Seed Science Research

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Seed traits and phylogenomics: prospects for the 21st century

Mariko Nonogaki[1], Satoru Yamazaki[1], Eri Nishiyama[2], Kazuhiko Ohshima[2] and Hiroyuki Nonogaki[1]

[1]Department of Horticulture, Oregon State University, Corvallis, OR 97331, USA and [2]Department of Bioscience, Nagahama Institute of Bio-Science and Technology, Nagahama, Shiga 526-0829, Japan

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Author for Correspondence:
Hiroyuki Nonogaki,
E-mail: hiro.nonogaki@oregonstate.edu

Abstract

Genetic and biochemical studies have greatly advanced our understanding of the biology of seeds in recent years. Another area of study, which could accelerate contemporary seed biology research, is phylogenomics that integrates the wealth of genome sequence data with evolutionary biology. The recent phylogenomic study of the *DELAY OF GERMINATION1* family genes exemplifies how the molecular evolution of seed genes can be traced back through early diverging plants and what implications can be obtained from the analysis of seed gene diversification at ancient times. The identification of possible ancestors of seed genes in non-seed plants could illuminate the ancient roots of the molecular mechanisms driving seed maturation programmes. It is possible that the origins of molecular mechanisms associated with the induction of seed storage proteins and desiccation tolerance proteins date back to the time of, or even prior to, early diverging land plants. Abscisic acid-dependent growth arrest or dormancy mechanisms might date back to red algae, one of the oldest algal groups. Thus, understanding algal cell biology will also be an integral part of future seed biology research. Unravelling key events associated with the evolution of seed- and non-seed plants will not only advance basic research but could also contribute to applied aspects of seed science, potentially leading to technology development for agriculture.

Introduction

The availability of plant genome sequences is growing exponentially, which opens new dimensions for seed science research. One of the flagship themes of the 13th International Society for Seed Science (ISSS) conference (Kew Gardens, UK) was to connect seed traits and phylogenomics. This article summarizes the opening plenary lecture '*Seed traits and phylogenomics*' given at the ISSS conference to highlight the utility of phylogenomics for future seed studies. Rather than discussing general aspects of phylogenomics, the focus of this article will be placed on the recent case study of the *DELAY OF GERMINATION1* (*DOG1*) family genes, which illustrates interesting research developments during a phylogenomic study, including the generation of new hypotheses and theories for future functional genomics. While the case study highlights specific information about the gene family, it also raises interesting questions about the origins of seed programmes, such as reserve accumulation, dormancy and desiccation tolerance. The discussion will be extended through the possible roots of the molecular mechanisms of seed maturation programmes in non-seed plants. Potential applications of the knowledge obtained from evolutionary studies to future research in both fundamental and applied seed science will also be discussed.

Diversification of the *DOG1* family genes in flowering plants

The *DOG1* family genes (termed *DFGs* hereafter) of *Arabidopsis* include the six genes *DOG1*, *DOG1-LIKE1* (*DOGL1*), *DOGL2*, *DOGL3*, *DOGL4* and *DOGL5* (Bentsink et al., 2006; Nishimura et al., 2018). A genomic survey of *DFGs* in other angiosperm species has identified *DOGL6*, another *DOGL* found in multiple species (Nishiyama et al., 2021). Extensive phylogenetic analysis of *DFGs* suggests that they have evolved in the four stem lineages such as *DOG1*, *DOGL4*, *DOGL5* and *DOGL6* in angiosperms, while *DOGL1*, *DOGL2* and *DOGL3* occurred within the *DOG1* lineage (Nishiyama et al., 2021) (Fig. 1). In terms of gene function, *DOG1* has intensively been characterized for its involvement in seed dormancy (Bentsink et al., 2006; Cyrek et al., 2016; Fedak et al., 2016; Née et al., 2017; Nishimura et al., 2018), while *DOGL4* was found to play a role in seed reserve accumulation (Sall et al., 2019). The *DOG1* involvement in seed dormancy has also been reported for *Lepidium*, another genus in Brassicaceae (Graeber et al., 2013, 2014). The *DOG1* function in dormancy or the *DOGL4* function in reserve accumulation seems to be specific to each gene, although they also have an overlapping role in desiccation tolerance (Dekkers et al., 2016; González-Morales et al.,

