers some clue to this puzzle [196]. Future study on Brachypodium homologs may provide valuable evidence with reduced complexity, as gene expression clearly suggests their involvement in germinating Brachypodium grains (**Supplementary Figure 12**).

6.2 *Seed dormancy 4 (Sdr4)*

The *Sdr4* locus plays a dominant role in shaping seed dormancy and domestication in rice [197]. This locus regulates rice seed dormancy through the ABA signalling pathway under the activation of ABI3/VP1. As a versatile regulator, *Sdr4* has been implicated in multiple processes and designated different nomenclatures, for example, *Dynamic Influencer of Gene Expression (DIG), ABA-induced transcription repressors (AITRs)* and *REVERSAL OF RDO5 1 (ODR1)* [198-200]. Phylogenetic analysis identified *Sdr4-like (SFL)* genes in Arabidopsis and temperate cereals (**Supplementary Figure 13A**). While *AtSFL1* clusters within the cereal SFL1 clade, all other Arabidopsis *SFL/AITR* genes form an independent clade. Experimental evidence suggests that *AtSFL1* (AT1G27461) plays a role in regulating Arabidopsis seed dormancy via multiple mechanisms, including ABA biosynthesis, DOG1, GA metabolism and signalling and potentially proanthocyanidin biosynthesis [200-202].

In temperate cereals, functional characterization of the wheat homolog *TaSdr* indicated association of alleles at *TaSdr-B1* and *TaSdr-A1* with PHS resistance [203, 204]. However, compared with *OsSdr4*, which has been extensively characterized and proved to be dominant in PHS [205], homologs in maize and barley have not been studied. Thus, research on the Brachypodium homologs may provide useful information considering its close relationship with temperate cereals.

6.3 *MITOGEN-ACTIVATED PROTEIN KINASE KINASE 3 (MKK3)*

MKK3 is responsible for critical loci regulating seed dormancy in barley and wheat [206, 207]. Natural variation of *MKK3* has been observed in multiple populations across geographical and climate conditions, highlighting its overall importance in both seed dormancy and end-use traits [183, 208]. Phylogenetic analysis identified three Brachypodium homologs, indicating possible gene duplication (**Supplementary Figure 13B**). The single rice homolog *OsMKK3* has been shown to modulate seed dormancy upstream of *OsMFT* through the ABA signalling pathway [209, 210]. While no dormancy phenotype was reported for the maize homolog *ZmMKK3*, it has been shown to play roles in mediating osmotic stress and ABA signalling responses [211].

6.4 *ZHOUPI (ZOU)* and *INDUCER OF CBP EXPRESSION 1 (ICE1)*

In Arabidopsis, two endosperm-expressed genes, *ZOU* and *ICE1* determine primary seed dormancy [212]. The endosperm-specific *AtZOU* was initially implicated in endosperm breakdown, embryonic epidermal development and cuticle formation [213, 214]. Further study proved the essential role of *AtICE1* in these processes and that the heterodimerization of AtZOU and AtICE1 is necessary to

regulate endosperm breakdown [215]. The involvement of *AtICE1* in seed dormancy and germination was further supported by its interaction with both ABI5 and DELLA proteins to fine-tune ABA signalling [216]. Phylogenetic analysis identified two *ICE* genes in temperate cereals, namely *ICE1* and *ICE2* (**Supplementary Figure 14**). In the *ICE1* clade, two homologs were found in maize, barley and wheat but only one in Brachypodium and rice. This suggests possible gene duplication after the diverge between Brachypodium and temperate cereals. The role of *AtZOU* in endosperm development seems to be conserved on the one hand, as the endosperm-specific ZmZOU could form functional heterodimers with AtICE1. On the other hand, ZmZOU seems to have diverged from AtZOU in that ZmZOU interacted more strongly with ZmICEa, and *ZmZOU* only partially complements the *Atzou-4* mutant [217]. In the *ICE2* clade, a single homolog was identified in all analysed species. The wheat gene *TaICE2* (also called *TaSD6*) has been proved to be responsible for PHS resistance in a GWAS study and was confirmed using triple-homozygous mutants. Similarly, *OsSD6/ICE2* has also been shown to be responsible for PHS resistance [218]. Although no interaction partner of ICE2 has been reported during seed dormancy and germination, it is tempting to consider ZOU due to its conserved interaction with ICE1.

Discussion

The central conserved hormonal pathway

Plant hormones are a central conserved mechanism underlying seed dormancy and germination. Homologs of proteins in the hormonal pathways were identified in all species analysed. The Brachypodium genome encodes homologs involved in key hormonal pathways regulating seed dormancy and germination, including but not limited to ABA, GA, BRs, ethylene and jasmonate. Preliminary evidence revealed their participation into diverse biological processes controlled by these phytohormones, which orchestrates results observed in other species. Thus, further investigation into Brachypodium homologs may provide useful insights into seed dormancy and germination control that are common in grass species with reduced complexity.

Gene duplication and deletion

Compared with Arabidopsis, gene duplication was observed in major genes regulating seed dormancy in grasses. In plant hormonal pathways, gene duplication could explain the existence of additional grass proteins in the LEC2, GA2ox, AUX3, AUX4, ETR4, ERS1 and AFP clades, which involve both Brachypodium, rice and other species. On top of this, gene duplication may also be responsible for increased protein members participating in epigenetic and environmental regulation, such as FIE1, REF6, VIL3 and ROS1 in the former, and RBOHB and CRY1 in the latter.

Meanwhile, no homologs of some Arabidopsis proteins were identified in grasses, which implies possible gene loss following the split of the two plant groups. This includes the VAL1 and VRN2 proteins in all grass species analyzed, VIL1 proteins in wheat and barley, AUX2 and AUX5 proteins in Brachypodium, and RBOHD, GA20ox5 and DOG1L4 in rice. Absence of these proteins in grasses may be confined to a specific accession such as Bd21 in the case of Brachypodium, but could also be extended into the wider grass linage.

Co-ordinated components integrating internal and external cues

As a quantitative trait, seed dormancy level and its induction, maintenance and release are influenced by multiple internal and external cues. These signals can be sensed, perceived and integrated into the central hormonal pathway via specific components to modulate downstream effects. Among the internal cues, phytohormones, epigenetic status and seed covering tissues play major roles. Homologs of genes involved in these aspects are present in Brachypodium and rice. For the external cues, temperature plays

the most potent role in seed dormancy. Multiple thermosensors and genes required for temperature-mediated seed dormancy and germination control have been revealed in Arabidopsis mostly, such as *PHYB*, *MFT*, *DOG1* and *FLC*. Their monocot homologs show high similarity as can be seen from the phylogenetic analysis, but functional interpretation would require more in depth investigation.

Towards an integrated molecular and genetic understanding of seed dormancy

In the framework of the central hormonal pathway, a range of components act in the regulation of seed dormancy, including genetic, epigenetic, hormonal and environmental components. Research in Arabidopsis indicated multifaceted interactions among these components, be them synergetic or antagonistic [58, 59, 219, 220]. While recent discoveries begin to uncover the molecular and genetic identities underlying these interactions, comparative perspective may provide important information towards an integrated understanding of seed dormancy regulation.

Ethics declarations

Source of the plant used

Not applicable. No plant materials were used in this study.

Permissions to collect the plants/plant parts

Not applicable. No plant materials were used in this study.

Plant guidelines

Not applicable. No plant materials were used in this study.

Plant Ethics

Not applicable. No plant materials were used in this study.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no conflict of interest.

Data availability

The sequence data used in this study can be found in the Materials and Methods section. The RNA-seq datasets of *B. distachyon* accession Bd21 analyzed in the study are available in the EMBL-EBI repository (https://www.ebi.ac.uk/biostudies/arrayexpress/studies/E-MTAB-4401).

Author contributions

RL and KG: conceptualization; RL: homolog search, phylogenetic analysis, writing — original draft; RL and KG: writing — revision and editing. All authors have read and approved the final version of the manuscript.

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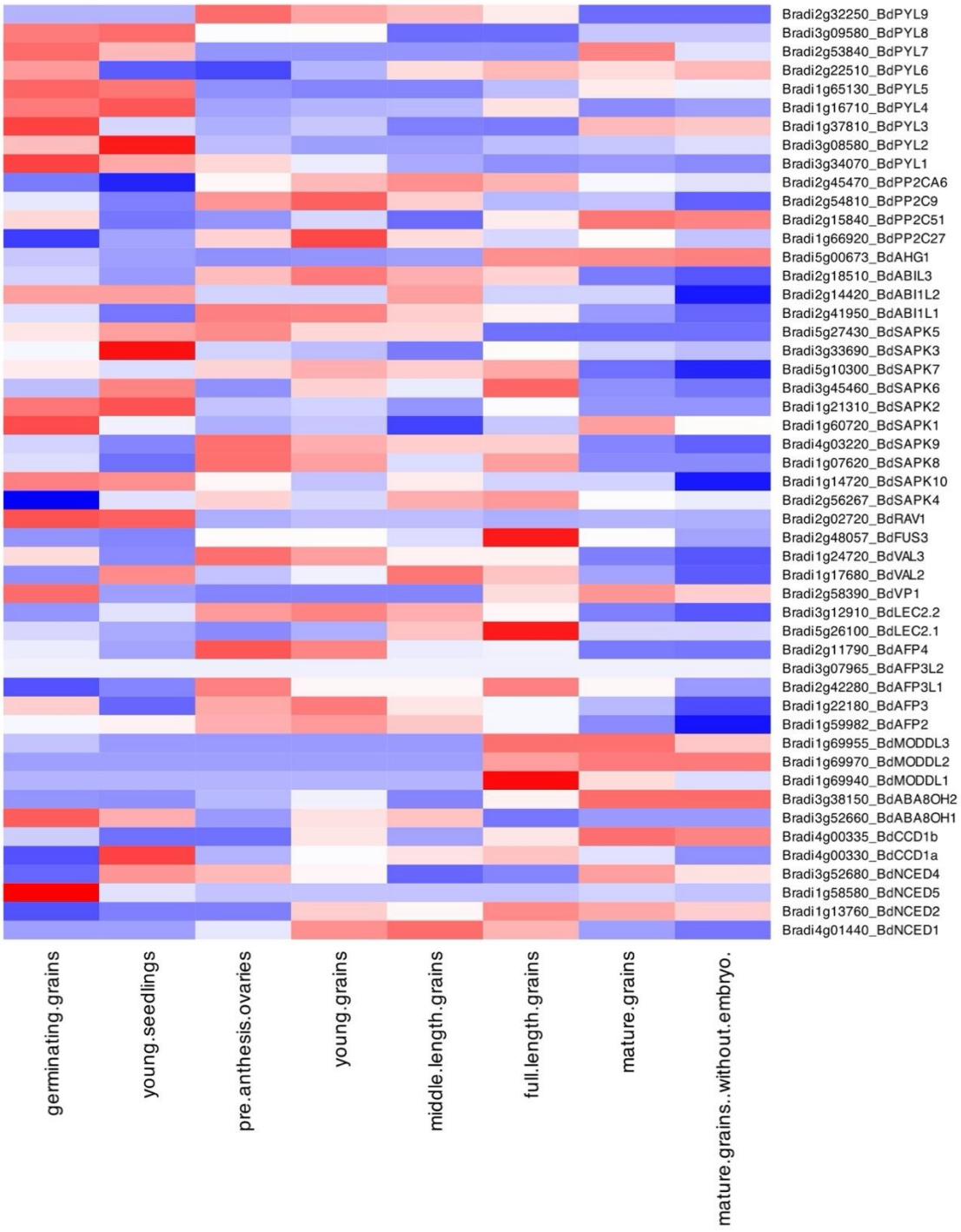
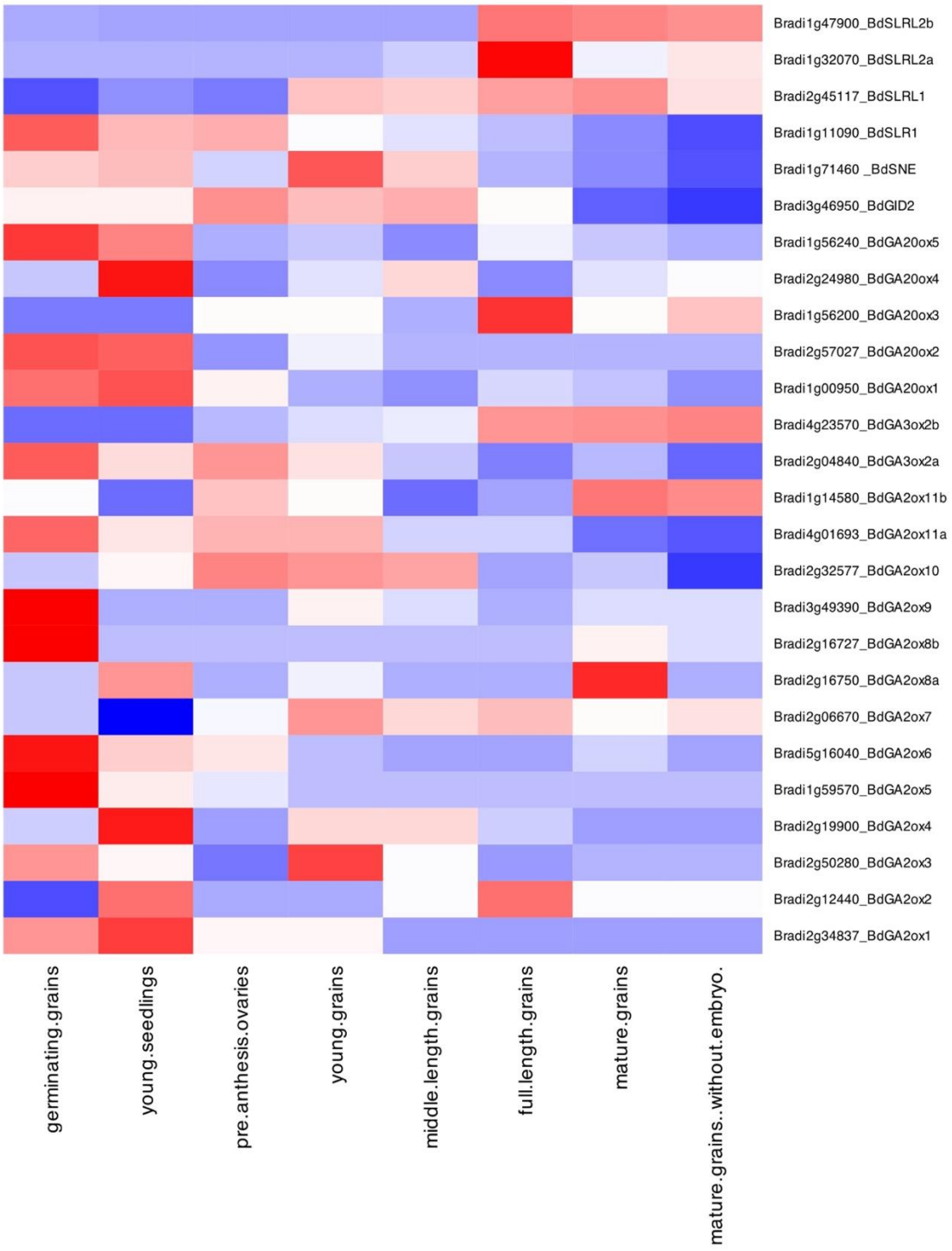
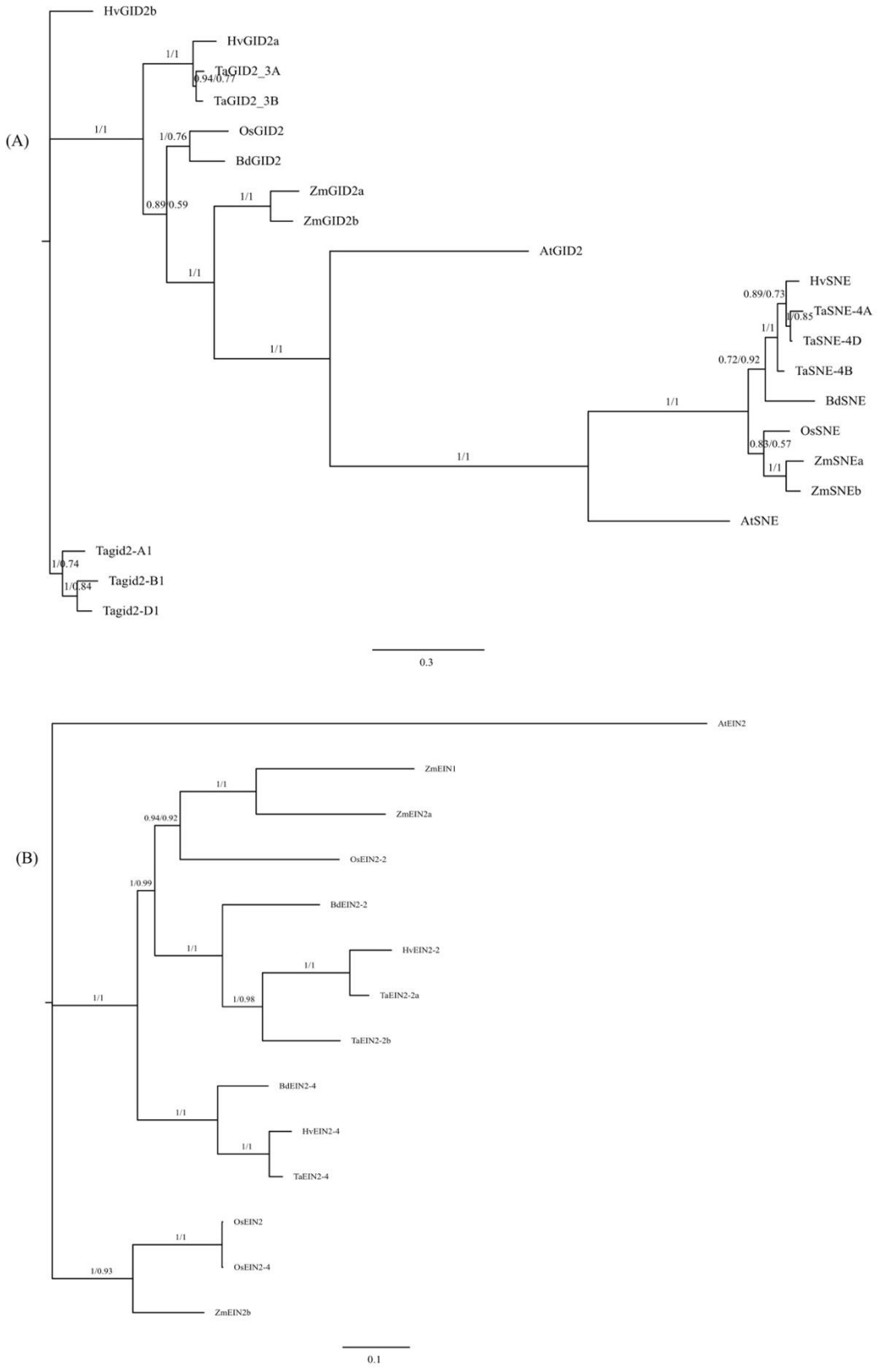
Supplementary Figure and Table



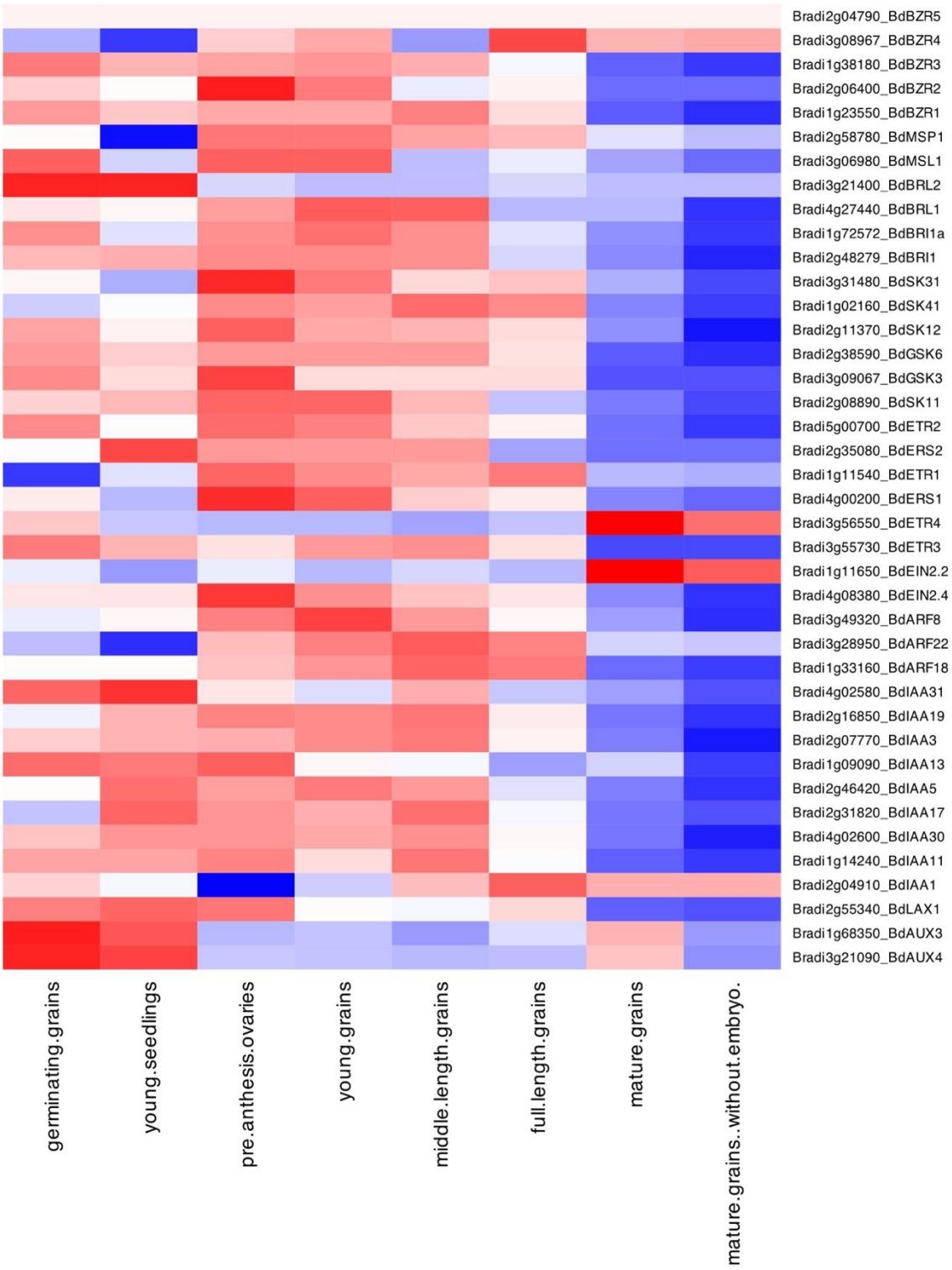
Supplementary Figure 1, Expression profile of Brachypodium genes encoding ABA metabolism and signalling proteins during seed germination and grain development. RNA-seq data of B. distachyon accession Bd21 were taken from published results [221] and visualized using R. Colour intensity indicates expression level. Red colour correlates with high expression and blue colour with low expression. Blank bar means no expression or data not available.



Supplementary Figure 2, Expression profile of Brachypodium genes encoding GA metabolism proteins during seed germination and grain development. RNA-seq data of B. distachyon accession Bd21 were taken from published results [1] and visualized using R. Colour intensity indicates expression level. Red colour correlates with high expression and blue colour with low expression. Blank bar means no expression or data not available.

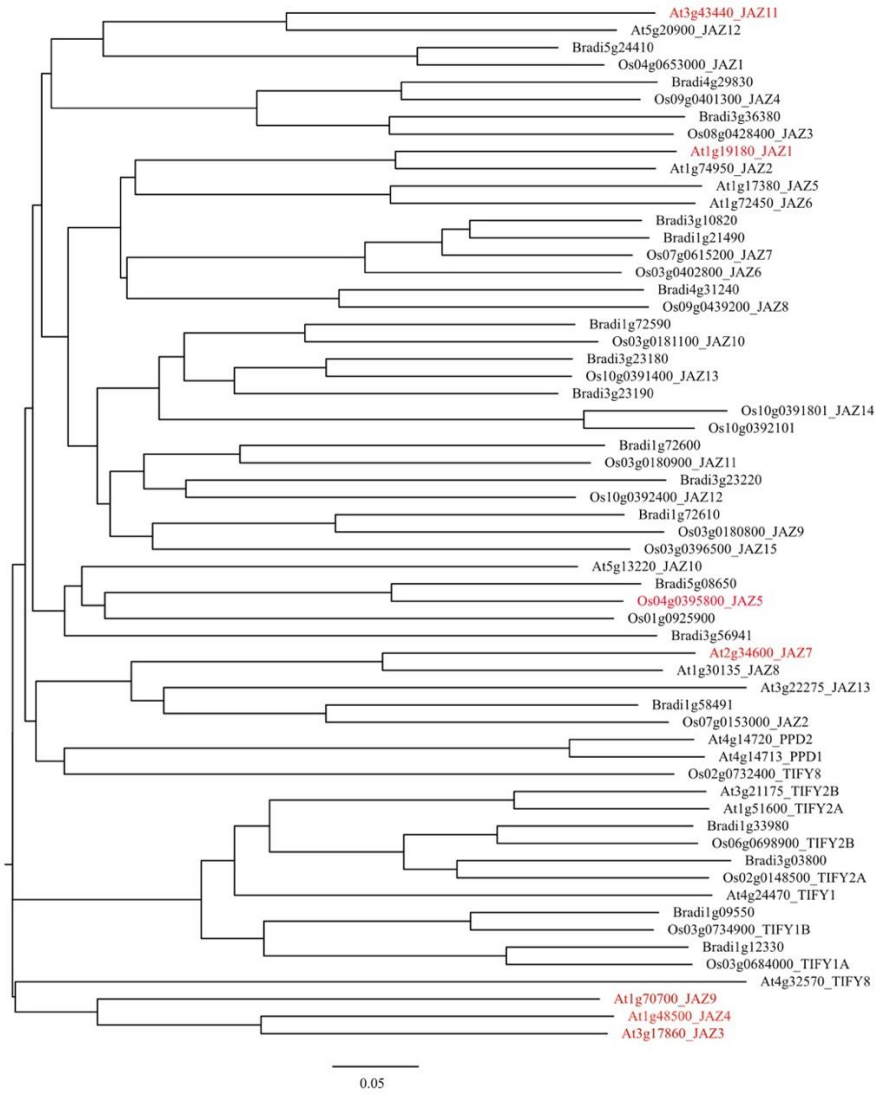


Supplementary Figure 3, Maximum likelihood phylogeny of (A) GID2 proteins and (B) EIN2 proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.