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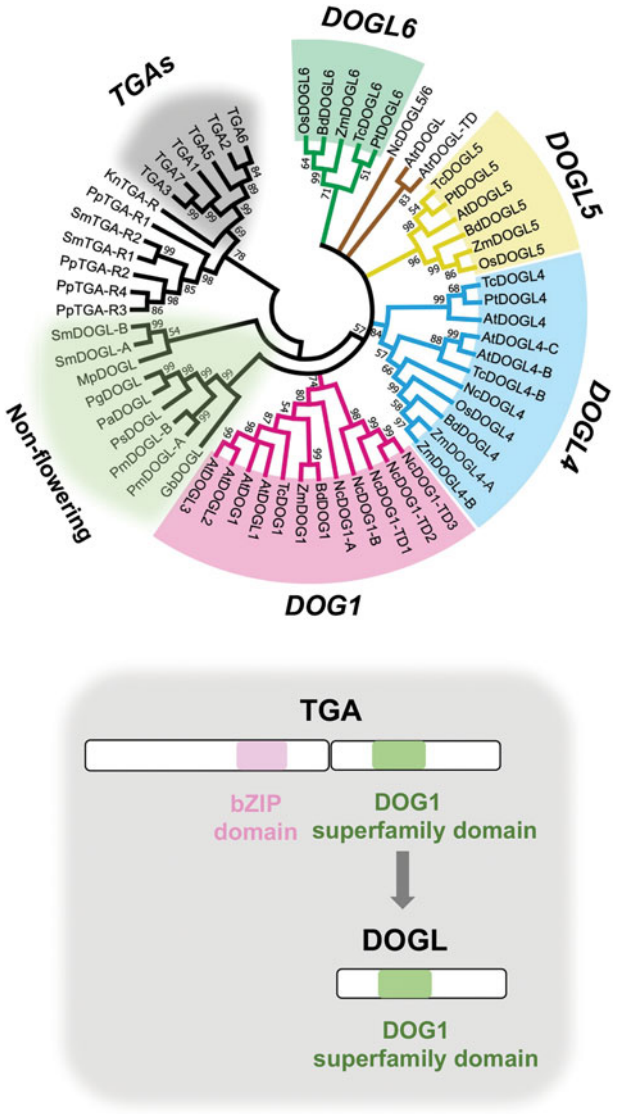


Fig. 1. Phylogeny of the *DOG1* family genes. (*Top*) Phylogenetic tree of the *DOG1* family genes (*DFGs*), including *DOG1s* and *DOG1-LIKEs* (*DOGLs*), which shows the diversification of *DFGs* in the four stem lineages (*DOG1*, *DOGL4*, *DOGL5* and *DOGL6*) in angiosperms and the presence of *DOGLs* in non-flowering plants. Note that *DOGL1*, *DOGL2* and *DOGL3* are confined to the *DOG1* lineage. The *TGACG motif-binding transcription factor* genes (*TGAs*) and *TGA-related* genes (*TGA-Rs*), which are associated with *DOGLs*, are used as an outgroup in the phylogeny (from Nishiyama et al. (2021)). (*Bottom*) Schematic representation of the possible evolution of *DOGLs* from *TGAs*. The basic leucine zipper (bZIP) domain and DOG1 superfamily domains are shown in the panel (based on Sall et al. (2019)). *At*, *Arabidopsis thaliana*; *Atr*, *Amborella trichopoda*; *Bd*, *Brachypodium distachyon*; *Gb*, *Ginkgo biloba*; *Mp*, *Marchantia polymorpha*; *Nc*, *Nymphaea colorata*; *Os*, *Oryza sativa*; *Pa*, *Picea abies*; *Pg*, *Picea glauca*; *Pm*, *Pseudotsuga menziesii*; *Pp*, *Physcomitrella patens*; *Ps*, *Pinus sylvestris*; *Pt*, *Populus trichocarpa*; *Sm*, *Selaginella moellendorffii*; *Tc*, *Theobroma cacao*; *Zm*, *Zea mays*.

2016; Sall et al., 2019), suggesting their common origin and functional diversification (Nonogaki et al., 2020).