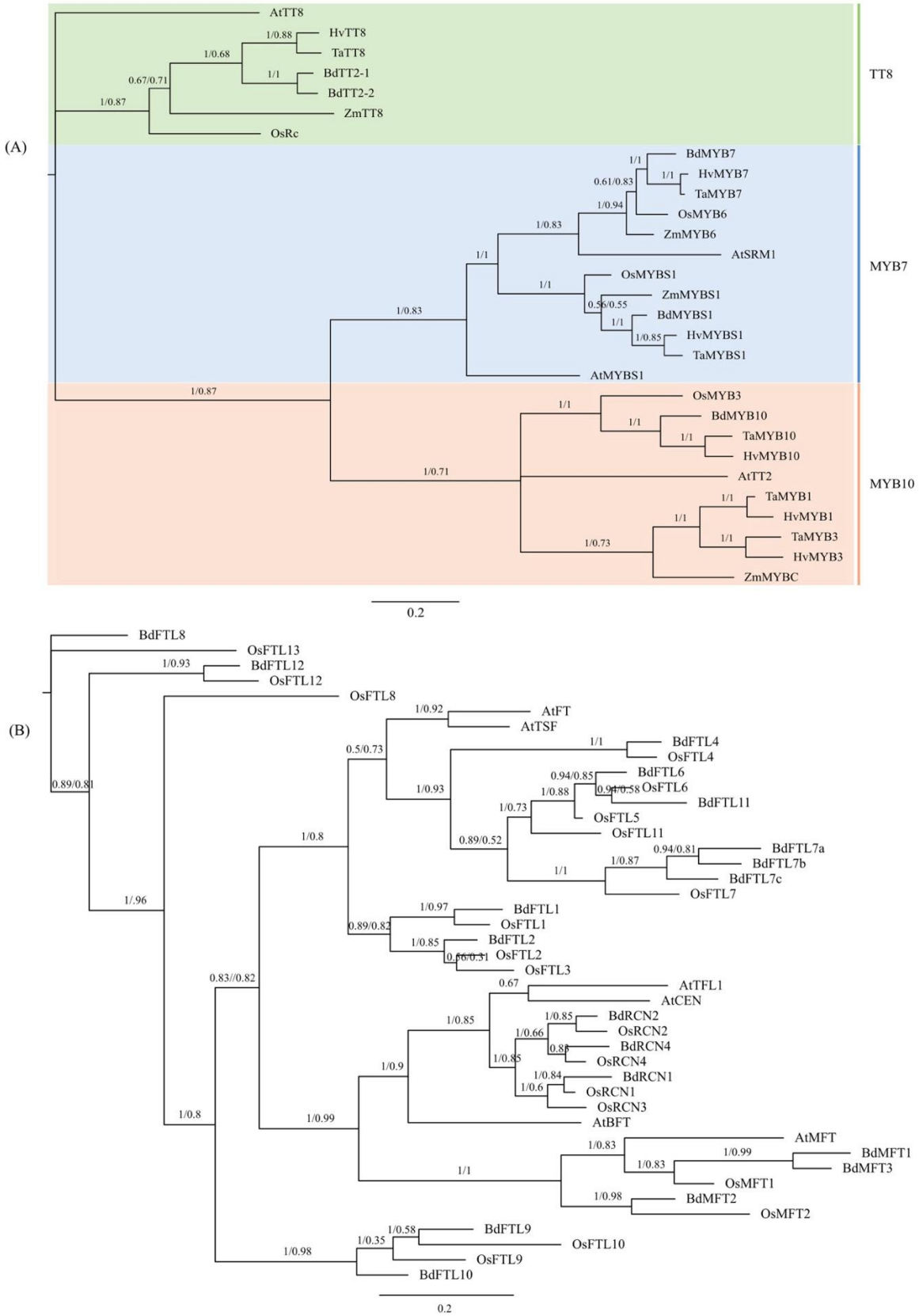


Supplementary Figure 4, Expression profile of Brachypodium genes encoding proteins related to auxin, ethylene and BRs during seed germination and grain development. RNA-seq data of B. distachyon accession Bd21 were taken from published results [1] and visualized using R. Colour intensity indicates expression level. Red colour correlates with high expression and blue colour with low expression. Blank bar means no expression or data not available.

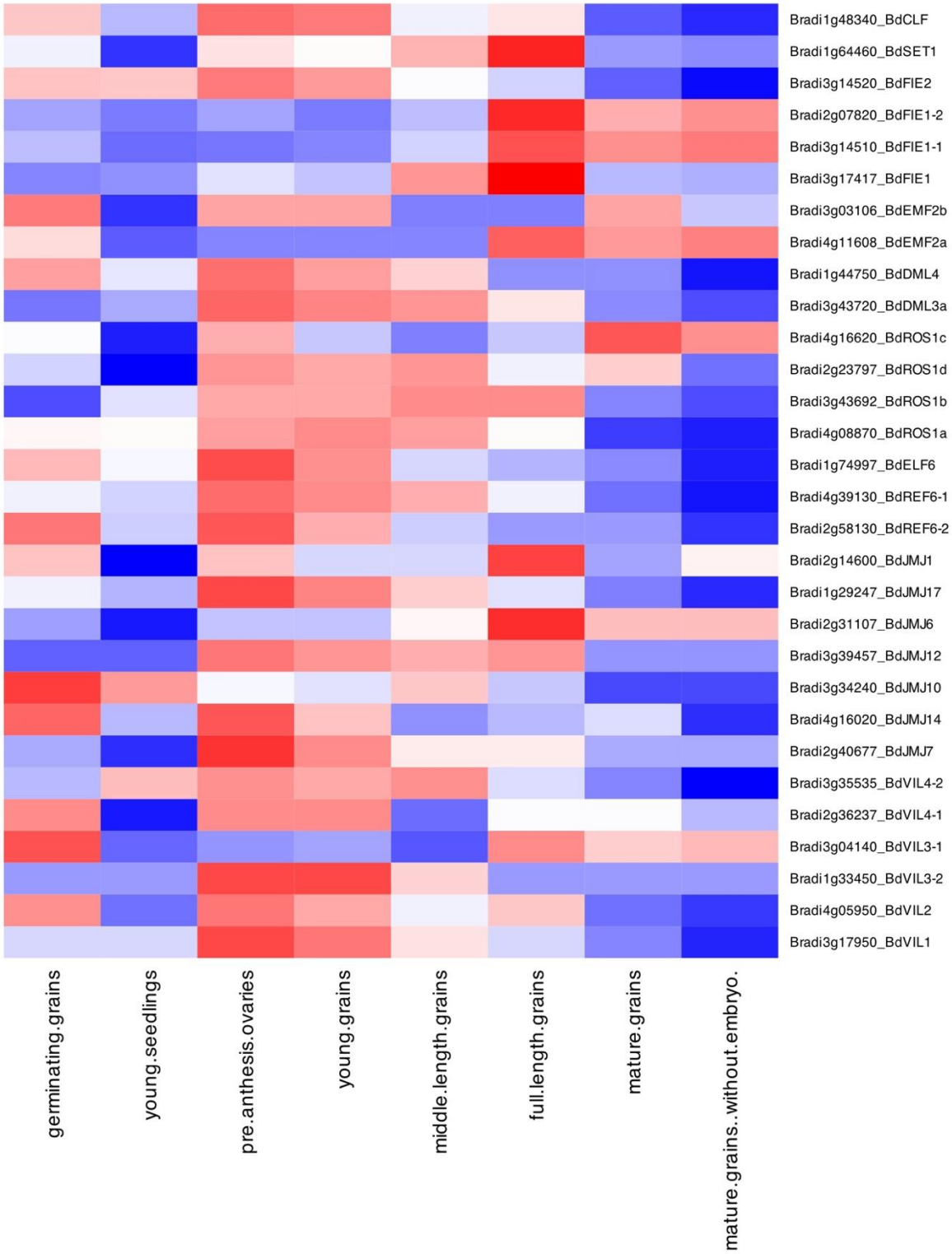
Supplementary Figure 5, Maximum likelihood phylogeny of BRI, BZR and BIN2 proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.



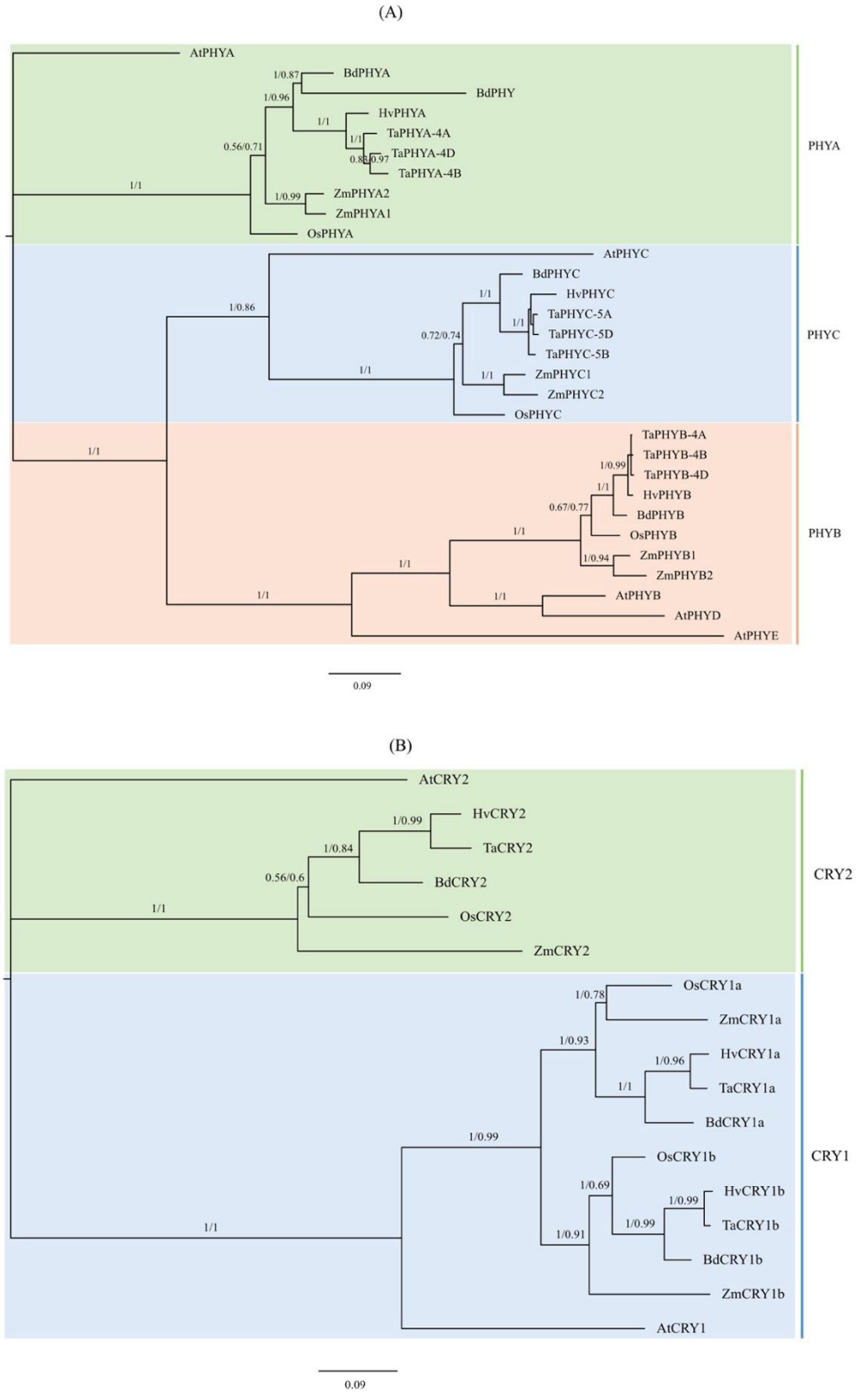
Supplementary Figure 6, Maximum likelihood phylogeny of JAZ proteins showing the relationships of the different subfamilies.



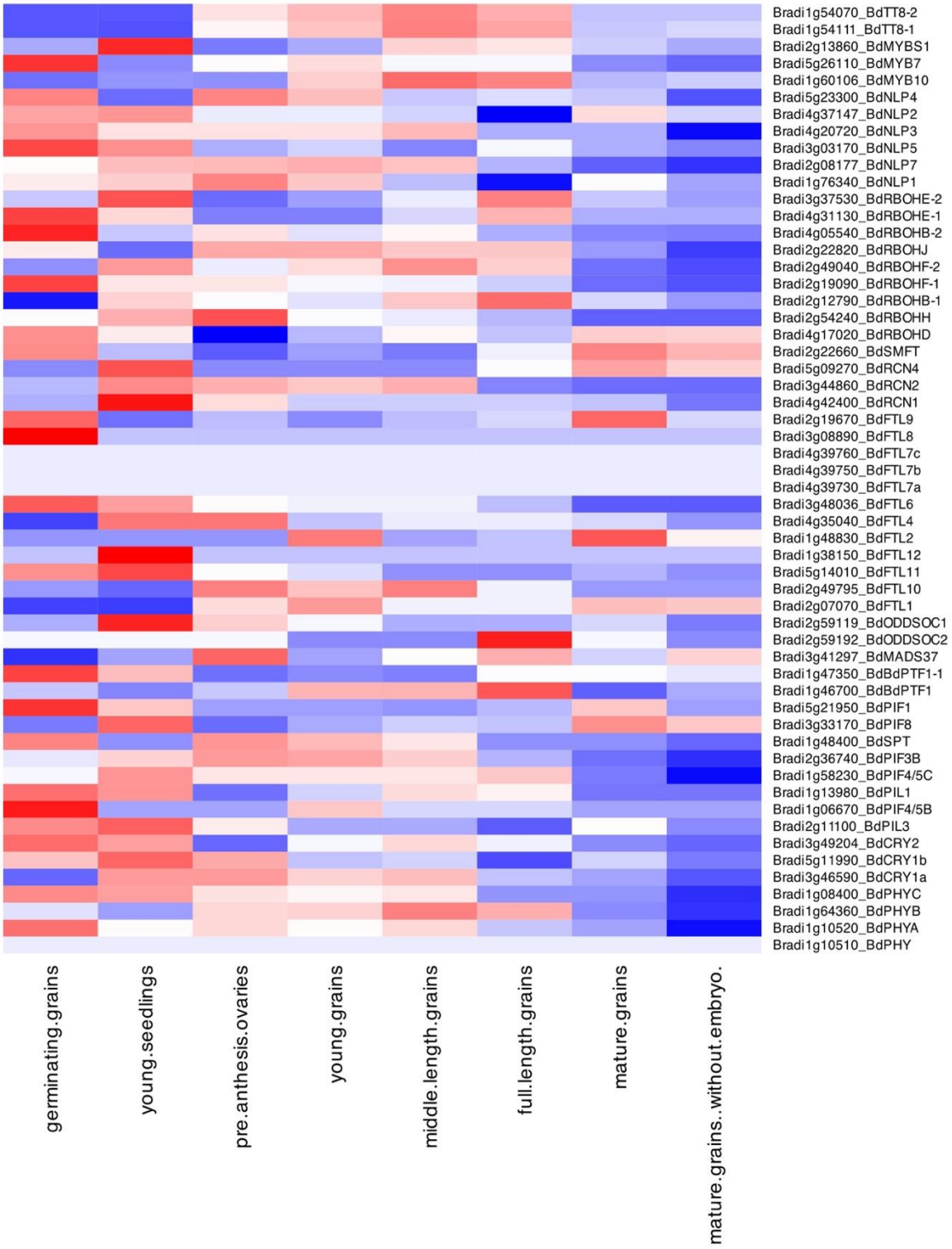
Supplementary Figure 7, Maximum likelihood phylogeny of (A) proteins related to covering mediated dormancy and (B) FT proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.