DFGs are found also in non-flowering plants where a single gene is a prevalent form (Nonogaki et al., 2020; Nishiyama et al., 2021) (Fig. 1). Those results and the presence of multiple *DOGLs* in angiosperms suggest that *DFG* duplications occurred after the divergence of gymnosperms and angiosperms. *DFG* diversification probably occurred in early diverging angiosperms, which are also called basal angiosperms. In the genome of the basal angiosperm *Nymphaea colorata* (tropical water lily), the three genes *DOG1*, *DOGL4* and *DOGL5/6* (resembling *DOGL5* and *DOGL6*) are detected. By contrast, a single form of *DOGL* is found in the genome of *Amborella trichopoda* that is supposedly the most ancient extant basal angiosperm, although another copy of this gene is found in its vicinity, probably due to tandem duplication (Nishiyama et al., 2021). It is difficult to identify this *A. trichopoda DOGL* (*AtrDOGL*) as either of *DOG1*, *DOGL4* or *DOGL5/6* through sequence alignments. However, genome synteny analysis focusing on its neighbouring genes indicates that the same set of genes is conserved in the vicinity of *N. colorata DOG1* (*NcDOG1*) and *Arabidopsis thaliana DOG1* (*AtDOG1*) (Fig. 2), suggesting their evolutionary relationship. Interestingly, the *Arabidopsis DOGL4* neighbourhood contains the genes similar to the *DOG1* 'signature' genes (Nishiyama et al., 2021), implying that *DOG1* and *DOGL4* originated from the same ancient locus possibly of a basal angiosperm species.

To support this notion, *DOG1* and *DOGL4* are found next to each other in the genome of *Theobroma cacao*, where a mixture of the *DOG1* and *DOGL4* signature genes is found in their vicinity (Fig. 2). Likewise, colocalization of *DOGL4* and *DOGL5* is found in the *Nelumbo nucifera* (lotus) genome (Nishiyama et al., 2021). While no gene is annotated next to the *NnDOGL4–NnDOGL5* region in the lotus genome, a *pseudo DOG1* that is comprised of two parts of collapsed open reading frames of a copy of *DOG1* has been identified next to *NnDOGL4*. In addition, a *pseudo NnDOGL4* has been found next to *NnDOG1*, which is annotated on a separate chromosome (Nishiyama et al., 2021). Taken together, it is likely that *DOG1*, *DOGL4* and *DOGL5/6* originated from tandem duplications at an ancient locus of the most recent common ancestor of angiosperms.

Possible origins of seed maturation programmes in non-seed plants

DFG diversification probably occurred in angiosperms, which must have contributed to functional diversification of the gene family as well. It is possible that *DOGLs* were already playing some biological roles in non-flowering plants. The *Amborella*-type of intron-less *DOGLs* are found in gymnosperms, lycophytes and bryophytes (Nishiyama et al., 2021). These findings raise interesting questions about the origins of the molecular mechanisms associated with seed maturation programmes, such as seed dormancy. In the liverwort *Marchantia polymorpha*, there is gemma dormancy where the germination of rhizoid from gemmae is blocked by abscisic acid (ABA) (Eklund et al., 2018), as is the case of seed dormancy. It would be interesting to examine in future research whether *M. polymorpha DOGL* (*MpDOGL*) functions as a repressor of protein phosphatase 2C (PP2C) to enhance ABA sensitivity of gemmae, just like *Arabidopsis DOG1* in seeds (Née et al., 2017; Nishimura et al., 2018) (see below for more discussion about PP2C repression).

Bryophytes are not the oldest group containing *DOGLs*. They are found even in the algae Zygnematophyceae (Fig. 3), which is an algal sister lineage of land plants (Wodniok et al., 2011; Wickett et al., 2014; Gitzendanner et al., 2018; Cheng et al., 2019). This timing coincides with the emergence of the ancestral form of ABA receptor *pre-PYR1-LIKE* (*pre-PYL*) (Sun et al., 2019). *Pre-PYL* has been found in *Zygnema circumcarinatum*, while *DOGLs* can be found in *Mesotaenium endlicherianum*