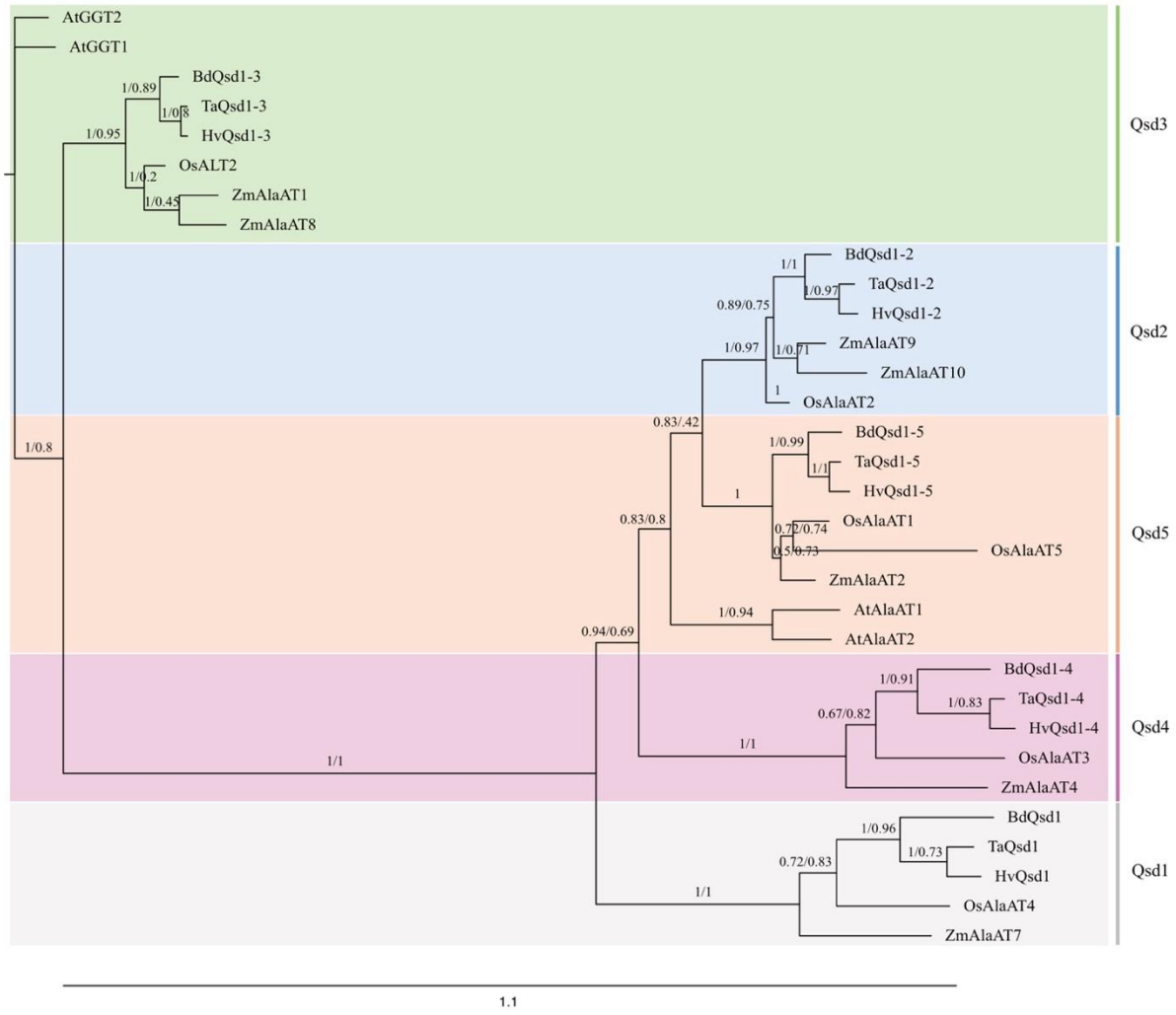
Supplementary Figure 8, Expression profile of Brachypodium genes encoding proteins related to epigenetic regulation during seed germination and grain development. RNA-seq data of B. distachyon accession Bd21 were taken from published results [1] and visualized using R. Colour intensity indicates expression level. Red colour correlates with high expression and blue colour with low expression. Blank bar means no expression or data not available.



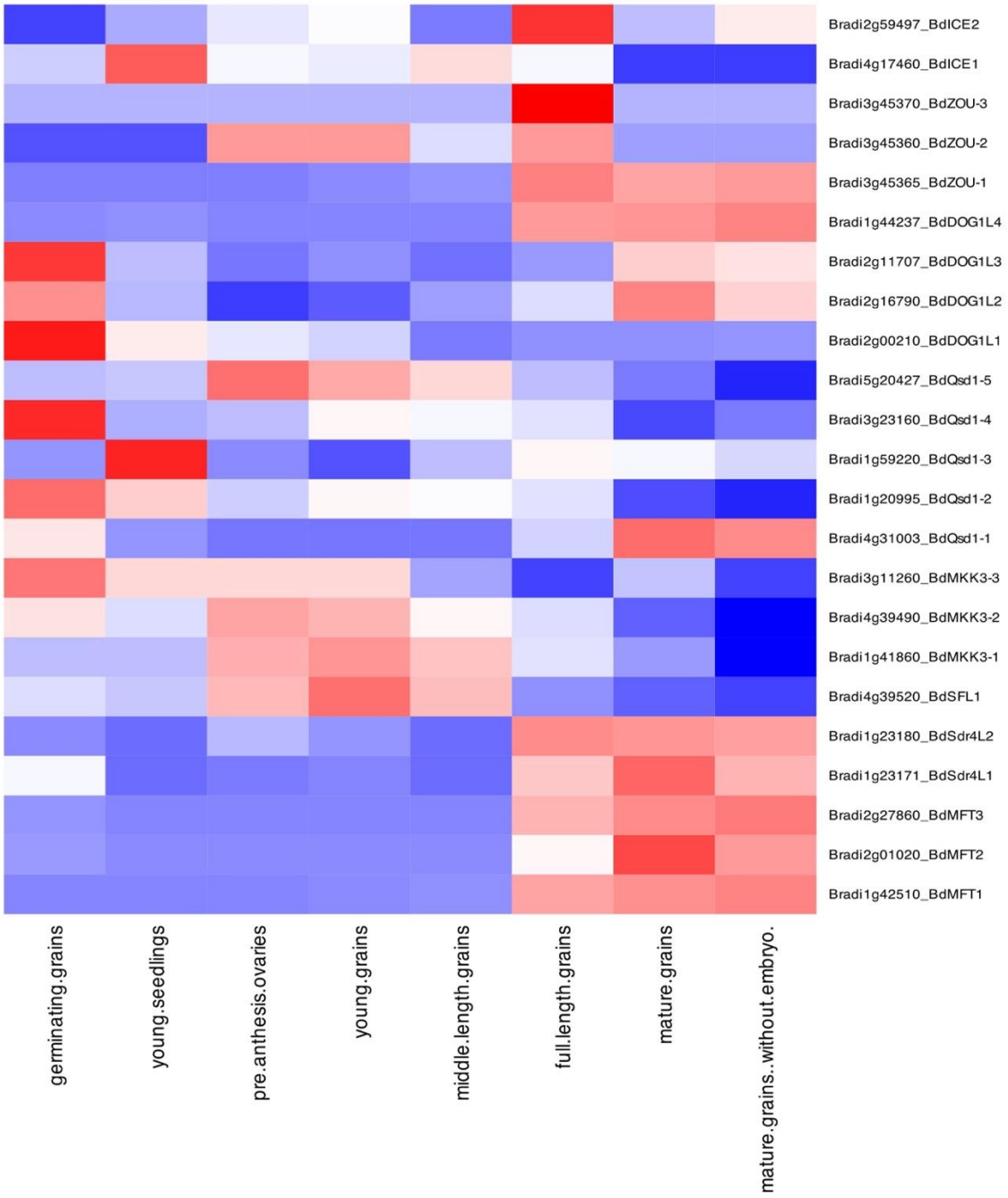
Supplementary Figure 9, Maximum likelihood phylogeny of PHY and CRY proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.



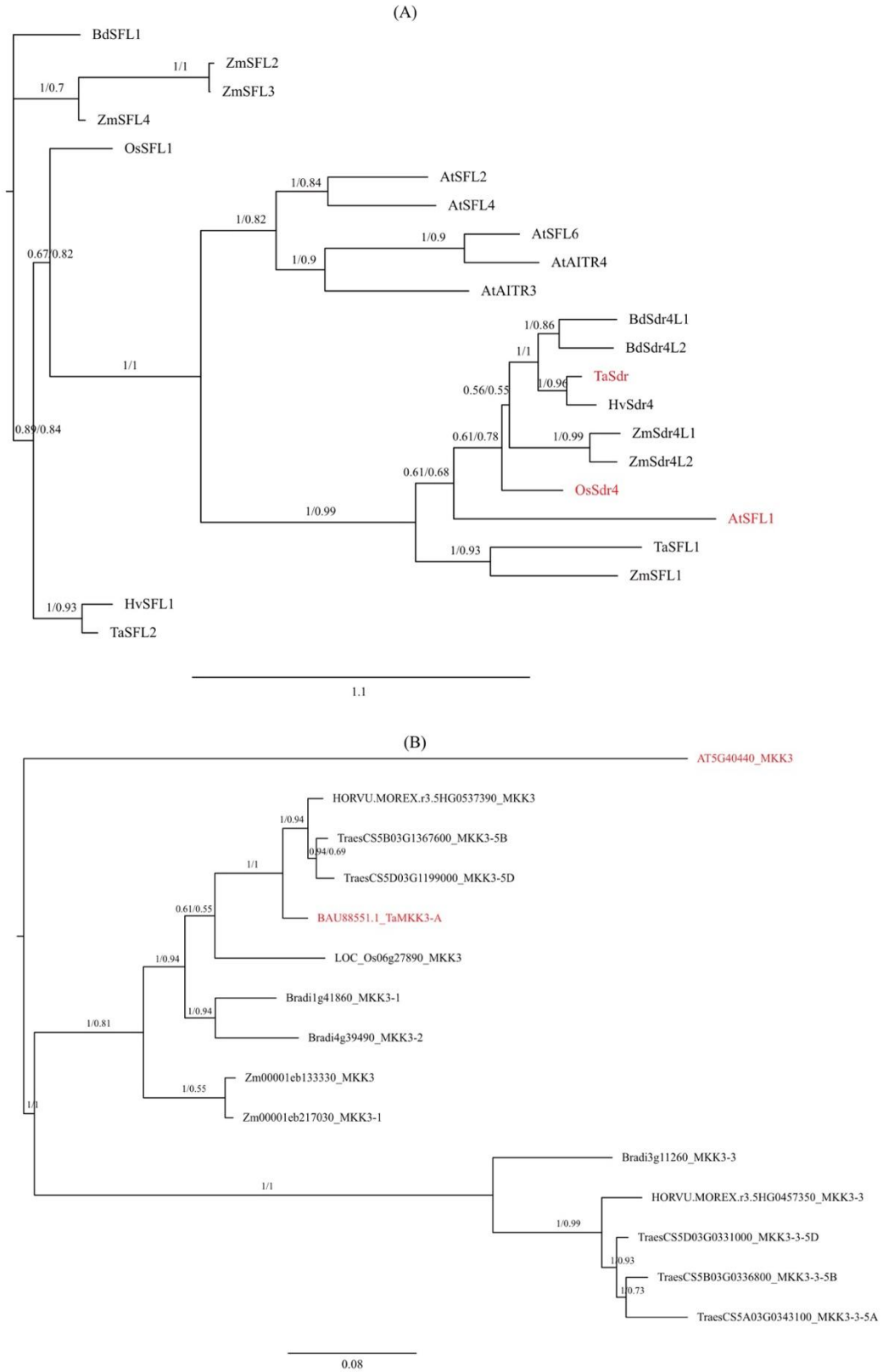
Supplementary Figure 10, Expression profile of Brachypodium genes encoding proteins involved in covering tissue and environmental regulation during seed germination and grain development. RNA-seq data of B. distachyon accession Bd21 were taken from published results [1] and visualized using R. Colour intensity indicates expression level. Red colour correlates with high expression and blue colour with low expression. Blank bar means no expression or data not available.