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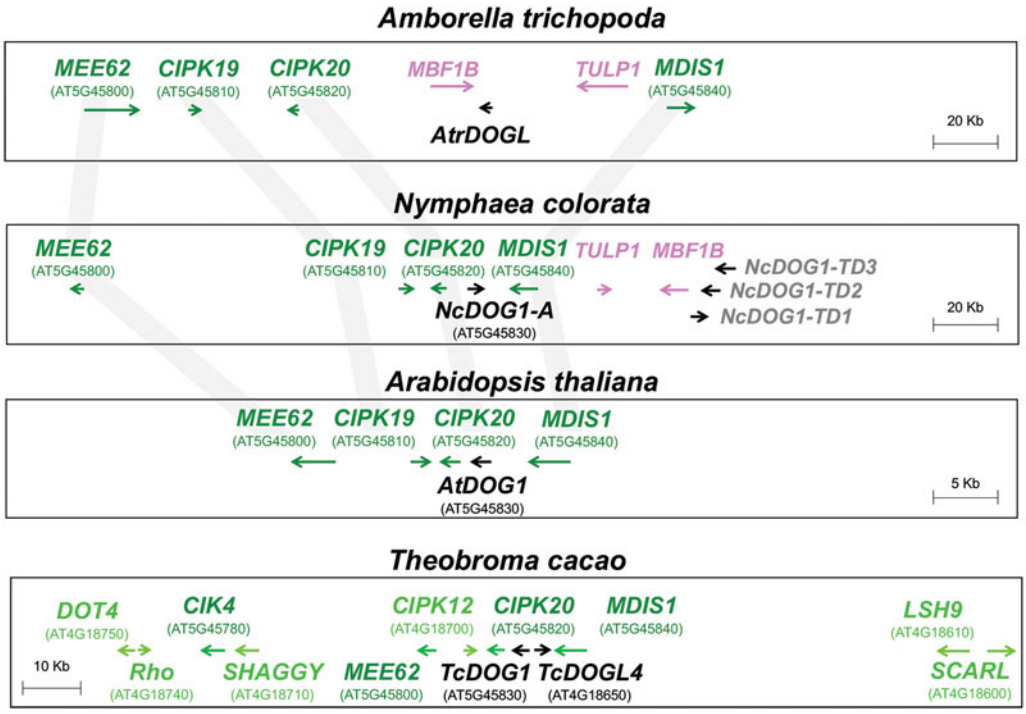


Fig. 2. The synteny of the *DOG1* family genes suggesting their diversification in the early diverging angiosperms. It is difficult to identify *AtrDOGL* as either of *DOG1*, *DOGL4*, *DOGL5* or *DOGL6*. However, the examination of its neighbouring genes, such as *MEE62*, *CIPK19*, *CIPK20* and *MDIS1*, suggests its evolutionary relationship with the *NcDOG1* (water lily) and *AtDOG1* (compare the top three panels). The *Arabidopsis DOGL4* neighbours also include similar genes like *CIPK12* and *MDIS2* (not shown in the figure), suggesting that *DOG1* and *DOGL4* originated from the same ancient locus. To support this idea, *DOG1* and *DOGL4* are found next to each other in the genome of *T. cacao* (bottom panel), with the mixture of the *DOG1* signature neighbouring genes (green) and the *DOGL4* signature neighbouring genes (light green). This type of genomic locus probably represents the ancient genomic arrangement of *DFGs* (from Nishiyama et al. (2021)). *CIK4*, *CLAVATA3 INSENSITIVE RECEPTOR KINASE 4*; *CIPK*, *CBL-INTERACTING PROTEIN KINASE*; *DOT4*, *DEFECTIVELY ORGANIZED TRIBUTARIES 4*; *LSH9*, *LIGHT-DEPENDENT SHORT HYPOCOTYLS 9*; *MBF*, *multiprotein-binding factor*; *MDIS*, *MALEDISCOVERER*; *MEE62*, *MATERNAL EFFECT EMBRYO ARREST 62*; *PP*, *protein phosphatase*; *Rho*, *Rho termination factor*; *SCARL*, *SCAR-LIKE*; *SHAGGY*, *SHAGGY-LIKE KINASE*; *TD*, *tandem duplication*; *TULP*, *Tubby-like F-box protein*.