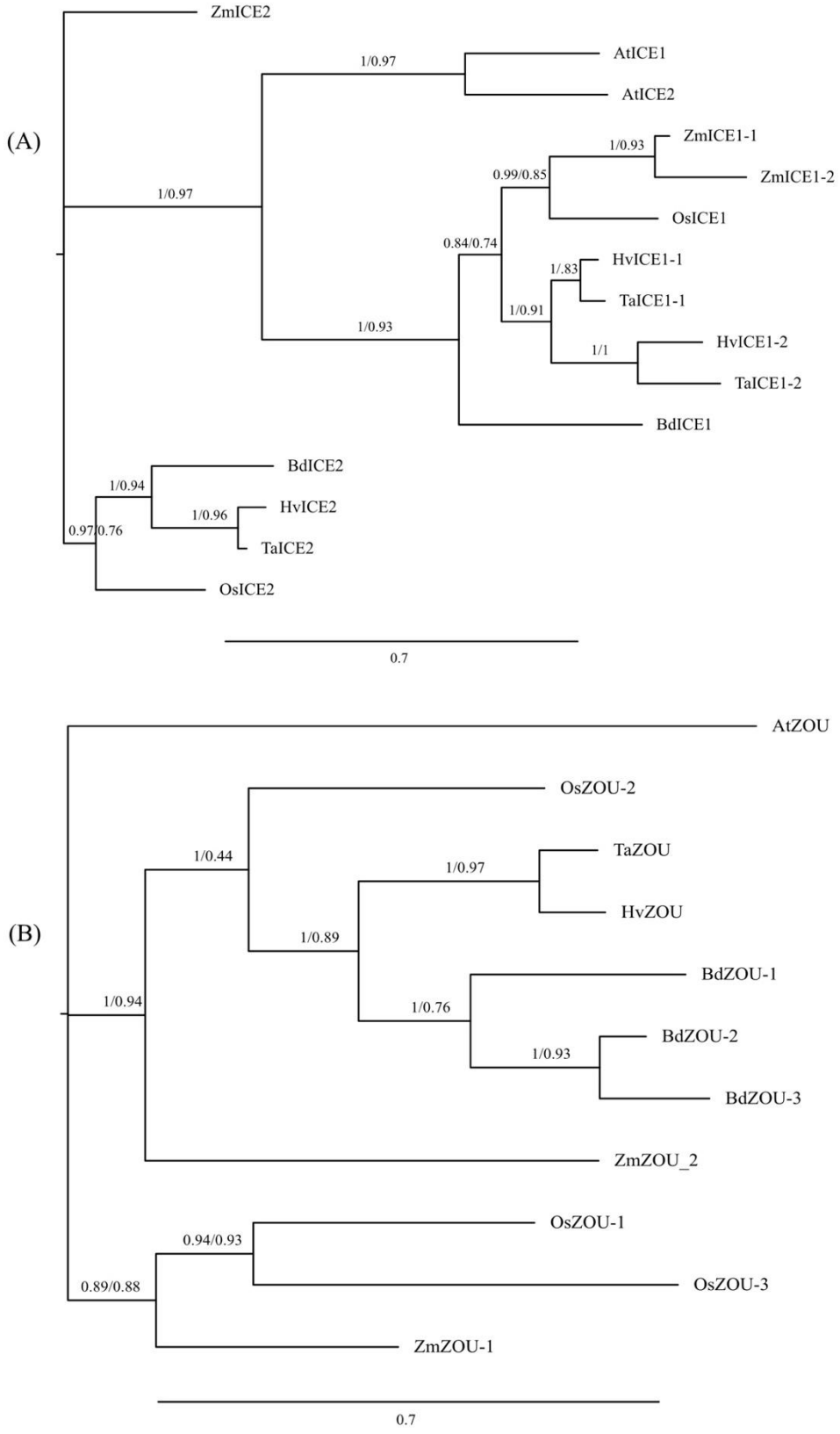
Supplementary Figure 11, Maximum likelihood phylogeny of Qsd proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.



Supplementary Figure 12, Expression profile of Brachypodium seed dormancy gene homologs during seed germination and grain development. RNA-seq data of B. distachyon accession Bd21 were taken from published results [1] and visualized using R. Colour intensity indicates expression level. Red colour correlates with high expression and blue colour with low expression. Blank bar means no expression or data not available.



Supplementary Figure 13, Maximum likelihood phylogeny of (A) Sdr4 and (B) MKK3 proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.



Supplementary Figure 14, Maximum likelihood phylogeny of ICE (A) and ZOU (B) proteins showing the relationships of the different subfamilies. The numbers next to the nodes represent Bayesian posterior probabilities and bootstrap values for the corresponding clades.

Supplementary Table 1, Seed dormancy genes in Arabidopsis, rice and their Brachypodium homologs.

	Arabidopsis		**Rice (Japonica group)**		**Brachypodium**		**Wheat**		**Barley**		**Maize**	
Group	Protein	TAIR 10	Protein	RAP-DB ID	Protein	Bd21 V3	Protein	Chinese Spring v2.1	Protein	Morex V3	Protein	B73 Reference
NCED	AtNCED5	AT1G30100	OsNCED1	LOC_Os02g47510	BdNCED1	Bradi4g01440	TaNCED3	TraesCS2A03G0026500	HvNCED2	HORVU.MOREX.r3.5HG0508150	ZmNCED4	Zm00001d007876
	AtNCED9	AT1G78390	OsNCED3	LOC_Os03g44380	BdNCED2	Bradi1g13760	TaNCED5	TraesCS2A03G0603200	HvNCED3	HORVU.MOREX.r3.5HG0419880	ZmNCED9	Zm00001d013689
	AtNCED3	AT3G14440	OsNCED4	LOC_Os07g05940	BdNCED5	Bradi1g58580	TaCCD1a	TraesCS5A03G0002500	HvNCED1	HORVU.MOREX.r3.5HG0426410	ZmNCED8	Zm00001d017766
	AtNCED6	AT3G24220	OsNCED2	LOC_Os12g24800	BdNCED4	Bradi3g52680	TaCCD1b	TraesCS5A03G0004500	HvNCED4	HORVU.MOREX.r3.6HG0607370	ZmNCED5	Zm00001d018819
	AtNCED1	AT3G63520	OsNCED5	LOC_Os12g42280	BdCCD1a	Bradi4g00330	TaCCD1c	TraesCS5A03G0004900	HvCCD1	HORVU.MOREX.r3.4HG0336120	ZmNCED2	Zm00001d031086
	AtNCED2	AT4G18350	OsCCD1	LOC_Os12g44310	BdCCD1b	Bradi4g00335	TaNCED1	TraesCS5B03G0068800			ZmNCED3	Zm00001d035724
	AtNCED4	AT4G19170					TaNCED2	TraesCS5A03G0898000			ZmNCED6	Zm00001d051556
							TaNCED4	TraesCS6A03G0725700			ZmNCED1	Zm00001eb218680
											ZmNCED	Zm00001eb309770
											ZmCCD1	Zm00001eb402840
CYP707A	AtCYP707A1	AT4G19230	OsABA8ox1	LOC_Os02g47470	BdABA8OH1	Bradi3g52660	TaCYP707A1	TraesCS6B03G0858400	HvCYP707A1	HORVU.MOREX.r2.6HG0503470	ZmCYP707A4	Zm00001eb314900
	AtCYP707A2	AT2G29090	OsABA8ox2	LOC_Os08g36860	BdABA8OH2	Bradi3g38150	TaCYP707A2	TraesCS5D03G0566800	HvCYP707A2	HORVU.MOREX.r2.5HG0402930	ZmCYP707A3	Zm00001eb176720
	AtCYP707A3	AT5G45340	OsABA8ox3	LOC_Os09g28390							ZmCYP707A2	Zm00001eb100780
	AtCYP707A4	AT3G19270									ZmCYP707A1	Zm00001eb251960
AFP	AtAFP1	AT1G69260	OsMODD	LOC_Os03g11550	BdMODDL1	Bradi1g69940	TaMODDL1	TraesCS4A03G0112900	HvAFP4	HORVU.MOREX.r3.1HG0086350	ZmMODD	Zm00001eb400170
	AtAFP2	AT1G13740	OsAFP2	Os03g0419100	BdMODDL2	Bradi1g69970	TaMODDL2	TraesCS4A03G0113600	HvAFP3	HORVU.MOREX.r3.2HG0126880	ZmAFP2	Zm00001eb393150
	AtAFP3	AT3G29575	OsAFP3	Os07g0602900	BdMODDL3	Bradi1g69955	TaMODDL3	TraesCS3B03G1485000	HvMODDL2	HORVU.MOREX.r3.4HG0396620	ZmAFP3	Zm00001eb326900
	AtAFP4	AT3G02140	OsAFP4	LOC_Os05g48500	BdAFP2	Bradi1g59982	TaAFP3	TraesCS2A03G0367800	HvMODDL1	HORVU.MOREX.r3.4HG0396670	ZmAFP4	Zm00001eb343360
	AtAFPH2	AT4G28910			BdAFP3	Bradi1g22180	TaAFP4	TraesCS1A03G0949800			ZmAFP2L1	Zm00001eb020120
					BdAFP3L1	Bradi2g42280						
					BdAFP3L2	Bradi3g07965						
					BdAFP4	Bradi2g11790						
VP1	AtVAL3	AT4G21550	OsVP1	LOC_Os01g68370	BdLEC2.1	Bradi5g26100	TaVAL2	TraesCS2A03G0217300	HvFUS3	HORVU.MOREX.r3.3HG0284730	ZmVAL3	Zm00001eb106940
	AtFUS3	AT3G26790	OsVAL3	LOC_Os07g37610	BdLEC2.2	Bradi3g12910	TaVAL3	TraesCS2A03G0785500	HvVAL2	HORVU.MOREX.r3.2HG0112030	ZmVAL2	Zm00001eb111570
	AtABI3	AT3G24650	OsLEC2.1-1	LOC_Os04g58010	BdVP1	Bradi2g58390	TaLEC2.1	TraesCS2A03G1285400	HvVAL3	HORVU.MOREX.r3.2HG0134870	ZmRAV1	Zm00001eb342850
	AtVAL2	AT4G32010	OsVAL2	LOC_Os07g48200	BdVAL2	Bradi1g17680	TaFUS3	TraesCS3A03G0639800	HvLEC2.1	HORVU.MOREX.r3.2HG0210050	ZmFUS3	Zm00001eb361390
	AtVAL1	AT2G30470	OsFUS3	LOC_Os01g51610	BdVAL3	Bradi1g24720	TaVP1	TraesCS3A03G0970200	HvLEC2.2	HORVU.MOREX.r3.7HG0708130	ZmVP1	Zm00001eb143690
	AtLEC2	AT1G28300	OsLEC2.2	LOC_Os08g01090	BdFUS3	Bradi2g48057	TaRAV1	TraesCS5A03G1166700	HvVP1	HORVU.MOREX.r3.3HG0308890	ZmLEC2.2	Zm00001eb259870
			OsLEC2.1	LOC_Os04g58000	BdRAV1	Bradi2g02720	TaLEC2.2	TraesCS7A03G0811800	HvRAV1	HORVU.MOREX.r3.3HG0227780	ZmLEC2.1	Zm00001eb066270
			OsRAV1	LOC_Os01g04800								
SNRK	AtSRK2I/SNRK2.3	AT5G66880	OsSAPK10	LOC_Os03g41460	BdSAPK4	Bradi2g56267			HvSAPK8	HORVU.MOREX.r3.5HG0512820	ZmSAPK4-1	Zm00001eb146500

	AtSRK2D/SNRK2.2	AT3G50500	OsSAPK8	LOC_Os03g55600	BdSAPK10	Bradi1g14720			HvSAPK7	HORVU.MOREX.r3.2HG0168730	ZmSAPK10-1	Zm00001eb219160
	AtSRK2E/OST1	AT4G33950	OsSAPK9	LOC_Os12g39630	BdSAPK8	Bradi1g07620			HvSAPK3	HORVU.MOREX.r3.1HG0057490	ZmSAPK8-1	Zm00001eb058470
	AtSRK2A/SNRK2.4	AT1G10940	OsSAPK2	LOC_Os07g42940	BdSAPK9	Bradi4g03220			HvSAPK5	HORVU.MOREX.r3.2HG0216470	ZmSAPK8-2	Zm00001eb214180
	AtSRK2H/SNRK2.5	AT5G63650	OsSAPK1	LOC_Os03g27280	BdSAPK1	Bradi1g60720			HvSAPK4-2	HORVU.MOREX.r3.1HG0075630	ZmSAPK10-2	Zm00001eb051510
	AtSRK2B/SNRK2.10	AT1G60940	OsSAPK3	LOC_Os10g41490	BdSAPK2	Bradi1g21310			HvSAPK10	HORVU.MOREX.r3.4HG0342860	ZmSAPK2	Zm00001eb327780
	AtSRK2G/SNRK2.1	AT5G08590	OsSAPK7	LOC_Os04g35240	BdSAPK6	Bradi3g45460			HvSAPK9	HORVU.MOREX.r3.5HG0438740	ZmSAPK1	Zm00001eb392580
	AtSRK2F/SNRK2.7	AT4G40010	OsSAPK6	LOC_Os02g34600	BdSAPK7	Bradi5g10300			HvSAPK2	HORVU.MOREX.r3.2HG0123910	ZmSAPK3	Zm00001eb023880
	AtSRK2C/SNRK2.8	AT1G78290	OsSAPK5	LOC_Os04g59450	BdSAPK3	Bradi3g33690			HvSAPK1	HORVU.MOREX.r3.2HG0201420	ZmSAPK7	Zm00001eb082720
	AtSRK2J/SNRK2.9	AT2G23030	OsSAPK4	LOC_Os01g64970	BdSAPK5	Bradi5g27430			HvSAPK4-1	HORVU.MOREX.r3.3HG0299220	ZmSAPK6-1	Zm00001eb181940
											ZmSAPK6-2	Zm00001eb243440
											ZmSAPK5	Zm00001eb434400
											ZmSAPK4-2	Zm00001eb366610
											ZmSAPK4-3	Zm00001eb289200
PP2C	AtABI1	AT4G26080	OsABIL1	LOC_Os01g40094	BdABI1L1	Bradi2g41950	TaABI1L1	TraesCS3A03G0542200	HvABI1L1	HORVU.MOREX.r3.3HG0267730	ZmPP2C10	Zm00001eb160470
	AtABI2	AT5G57050	OsABIL2	LOC_Os05g51510	BdABI1L2	Bradi2g14420	TaABI1L2	TraesCS1A03G1073800	HvABI1L2	HORVU.MOREX.r3.1HG0094890	ZmPP2C11	Zm00001eb309920
	AtAHG1	AT5G51760	OsABIL3	LOC_Os05g46040	BdABIL3	Bradi2g18510	TaABIL3	TraesCS1A03G0875600	HvABIL3	HORVU.MOREX.r3.1HG0080890	ZmPP2C12	Zm00001eb344210
	AtAHG3	AT3G11410	OsPP2C30	LOC_Os03g16170	BdAHG1	Bradi5g00673	TaABIL3-1	TraesCS3A03G0639700	HvABIL3-1	HORVU.MOREX.r3.3HG0284740	ZmPP2C13	Zm00001eb419870
	AtHAB1	AT1G72770	OsPP2C37	LOC_Os04g08560	BdPP2C27	Bradi1g66920	TaPP2C-a10	TraesCS2A03G0000700	HvAHG1	HORVU.MOREX.r3.2HG0095500	ZmPP2C14	Zm00001eb012040
	AtHAB2	AT1G17550	OsPP2C49	LOC_Os05g38290	BdPP2C51	Bradi2g15840	TaPP2C30	TraesCS4A03G0193400	HvPP2C30	HORVU.MOREX.r3.4HG0389000	ZmPP2C15	Zm00001eb359460
	AtHAI1	AT5G59220	OsPP2C51	LOC_Os05g49730	BdPP2C9	Bradi2g54810	TaPP2C49	TraesCS3A03G0860100	HvPP2C49	HORVU.MOREX.r3.3HG0302180	ZmPP2C16	Zm00001eb098220
	AtHAI2	AT1G07430	OsPP2C68	LOC_Os09g15670	BdPP2CA6	Bradi2g45470	TaPP2C51	TraesCS1A03G1005000	HvPP2C51	HORVU.MOREX.r3.1HG0090670	ZmPP2C17	Zm00001eb357040
	AtHAI3	AT2G29380	OsPP2C8	LOC_Os01g46760			TaPP2C68	TraesCS5A03G0486100	HvPP2C68	HORVU.MOREX.r3.5HG0473680	ZmPP2C19	Zm00001eb158020
			OsPP2C9	LOC_Os01g62760			TaPP2C8	TraesCS3A03G0611800	HvPP2C8	HORVU.MOREX.r3.3HG0276740	ZmPP2C3	Zm00001eb356420
											ZmPP2C4	Zm00001eb294200
											ZmPP2C6	Zm00001eb367840
											ZmPP2C7	Zm00001eb345270
											ZmPP2C8	Zm00001eb297300
											ZmPP2C9	Zm00001eb148130
RCAR	AtPYR1	AT4G17870	OsPYL1	LOC_Os10g42280	BdPYL1	Bradi3g34070	TaPYL1	TraesCS1B03G0603200	HvPYL2	HORVU.MOREX.r3.3HG0248870	ZmPYL1	Zm00001eb024490
	AtPYL1	AT5G46790	OsPYL2	LOC_Os06g36670	BdPYL2	Bradi3g08580	TaPYL2	TraesCS3D03G0346100	HvPYL3	HORVU.MOREX.r3.7HG0717820	ZmPYR1-1	Zm00001eb390480
	AtPYL2	AT2G26040	OsPYL3	LOC_Os02g13330	BdPYL3	Bradi1g37810	TaPYL3	TraesCS7A03G0875800	HvPYL4	HORVU.MOREX.r3.2HG0108630	ZmPYL2	Zm00001eb239670
	AtPYL3	AT1G73000	OsPYL4	LOC_Os01g61210	BdPYL4	Bradi1g16710	TaPYL4	TraesCS2B03G0246300	HvPYL5	HORVU.MOREX.r3.1HG0071710	ZmPYL4	Zm00001eb396710
	AtPYL4	AT2G38310	OsPYL5	LOC_Os05g39580	BdPYL5	Bradi1g65130	TaPYL5	TraesCS1B03G0846200	HvPYL6	HORVU.MOREX.r3.4HG0383820	ZmPYL5-0	Zm00001eb149160
	AtPYL5	AT5G05440	OsPYL6	LOC_Os03g18600	BdPYL6	Bradi2g22510	TaPYL6	TraesCS4B03G0534100	HvPYL7	HORVU.MOREX.r3.3HG0304260	ZmPYL5-1	Zm00001eb290140

	AtPYL6	AT2G40330	OsPYL7	LOC_Os06g33480	BdPYL7	Bradi2g53840	TaPYL7	TraesCS3D03G0763400	HvPYL8	HORVU.MOREX.r3.7HG0708570	ZmPYL7	Zm00001eb013780
	AtPYL7	AT4G01026	OsPYL8	LOC_Os06g33640	BdPYL8	Bradi3g09580	TaPYL8	TraesCS7B03G0653400	HvPYL9	HORVU.MOREX.r3.1HG0032540	ZmPYL8	Zm00001eb368560
	AtPYL8	AT5G53160	OsPYL9	LOC_Os06g33690	BdPYL9	Bradi2g32250	TaPYL9	TraesCS1A03G0316200			ZmPYL8-0	Zm00001eb283810
	AtPYL9	AT1G01360	OsPYL10	LOC_Os02g15640							ZmPYL8-1	Zm00001eb238230
	AtPYL10	AT4G27920	OsPYL11	LOC_Os05g12260							ZmPYL8-2	Zm00001eb350630
	AtPYL11	AT5G45860	OsPYL12	LOC_Os02g15620							ZmPYL9	Zm00001eb204180
	AtPYL12	AT5G45870										
	AtPYL13	AT4G18620										
GA2ox	AtGA2ox1	AT1G78440	OsGA2ox1	LOC_Os05g06670	BdGA2ox1	Bradi2g34837						
	AtGA2ox2	AT1G30040	OsGA2ox2	LOC_Os01g22910	BdGA2ox2	Bradi2g12440						
	AtGA2ox3	AT2G34555	OsGA2ox3	LOC_Os01g55240	BdGA2ox3	Bradi2g50280						
	AtGA2ox4	AT1G47990	OsGA2ox4	LOC_Os05g43880	BdGA2ox4	Bradi2g19900						
	AtGA2ox6	AT1G02400	OsGA2ox5	LOC_Os07g01340	BdGA2ox5	Bradi1g59570						
	AtGA2ox7	AT1G50960	OsGA2ox6	LOC_Os04g44150	BdGA2ox6	Bradi5g16040						
	AtGA2ox8	AT4G21200	OsGA2ox7	Os01g0209700	BdGA2ox7	Bradi2g06670						
	AtGA2ox9	AT5G58660	OsGA2ox8	LOC_Os05g48700	BdGA2ox8a	Bradi2g16750						
	AtGA2ox10	AT3G47190	OsGA2ox9	LOC_Os02g41954	BdGA2ox8b	Bradi2g16727						
			OsGA2ox10	Os05g0208550	BdGA2ox9	Bradi3g49390						
			OsGA2ox11	Os04g0407800	BdGA2ox10	Bradi2g32577						
					BdGA2ox11a	Bradi4g01693						
					BdGA2ox11b	Bradi1g14580						
GA3ox	AtGA3ox3	AT4G21690	OsGA3ox1	LOC_Os05g08540	BdGA3ox2a	Bradi2g04840						
	AtGA3ox4	AT1G80330	OsGA3ox2	LOC_Os01g08220	BdGA3ox2b	Bradi4g23570						
	AtGA3ox1	AT1G15550										
	AtGA3ox2	AT1G80340										
GA20ox	AtGA20ox1	AT4G25420	OsGA20ox1	LOC_Os03g63970	BdGA20ox1	Bradi1g00950						
	AtGA20ox2	AT5G51810	OsGA20ox2	LOC_Os01g66100	BdGA20ox2	Bradi2g57027						
	AtGA20ox3	AT5G07200	OsGA20ox3	LOC_Os07g07420	BdGA20ox3	Bradi1g56200						
	AtGA20ox4	AT1G60980	OsGA20ox4	LOC_Os05g34854	BdGA20ox4	Bradi2g24980						
	AtGA20ox5	AT1G44090			BdGA20ox5	Bradi1g56240						
SLY	AtSLY2/SNE	AT5G48170	OsSNE	Os03g0196500	BdGID2	Bradi3g46950	TaGID2-3A	TraesCS3A03G0116100	HvGID2a	HORVU.MOREX.r3.3HG0228040	ZmGID2a	Zm00001eb245180
	AtSLY1/GID2	AT4G24210	OsGID2	LOC_Os02g36974	BdSNE	Bradi1g71460	TaGID2-3B	TraesCS3B03G0153700	HvGID2b	HORVU.MOREX.r3.3HG0228120	ZmSNEa	Zm00001eb008130
							Tagid2-A1	TraesCS3A03G0117900	HvSNE	HORVU.MOREX.r3.4HG0399750	ZmGID2b	Zm00001eb183250
							Tagid2-B1	TraesCS3B03G0155200			ZnSNEb	Zm00001eb401080

							Tagid2-D1	TraesCS3D03G0104000				
							TaSNE-4A	TraesCS4A03G0083500				
							TaSNE-4B	TraesCS4B03G0701600				
							TaSNE-4D	TraesCS4D03G0627700				
DELLA	AtGAI	AT1G14920	OsSLR1	LOC_Os03g49990	BdSLR1	Bradi1g11090	TaRht-A	TraesCS4A03G0701300	HvD8	HORVU.MOREX.r3.3HG0275650	ZmD8	Zm00001eb054480
	AtRGL1	AT1G66350	OsSLRL1	LOC_Os01g45860	BdSLRL1	Bradi2g45117	TaRht-B	TraesCS4B03G0093100	HvSLN1	HORVU.MOREX.r3.4HG0336620	ZmD9	Zm00001eb216610
	AtRGA	AT2G01570	OsSLRL2	LOC_Os05g49930	BdSLRL2a	Bradi1g32070	TaRht-D	TraesCS4D03G0067100	HvSLRL2	HORVU.MOREX.r3.1HG0091000	ZmRGA	Zm00001eb158520
	AtRGL2	AT3G03450			BdSLRL2b	Bradi1g47900	TaSLRL1-3A	TraesCS3A03G0600000			ZmSLRL2	Zm00001eb344400
	AtRGL3	AT5G17490					TaSLRL1-3B	TraesCS3B03G0682500				
							TaSLRL1-3D	TraesCS3D03G0554000				
							TaSLRL2-1A	TraesCS1A03G1011200				
							TaSLRL2-1B	TraesCS1B03G1192200				
							TaSLRL2-1D	TraesCS1D03G0972200				
							TaSLRL2-4B	TraesCS4B03G0890100				
							TaSLRL2-4D	TraesCS4D03G0786700				
							TaSLRL2-5A	TraesCS5A03G1201000				
LAX	AtLAX3	AT1G77690	OsAUX2	LOC_Os05g37470	BdAUX4	Bradi3g21090	TaAUX4	TraesCS1A03G0190200	HvAUX3	HORVU.MOREX.r3.4HG0392470	ZmAUX5	Zm00001eb200830
	AtAUX1	AT2G38120	OsAUX4	LOC_Os10g05690	BdAUX3	Bradi1g68350	TaAUX2	TraesCS1A03G0702700	HvLAX1	HORVU.MOREX.r3.3HG0301040	ZmLAX1	Zm00001eb147480
	AtLAX2	AT2G21050	OsAUX3	LOC_Os03g14080	BdLAX1	Bradi2g55340	TaLAX1	TraesCS3A03G0876100	HvAUX4	HORVU.MOREX.r3.1HG0017310	ZmAUX3	Zm00001eb010460
	AtLAX1	AT5G01240	OsAUX5	LOC_Os11g06820			TaAUX3	TraesCS4A03G0141800	HvAUX5	HORVU.MOREX.r3.4HG0349300	ZmAUX2	Zm00001eb288800
			OsLAX1	LOC_Os01g63770			TaAUX5	TraesCS4A03G0553400	HvAUX2	HORVU.MOREX.r3.1HG0074390	ZmAUX4	Zm00001eb026490
IAA	AtIAA8	AT2G22670	OsIAA30	Os12g0601300	BdIAA1	Bradi2g04910						
	AtIAA7	AT3G23050	OsIAA21	LOC_Os06g22870	BdIAA11	Bradi1g14240						
	AtIAA9	AT5G65670	OsIAA17	LOC_Os05g14180	BdIAA30	Bradi4g02600						
	AtIAA14	AT4G14550	OsIAA3	LOC_Os01g13030	BdIAA17	Bradi2g31820						
	AtIAA17	AT1G04250	OsIAA19	Os05g0559400	BdIAA5	Bradi2g46420						
	AtIAA16	AT3G04730	OsIAA11	LOC_Os03g43400	BdIAA13	Bradi1g09090						
	AtIAA27	AT4G29080	OsIAA5	Os01g0675700	BdIAA3	Bradi2g07770						
	AtIAA3	AT1G04240	OsIAA13	LOC_Os03g53150	BdIAA19	Bradi2g16850						
	AtIAA4	AT5G43700	OsIAA31	LOC_Os12g40900	BdIAA31	Bradi4g02580						
			OsIAA15	Os05g0178600								
			OsIAA12	LOC_Os03g43410								
			OsIAA1	LOC_Os01g08320								
ARF	AtARF10	AT2G28350	OsARF18	LOC_Os06g47150	BdARF18	Bradi1g33160						