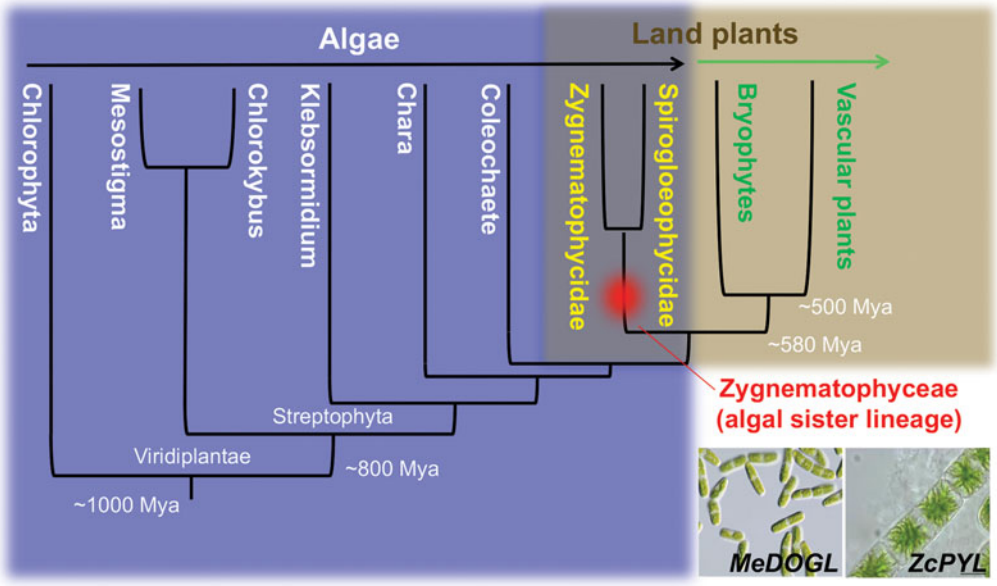


Fig. 3. Ancestral *DOGL* and ABA receptor found in algae. *DOGLs* can be found in as early as *MeDOGL* in Zygnematophyceae, which is an algal sister lineage of land plants. Interestingly, this timing coincides with the timing of the emergence of the ancestral ABA receptor *pre-PYRABACTIN RESISTANCE 1-LIKE* (*pre-PYL*) found in *Z. circumcarinatum* (*ZcPYL*) in the same class (Sun et al., 2019). Phylogeny is based on Cheng et al. (2019). Photos: *Mesotaenium* and *Zygnema*, T. Friedl CC BY-SA 4.0 (sagdb.uni-goettingen.de) and Feng et al. (2021), CC BY, respectively.

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Fig. 4. ABA-independent PP2C repression by the algal pre-PYL and seed DOG1. In *Arabidopsis*, the ABA receptor PYRABACTIN RESISTANCE 1-LIKE (PYL) represses protein phosphatase 2C (PP2C) upon ABA perception (*right*), which in turn activates SNF1-related protein kinase 2 (SnRK2) to phosphorylate (P) transcription factors downstream, such as basic leucine zipper protein (bZIP), leading to stress responses, including seed dormancy (Cutler et al., 2010). The ancestral ABA receptor pre-PYL (*middle*), which represses PP2C without requiring ABA, has been found in *Z. circumcarinatum* (Sun et al., 2019). This is interesting because it is exactly how DOG1 functions in seeds (*left*): DOG1 is a PP2C repressor independent of ABA (Nishimura et al., 2018). Thus, pre-PYL and DOG1 play similar roles in terms of enhancing stress responses without binding ABA. *Note that alternate mechanisms downstream of the DOG1 function have been predicted (Nonogaki, 2020). Photo (*Zygnema*): Feng et al. (2021), CC BY.

(*MeDOGLs*) of the same Zygnematophyceae (Fig. 3) (ME000109S10872 and ME000088S10108 in PhycoCosm; https://phycocosm.jgi.doe.gov/phycocosm/home). In *Arabidopsis* seeds, PYLs repress PP2C upon ABA perception and enhance ABA sensitivity, which results in dormancy (Cutler et al., 2010), while pre-PYL in *Zygnema* represses PP2C without requiring ABA (Sun et al., 2019) (Fig. 4). This is intriguing because it is exactly what DOG1 is doing in seeds; DOG1 is a PP2C repressor independent of ABA (Nishimura et al., 2018).