	AtARF16	AT4G30080	OsARF8	LOC_Os02g41800	BdARF22	Bradi3g28950						
			OsARF22	LOC_Os10g33940	BdARF8	Bradi3g49320						
			OsARF10	Os04g0519700								
EIN2	AtEIN2	AT5G03280	OsEIN2	LOC_Os07g06130	BdEIN2.4	Bradi4g08380	TaEIN2.2b	TraesCS4A03G0710900	HvEIN2.4	HORVU.MOREX.r3.5HG0467950	ZmEIN1	Zm00001eb054060
			OsEIN2.2	Os03g0700800	BdEIN2.2	Bradi1g11650	TaEIN2.2a	TraesCS5A03G1278000	HvEIN2.2	HORVU.MOREX.r3.4HG0418520	ZmEIN2a	Zm00001eb216860
			OsEIN2.4	Os07g0156732			TaEIN2.4	TraesCS5A03G0437700			ZmEIN2b	Zm00001eb119690
ETR/ERS	AtETR1	AT1G66340	OsETR3	LOC_Os02g57530	BdETR3	Bradi3g55730	TaETR1.1	TraesCS4A03G0855000	HvETR3	HORVU.MOREX.r3.6HG0630560	ZmETR2	Zm00001eb419810
	AtERS1	AT2G40940	OsERS1	LOC_Os03g49500	BdETR4	Bradi3g56550	TaETR3	TraesCS6A03G1001600	HvERS1	HORVU.MOREX.r3.5HG0420000	ZmETR40	Zm00001eb088180
	AtERS2	AT1G04310	OsETR2	LOC_Os04g08740	BdERS1	Bradi4g00200	TaERS1	TraesCS5A03G0005300	HvETR1	HORVU.MOREX.r3.4HG0336040	ZmETR6	Zm00001eb191130
	AtEIN4	AT3G04580	OsERS2	LOC_Os05g06320	BdETR1	Bradi1g11540	TaETR1	TraesCS4A03G0708500	HvERS2	HORVU.MOREX.r3.1HG0023840	ZmETR5	Zm00001eb205280
	AtETR2	AT3G23150	OsETR4	LOC_Os07g15540	BdERS2	Bradi2g35080	TaERS2	TraesCS1A03G0232900	HvETR4b	HORVU.MOREX.r3.6HG0619140	ZmERS25	Zm00001eb054170
					BdETR2	Bradi5g00700	TaETR4b	TraesCS6A03G0852600	HvETR4a	HORVU.MOREX.r3.6HG0610830	ZmERS14	Zm00001eb216810
							TaETR4a	TraesCS6A03G0759100	HvETR1.1	HORVU.MOREX.r3.5HG0532040	ZmERS2	Zm00001eb282800
							TaETR2	TraesCS2A03G0000300	HvETR2	HORVU.MOREX.r3.2HG0095490		
BIN2	AtKSG10	AT1G09840	OsGSK1	LOC_Os01g10840	BdSK11	Bradi2g08890						
	AtKSG2	AT3G61160	OsGSK2	LOC_Os05g11730	BdGSK3	Bradi3g09067						
	AtKSG4	AT1G57870	OsGSK3	LOC_Os02g14130	BdGSK6	Bradi2g38590						
	AtKSG5	AT5G14640	OsGSK4	LOC_Os06g35530	BdSK12	Bradi2g11370						
	AtKSG3	AT3G05840	OsSK11	Os01g0252100	BdSK41	Bradi1g02160						
	AtKSG1	AT5G26751	OsSK31	LOC_Os10g37740	BdSK31	Bradi3g31480						
	AtKSG8	AT4G00720	OsGSK6	Os05g0134000	BdGSK2	Bradi2g32620						
	AtKSG7	AT4G18710	OsSK12	Os01g0296100	BdGSK1	Bradi2g06490						
	AtKSG6	AT2G30980	OsSK41	LOC_Os03g62500								
	AtKSG9	AT1G06390										
BRI1	AtBRI1	AT4G39400	OsBRI1	LOC_Os01g52050	BdBRI1	Bradi2g48279						
	AtBRL1	AT1G55610	OsBRL1	LOC_Os09g12240	BdBRI1a	Bradi1g72572						
	AtBRL2	AT2G01950	OsBRL2	LOC_Os10g02500	BdBRL1	Bradi4g27440						
	AtBRL3	AT3G13380	OsBRL3	LOC_Os08g25380	BdBRL2	Bradi3g21400						
	AtEMS1	AT5G07280	OsMSL1	LOC_Os02g10100	BdMSL1	Bradi3g06980						
			OsMSP1	LOC_Os01g68870	BdMSP1	Bradi2g58780						
BZR	AtBZR1	AT1G75080	OsBZR1	LOC_Os07g39220	BdBZR1	Bradi1g23550	TaBZR1	TraesCS2B03G0529800	HvBZR1	HORVU.MOREX.r3.2HG0131380	ZmBZR1	Zm00001d021927
	AtBES1	AT1G19350	OsBZR2	Os01g0203000	BdBZR2	Bradi2g06400	TaBZR3	TraesCS7A03G0867300	HvBZR2	HORVU.MOREX.r3.3HG0243560	ZmBZR2	Zm00001d039439
	AtBEH2	AT4G36780	OsBZR3	Os06g0552300	BdBZR3	Bradi1g38180	TaBZR2	TraesCS3A03G0309300	HvBZR3	HORVU.MOREX.r3.7HG0718610	ZmBZR4	Zm00001eb003120
	AtBEH1	AT3G50750	OsBZR4	Os02g0233200	BdBZR4	Bradi3g08967	TaBZR4	TraesCS6A03G0871600	HvBZR4	HORVU.MOREX.r3.6HG0620450	ZmBZR6	Zm00001eb239100

	AtBEH3	AT4G18890	OsBZR5	LOC_Os01g08180	BdBZR5	Bradi2g04790	TaBZR5	TraesCS3B03G0338300	HvBZR5	HORVU.MOREX.r3.3HG0240300	ZmBZR5	Zm00001eb122520
	AtBEH4	AT1G78700									ZmBZR3	Zm00001eb384820
JAZ	AtJAZ11	AT3G43440	OsJAZ1	LOC_Os04g55920		Bradi5g24410						
	AtJAZ9	AT1G70700	OsJAZ7	LOC_Os07g42370		Bradi3g10820						
	AtJAZ1	AT1G19180	OsJAZ6	LOC_Os03g28940		Bradi1g21490						
	AtJAZ2	AT1G74950	OsJAZ4	Os09g0401300		Bradi4g29830						
	AtJAZ4	AT1G48500	OsJAZ3	Os08g0428400		Bradi1g72590						
	AtJAZ3	AT3G17860	OsJAZ11	LOC_Os03g08320		Bradi4g31240						
	AtJAZ12	AT5G20900	OsJAZ10	LOC_Os03g08330		Bradi3g36380						
	AtJAZ5	AT1G17380	OsJAZ8	LOC_Os09g26780		Bradi1g72600						
	AtJAZ6	AT1G72450	OsJAZ12	LOC_Os10g25290		Bradi3g23180						
	AtJAZ10	AT5G13220	OsJAZ5	Os04g0395800		Bradi3g56941						
	AtJAZ7	AT2G34600	OsJAZ13	LOC_Os10g25230		Bradi5g08650						
	AtJAZ8	AT1G30135		Os01g0925900		Bradi3g23190						
	AtPPD2	AT4G14720	OsJAZ2	LOC_Os07g05830		Bradi3g23220						
	AtPPD1	AT4G14713	OsJAZ9	LOC_Os03g08310		Bradi1g72610						
	AtTIFY8	AT4G32570	OsJAZ15	Os03g0396500		Bradi1g58491						
	AtTIFY2B	AT3G21175	OsJAZ14	Os10g0391801		Bradi2g05850						
	AtTIFY1	AT4G24470	OsTIFY1A	Os03g0684000		Bradi1g09550						
	AtTIFY2A	AT1G51600		Os10g0392101		Bradi1g12330						
	AtJAZ13	AT3G22275	OsTIFY2B	Os06g0698900		Bradi1g33980						
			OsTIFY1B	Os03g0734900		Bradi3g03800						
			OsTIFY2A	Os02g0148500								
			OsTIFY8	Os02g0732400								
DOG1	AtDOG1	AT5G45830	OsDOG1L1	Os01g0159000	BdDOG1L1	Bradi2g00210	TaDOG1L1	TraesCS3A03G0226600	HvDOG1L1	HORVU.MOREX.r3.3HG0235930	ZmDOG1L1	Zm00001eb123660
	AtDOGL1	AT4G18660	OsDOG1L2	Os05g0560200	BdDOG1L2	Bradi2g16790	TaDOG1L2	TraesCS1A03G0955500	HVDOG1L2	HORVU.MOREX.r3.1HG0086840	ZmDOG1L2	Zm00001eb295650
	AtDOGL2	AT4G18680	OsDOG1L3	LOC_Os01g20030	BdDOG1L3	Bradi2g11707	TaDOG1L3	TraesCS2A03G1135700	HvDOG1L3	HORVU.MOREX.r3.2HG0199880	ZmDOG1L4	Zm00001d043390
	AtDOGL3	AT4G18690			BdDOG1L4	Bradi1g44237	TaDOG1L4	TraesCS3A03G0736200	HvDOG1L4	HORVU.MOREX.r3.3HG0290160	ZmRAS1-1	Zm00001d040624
	AtDOGL4	AT4G18650									ZmRAS1-2	Zm00001d009087
	AtDOGL5	AT3G14880										
	AtRAS1	AT1G09950										
	AtZW2	AT1G58330										
Covering	AtMYBS1	AT1G49010	OsMYB3	LOC_Os03g29614	BdMYB10	Bradi1g60106	TaMYB1	TraesCS7A03G0392800	HvMYB1	HORVU.MOREX.r3.7HG0662710	ZmMYB6	Zm00001d001837
	AtMYBS2	AT5G08520	OsMYB6		BdMYB7	Bradi5g26110	TaMYB10	TraesCS3D03G1031600	HvMYB10	HORVU.MOREX.r3.3HG0316260	ZmMYBC	Zm00001eb373660

	AtTT2	AT5G35550	OsMYBS1	LOC_Os01g34060	BdMYBS1	Bradi2g13860	TaMYB3	TraesCS4B03G0838600	HvMYB3	HORVU.MOREX.r3.4HG0410500	ZmMYBS1	Zm00001eb332640
	AtTT8	AT4G09820	OsRc	LOC_Os07g11020	BdTT8-1	Bradi1g54111	TaMYB7	TraesCS2A02G554200	HvMYB7	HORVU.MOREX.r3.2HG0210040	ZmTT8	Zm00001eb303250
					BdTT8-2	Bradi1g54070	TaMYBS1	TraesCS4A03G1133400	HvMYBS1	HORVU.MOREX.r3.7HG0639370		
							TaTT8	TraesCS1A03G0248200	HvTT8	HORVU.MOREX.r3.1HG0021280		
VEL3	AtVEL1	AT4G30200	OsVIL1	LOC_Os08g12430	BdVIL1	Bradi3g17950	TaVIL3-2	TraesCS7A03G1050100	HvVIL3-2	HORVU.MOREX.r3.7HG0729670	ZmVIL1-1	Zm00001d024318
	AtVEL2	AT2G18880	OsVIL2	LOC_Os12g34850	BdVIL2	Bradi4g05950	TaVIL3	TraesCS6A03G0291300	HvVIL2	HORVU.MOREX.r3.5HG0446560	ZmVIL1-2	Zm00001eb171090
	AtVEL3	AT2G18870	OsVIL3	LOC_Os02g05840	BdVIL3-2	Bradi1g33450	TaVIL2	TraesCS5A03G0244500	HvVIL4	HORVU.MOREX.r3.1HG0020220	ZmVIL2-1	Zm00001d041715
	AtVIN3	AT5G57380	OsVIL4	LOC_Os05g05310	BdVIL3-1	Bradi3g04140	TaVIL4	TraesCS1A03G0263600	HvVIL3	HORVU.MOREX.r3.6HG0560710	ZmVIL2-2	Zm00001d023897
	AtVRN5	AT3G24440			BdVIL4-1	Bradi2g36237					ZmVIL3-1	Zm00001d015293
					BdVIL4-2	Bradi3g35535					ZmVIL3-2	Zm00001d053875
											ZmVIL4	Zm00001eb417960
JMJ	AtJMJ20	AT5G63080	OsJMJ709	Os01g0546900	BdJMJ7	Bradi2g40677						
	AtJMJ16	AT1G08620	OsJMJ705	LOC_Os01g67970	BdJMJ14	Bradi4g16020						
	AtJMJ18	AT1G30810	OsELF6	LOC_Os03g05680	BdJMJ10	Bradi3g34240						
	AtJMJ15	AT2G34880	OsJMJ703	LOC_Os05g10770	BdJMJ12	Bradi3g39457						
	AtJMJ19	AT2G38950	OsJMJ704	LOC_Os05g23670	BdJMJ6	Bradi2g31107						
	AtREF6	AT3G48430	OsJMJ17	Os06g0731600	BdJMJ17	Bradi1g29247						
	AtJMJ14	AT4G20400	OsJM706	LOC_Os10g42690	BdJMJ1	Bradi2g14600						
	AtELF6	AT5G04240	OsJMJ710	LOC_Os11g36450	BdREF6-2	Bradi2g58130						
	AtJMJ22	AT5G06550	OsJMJ702	Os12g0279100	BdREF6-1	Bradi4g39130						
	AtJMJ13	AT5G46910			BdELF6	Bradi1g74997						
PRC2	AtVRN2	AT4G16845	OsEMF2a	LOC_Os04g08034	BdEMF2a	Bradi4g11608	TaEMF2a	TraesCS2A03G0005800	HvEMF2a	HORVU.MOREX.r3.2HG0095780	ZmEMF2b-1	Zm00001eb309520
	AtEMF2	AT5G51230	OsEMF2b	LOC_Os09g13630	BdEMF2b	Bradi3g03106	TaEMF2b-1	TraesCS2A03G0000200	HvEMF2b-1	HORVU.MOREX.r3.2HG0095480	ZmEMF2b-2	Zm00001eb057460
							TaEMF2b-2	TraesCS5A03G0476700	HvEMF2b-2	HORVU.MOREX.r3.5HG0472220		
	AtFIE2/FIS2	AT2G35670	OsFIE1	LOC_Os08g04290	BdFIE1	Bradi3g17417	TaFIE1	TraesCS4A03G0970400	HvFIE1	HORVU.MOREX.r3.7HG0702190	ZmFIE1	Zm00001eb173090
	AtFIE1/FIS3	AT3G20740	OsFIE2	LOC_Os08g04270	BdFIE1-1	Bradi3g14510	TaFIE1-1	TraesCS7A03G0213500			ZmFIE2	Zm00001eb416950
					BdFIE1-2	Bradi2g07820	TaFIE1-2	TraesCS7A03G0213600				
					BdFIE2	Bradi3g14520	TaFIE2	TraesCS7A03G0760100				
	AtSWN/SDG10	AT4G02020	OsSET1	LOC_Os03g19480	BdSET1	Bradi1g64460	TaCLF-1	TraesCS7A03G0303400	HvSET1	HORVU.MOREX.r3.4HG0382250	ZmEZ1	Zm00001eb271490
	AtFIS1/MEA/SDG5	AT1G02580	OsCLF	LOC_Os06g16390	BdCLF	Bradi1g48340	TaCLF-2	TraesCS7A03G0303800	HvCLF-1	HORVU.MOREX.r3.7HG0655900	ZmEZ2-1	Zm00001eb014730
	AtCLF/SDG1/SET1	AT2G23380					TaSET1	TraesCS4A03G0249600	HvCLF-2	HORVU.MOREX.r3.7HG0655960	ZmEZ2	Zm00001eb396070
	AT4G16810	AT4G16810										

ROS1	AtROS1	AT2G36490	OsDML4		BdROS1a	Bradi4g08870	TaROS1a	TraesCS5A03G0455000	HvROS1a	HORVU.MOREX.r3.5HG0469860	ZmDML1b	Zm00001eb241240
	AtDME	AT5G04560	OsROS1a	LOC_Os01g11900	BdROS1b	Bradi3g43692	TaROS1c	TraesCS1B03G0992100	HvROS1d	HORVU.MOREX.r3.1HG0074440	ZmROS1d	Zm00001eb202980
	AtDML2	AT3G10010	OsROS1d		BdROS1d	Bradi2g23797	TaROS1d	TraesCS1A03G0701700	HvDML3a	HORVU.MOREX.r3.3HG0221280	ZmROS1c	Zm00001eb289030
	AtDML3	AT4G34060	OsROS1c	LOC_Os05g37350	BdROS1c	Bradi4g16620	TaDML3a	TraesCS3A03G0045600	HvDML4	HORVU.MOREX.r3.7HG0667760	ZmDML3a	Zm00001eb241310
			OsDML3a	LOC_Os02g29380	BdDML3a	Bradi3g43720	TaDML4	TraesCS7A03G0453900			ZmDML4	Zm00001eb279940
			OsDML3b		BdDML4	Bradi1g44750						
			OsROS1b									
PHY	AtPHYA	AT1G09570	OsPHYA	LOC_Os03g51030	BdPHY	Bradi1g10510	TaPHYB-4A	TraesCS4A03G0251700	HvPHYA	HORVU.MOREX.r3.4HG0338060	ZmPHYB1	Zm00001eb014850
	AtPHYB	AT2G18790	OsPHYB	LOC_Os03g19590	BdPHYA	Bradi1g10520	TaPHYA-4A	TraesCS4A03G0683800	HvPHYB	HORVU.MOREX.r3.4HG0381880	ZmPHYA2	Zm00001eb055460
	AtPHYD	AT4G16250	OsPHYC	LOC_Os03g54084	BdPHYB	Bradi1g64360	TaPHYA-4B	TraesCS4B03G0112200	HvPHYC	HORVU.MOREX.r3.5HG0511090	ZmPHYC1	Zm00001eb057490
	AtPHYE	AT4G18130			BdPHYC	Bradi1g08400	TaPHYB-4B	TraesCS4B03G0513700			ZmPHYC2	Zm00001eb214800
	AtPHYC	AT5G35840					TaPHYA-4D	TraesCS4D03G0095200			ZmPHYA1	Zm00001eb216020
							TaPHYB-4D	TraesCS4D03G0456400			ZmPHYB2	Zm00001eb396030
							TaPHYC-5A	TraesCS5A03G0934800				
							TaPHYC-5B	TraesCS5B03G0985300				
							TaPHYC-5D	TraesCS5D03G0893400				
CRY	AtCRY1	AT4G08920	OsCRY1a	LOC_Os02g36380	BdCRY1a	Bradi3g46590	TaCRY1a	TraesCS6A03G0549000	HvCRY1a	HORVU.MOREX.r3.6HG0587680	ZmCRY1a	Zm00001eb182820
	AtCRY2	AT1G04400	OsCRY1b	LOC_Os04g37920	BdCRY1b	Bradi5g11990	TaCRY1b	TraesCS2A03G0793800	HvCRY1b	HORVU.MOREX.r3.2HG0172510	ZmCRY1b	Zm00001eb081200
			OsCRY2	LOC_Os02g41550	BdCRY2	Bradi3g49204	TaCRY2	TraesCS6B03G0754600	HvCRY2	HORVU.MOREX.r3.6HG0596460	ZmCRY2	Zm00001eb382070
PIF	AtPIF6	AT3G62090	OsPIL1	LOC_Os03g56950	BdPIL3	Bradi2g11100						
	AtPIL1	AT2G46970	OsPIL16	LOC_Os05g04740	BdPIF4/5B	Bradi1g06670						
	AtPIF1	AT2G20180	OsPIL15	Os01g0286100	BdPIL1	Bradi1g13980						
	AtSPT	AT4G36930	OsPIL11	LOC_Os12g41650	BdPIF4/5C	Bradi1g58230						
	AtHFR1	AT1G02340	OsPIF14	LOC_Os07g05010	BdPIF3B	Bradi2g36740						
	AtPIF3	AT1G09530	OsbHLH107	LOC_Os02g56140	BdSPT	Bradi1g48400						
	AtPIF4	AT2G43010	OsPIF1	Os04g0618600	BdPIF8	Bradi3g33170						
	AtPIF5	AT3G59060	OsPIF8	Os10g0556200	BdPIF1	Bradi5g21950						
	AtPIF8	AT4G00050	OsSPT	LOC_Os06g06900	BdBdPTF1	Bradi1g46700						
	AtPIF7	AT5G61270	PTF1	LOC_Os06g09370	BdBdPTF1-1	Bradi1g47350						
FLC	AtFLC	AT5G10140	OsMADS37	LOC_Os08g41960	BdMADS37	Bradi3g41297	TaAGL12	ABF57951.1	HvODDSOC1	HORVU.MOREX.r3.3HG0310820		
			OsMADS51	LOC_Os01g69850	BdODDSOC2	Bradi2g59192	TaAGL22	ABF57949.1	HvODDSOC2	HORVU.MOREX.r3.3HG0311160		
					BdODDSOC1	Bradi2g59119	TaAGL41	ABF57941.1				
							TaAGL42	ABF57942.1				
MFT	AtMFT	AT1G18100	OsMFT1	LOC_Os06g30370	BdMFT1	Bradi1g42510	TaMFT-3A	TraesCS3A03G0015600	HvMFT1	HORVU.MOREX.r3.7HG0675890	ZmMFT1/ZCN11	Zm00001eb281410

			OsMFT2	LOC_Os01g02120	BdMFT2	Bradi2g01020	TaMFT-3B-1	TraesCS3B03G0035200	HvMFT2	HORVU.MOREX.r3.3HG0219250	ZmMFT2/ZCN10	Zm00001eb126300
					BdMFT3	Bradi2g27860	TaMFT-3B-2	TraesCS3B03G0016000				
							TaMFT-3D	TraesCS3D03G0012600				
FT	AtBFT	AT5G62040	OsFTL1	LOC_Os01g11940	BdFTL1	Bradi2g07070						
	AtCEN	AT2G27550	OsFTL10	LOC_Os05g44180	BdFTL10	Bradi2g49795						
	AtFT	AT1G65480	OsFTL11	LOC_Os11g18870	BdFTL11	Bradi5g14010						
	AtSMFT	AT5G01300	OsFTL12	LOC_Os06g35940	BdFTL12	Bradi1g38150						
	AtTFL1	AT5G03840	OsFTL13	LOC_Os02g13830	BdFTL2	Bradi1g48830						
	AtTSF	AT4G20370	OsFTL2	LOC_Os06g06320	BdFTL4	Bradi4g35040						
			OsFTL3	LOC_Os06g06300	BdFTL6	Bradi3g48036						
			OsFTL4	LOC_Os09g33850	BdFTL7a	Bradi4g39730						
			OsFTL5	LOC_Os02g39064	BdFTL7b	Bradi4g39750						
			OsFTL6	LOC_Os04g41130	BdFTL7c	Bradi4g39760						
			OsFTL7	LOC_Os12g13030	BdFTL8	Bradi3g08890						
			OsFTL8	LOC_Os01g10590	BdFTL9	Bradi2g19670						
			OsFTL9	LOC_Os01g54490	BdRCN1	Bradi4g42400						
			OsRCN1	LOC_Os11g05470	BdRCN2	Bradi3g44860						
			OsRCN2	LOC_Os02g32950	BdRCN4	Bradi5g09270						
			OsRCN3	LOC_Os12g05590	BdSMFT	Bradi2g22660						
			OsRCN4	LOC_Os04g33570								
			OsSMFT	LOC_Os05g39250								
RBOH	AtRBOHD	AT5G47910	OsNOX3	Os01g0835500	BdRBOHD	Bradi4g17020						
	AtRBOHH	AT5G60010	OsNOX4	Os05g0465800	BdRBOHH	Bradi2g54240						
	AtRBOHJ	AT3G45810	OsRBOHB	Os01g0360200	BdRBOHB-1	Bradi2g12790						
	AtRBOHC	AT5G51060	OsNOX5	LOC_Os05g45210	BdRBOHF-1	Bradi2g19090						
	AtRBOHA	AT5G07390	OsNOX9	LOC_Os12g35610	BdRBOHF-2	Bradi2g49040						
	AtRBOHB	AT1G09090	OsNOX7	LOC_Os09g26660	BdRBOHJ	Bradi2g22820						
	AtRBOHF	AT1G64060	OsNOX2	Os01g0734466	BdRBOHB-2	Bradi4g05540						
	AtRBOHG	AT4G25090	OsNOX6	LOC_Os08g35210	BdRBOHE-1	Bradi4g31130						
	AtRBOHE	AT1G19230			BdRBOHE-2	Bradi3g37530						
	AtRBOHI	AT4G11230										
NLP	AtNLP4	AT1G20640	OsNLP1	LOC_Os03g03900	BdNLP1	Bradi1g76340						
	AtNLP6	AT1G64530	OsNLP2	LOC_Os04g41850	BdNLP7	Bradi2g08177						
	AtNLP5	AT1G76350	OsNLP3	LOC_Os01g13540	BdNLP5	Bradi3g03170						

	AtNLP8	AT2G43500	OsNLP6	LOC_Os02g04340	BdNLP3	Bradi4g20720						
	AtNLP9	AT3G59580	OsNLP4	LOC_Os09g37710	BdNLP2	Bradi4g37147						
	AtNLP7	AT4G24020	OsNLP5	LOC_Os11g16290	BdNLP4	Bradi5g23300						
	AtNLP2	AT4G35270										
	AtNLP3	AT4G38340										
	AtNLP1	AT2G17150										
ZOU	AtZOU	AT1G49770	OsZOU-1	LOC_Os04g35010	BdZOU-1	Bradi3g45365	TaZOU	TraesCS6A02G114100	HvZOU	BAK04352.1	ZmZOU-1	ONM17464.1
			OsZOU-2	LOC_Os02g34320	BdZOU-2	Bradi3g45360					ZmZOU-2	Zm00001eb261420
			OsZOU-3	Os04g0429300	BdZOU-3	Bradi3g45370						
ICE	AtICE1	AT3G26744	OsICE1	LOC_Os11g32100	BdICE1	Bradi4g17460	TaICE1-1	TraesCS7A03G0766800	HvICE1-1	HORVU.MOREX.r3.7HG0703220	ZmICE1-1	Zm00001d049294
	AtICE2	AT1G12860	OsICE2	LOC_Os01g70310	BdICE2	Bradi2g59497	TaICE2	TraesCS3A03G1027800	HvICE2	HORVU.MOREX.r3.3HG0312340	ZmICE1-2	Zm00001d007382
							TaICE1-2	TraesCS4A03G0685000	HvICE1-2	HORVU.MOREX.r3.4HG0337970	ZmICE2	Zm00001eb142500
Sdr4	AtSFL1	AT1G27461	OsSdr4	LOC_Os07g39700	BdSdr4L1	Bradi1g23171	TaSdr	TraesCS2B03G0519300	HvSdr4		ZmSFL1	Zm00001eb020940
	AtSFL2	AT3G48510	OsSFL1	LOC_Os12g13910	BdSdr4L2	Bradi1g23180	TaSFL1	TraesCS5A03G0219000	HvSFL1	HORVU.MOREX.r3.3HG0270610	ZmSFL2	Zm00001eb002650
	AtSFL4	AT5G50360			BdSFL1	Bradi4g39520	TaSFL2	TraesCS3B03G0646500			ZmSFL3	Zm00001eb016430
	AtSFL6	AT3G27250									ZmSFL4	Zm00001eb409910
	AtAITR3	AT5G40790									ZmSdr4L1	Zm00001eb325870
	AtAITR4	AT5G40800									ZmSdr4L2	Zm00001eb108020
MKK3	AtMKK3	AT5G40440	OsMKK3	LOC_Os06g27890	BdMKK3-1	Bradi1g41860	TaMKK3-A	BAU88551.1	HvMKK3	HORVU.MOREX.r3.5HG0537390, HORVU.MOREX.r3.5HG0537440	ZmMKK3	Zm00001eb133330
					BdMKK3-2	Bradi4g39490	TaMKK3-5D	TraesCS5D03G1199000	HvMKK3-3	HORVU.MOREX.r3.5HG0457350		
					BdMKK3-3	Bradi3g11260	TaMKK3-3	TraesCS5D03G0331000				
Qsd1	AtAlaAT1	AT1G17290	OsALT2	LOC_Os07g01760	BdQsd1	Bradi4g31003	TaQsd1	TraesCS5A03G0558200	HvQsd1	HORVU.MOREX.r3.5HG0481320	ZmAlaAT1	Zm00001eb298440
	AtAlaAT2	AT1G72330	OsAlaAT5	LOC_Os03g08530	BdQsd1-2	Bradi1g20995	TaQsd1-2	TraesCS2A03G0347900	HvQsd1-2	HORVU.MOREX.r3.2HG0124810	ZmAlaAT2	Zm00001eb028030
	AtGGT2	AT1G70580	OsAlaAT4	LOC_Os09g26380	BdQsd1-3	Bradi1g59220	TaQsd1-3	TraesCS2A03G0643800	HvQsd1-3	HORVU.MOREX.r3.2HG0156760	ZmAlaAT4	Zm00001eb223670
	AtGGT1	AT1G23310	OsAlaAT3	LOC_Os10g25140	BdQsd1-4	Bradi5g20427	TaQsd1-4	TraesCS5A03G0151800	HvQsd1-4	HORVU.MOREX.r3.5HG0433990	ZmAlaAT7	Zm00001eb313780
			OsAlaAT2	LOC_Os07g42600	BdQsd1-5	Bradi3g23160	TaQsd1-5	TraesCS1A03G0207600	HvQsd1-5	HORVU.MOREX.r3.1HG0019260	ZmAlaAT8	Zm00001eb118240
			OsAlaAT1	LOC_Os10g25130							ZmAlaAT9	Zm00001eb327530
											ZmAlaAT10	Zm00001eb109370