Although molecular function of non-flowering plant *DOGLs* is not known yet, possible concurrent emergence of the ancestral ABA receptor and *DOGL* in the algal sister lineage of land plants is interesting. It is the time when plants were 'landing' from an aqueous environment, consequently exposing themselves to diverse stresses, such as drought and UV irradiance (de Vries and Archibald, 2018; de Vries et al., 2018; Cheng et al., 2019). This window of terrestrial adaptation is where we can start to find the algal *pre-PYL* and *DOGL*. *Pre-PYL* later became an ABA receptor, which is an ABA-dependent PP2C repressor (Sun et al., 2019), while *DOGL* evolved to *DOG1*, an ABA-independent PP2C repressor (Nishiyama et al., 2021).

The timings of *pre-PYL* and *DOGL* emergence are similar; however, their evolutionary origins seem to be distinct. It has been proposed that *pre-PYL* originated from soil bacteria through horizontal gene transfer (Cheng et al., 2019) (Fig. 5). By contrast, *DOGLs* presumably evolved from the *TGACG motif-binding transcription factors* (*TGAs*) (Nishiyama et al., 2021), which can be found in *Klebsormidium nitens* (GAQ81419.1 and GAQ90893.1) and *Mesostigma viride* (Mv17328-RA, PhycoCosm), more ancestral algae than Zygnematophyceae (Fig. 5). Interestingly, *Klebsormidium* already has PP2C and SNF1-related kinase 2 (SnRK2) (Hori et al., 2014; Shinozawa et al., 2019), and *Mesostigma* has SnRK2 (de Vries et al., 2018). ABA might have been mediated by another type of receptor (?) in those ancestral algae. Alternatively, PP2C–SnRK2 antagonism could have been modulated by another ligand rather than ABA at ancient times. In any event, outstanding questions about *DOGLs* are: When did they become PP2C repressors? Is it only in flowering plants, or it was from much more ancient time of non-seed plants? Those are the questions to be addressed by future research through international collaboration in the global seed research community.

Algal genome analysis, which sounds somewhat immaterial to seed biology, could further advance our understanding about the history of the molecular mechanisms associated with seed maturation. Genome analysis of *Chara* (see Figs 3 and 5) indicates that the transcripts related to seed storage proteins, oleosins and LATE EMBRYOGENESIS ABANDUNT (LEA) proteins accumulate in its zygotes, which also germinate like seeds (after meiosis) (Nishiyama et al., 2018). Those proteins are induced by *DOGL4* in *Arabidopsis* seeds (Sall et al., 2019). *DOGLs* are not found in *Chara*; however, these results imply that the very origin of the molecular mechanisms driving seed maturation programmes, such as reserve accumulation and desiccation tolerance, dates back through the ancient time of algae.

Concerning dormancy, the roots of its molecular mechanism could go back even further through red algae, one of the oldest groups of algae. In the unicellular red alga *Cyanidioschyzon merolae*, stress-induced ABA causes growth arrest of the cell (Kobayashi et al., 2016) (Fig. 6), which is similar to dormancy in a sense. In this alga, which contains a single mitochondrion, a single chloroplast and the nucleus, ABA is likely produced in the chloroplast, while haeme, another signalling molecule, is probably produced in the mitochondrion (Watanabe et al., 2013; Kobayashi et al., 2016). These molecules are thought to play important roles for interorganelle communication and possibly retrograde signalling to the nucleus in the alga. A substantial volume of recent literature started to highlight the importance of intracellular signalling, including interorganelle communication and anterograde and retrograde signalling, in the seed cells for the regulation of dormancy and germination (summarized in Nonogaki, 2019). Therefore, it is crucial to go back through algae (and earlier organisms) and understand how mitochondrion and chloroplast started to live together in a cell and how they have established the well-orchestrated interaction with the nucleus. Thus, understanding even algal cell biology will be an integral part of seed biology in the future.

Integration of the outcomes of phylogenomic studies with experimental seed biology

While genomic information from non-flowering plants is useful to deduce the evolution of the molecular mechanism of seed maturation programmes, phylogenetic information of the actual seed genes, such as *DOG1*, *DOGL4* and *DOGL5/6* found in basal angiosperms (Nishiyama et al., 2021), could address important biological questions about seeds in a more direct manner. For example, the basal angiosperms' *DOG1* and *DOGL4* that were identified by phylogenomic studies can be used in genetic studies, including their heterologous expression in *Arabidopsis*. It is possible that *Nymphaea DOG1* rescues the non-dormancy phenotype of the *Arabidopsis dog1* mutants. Alternatively,

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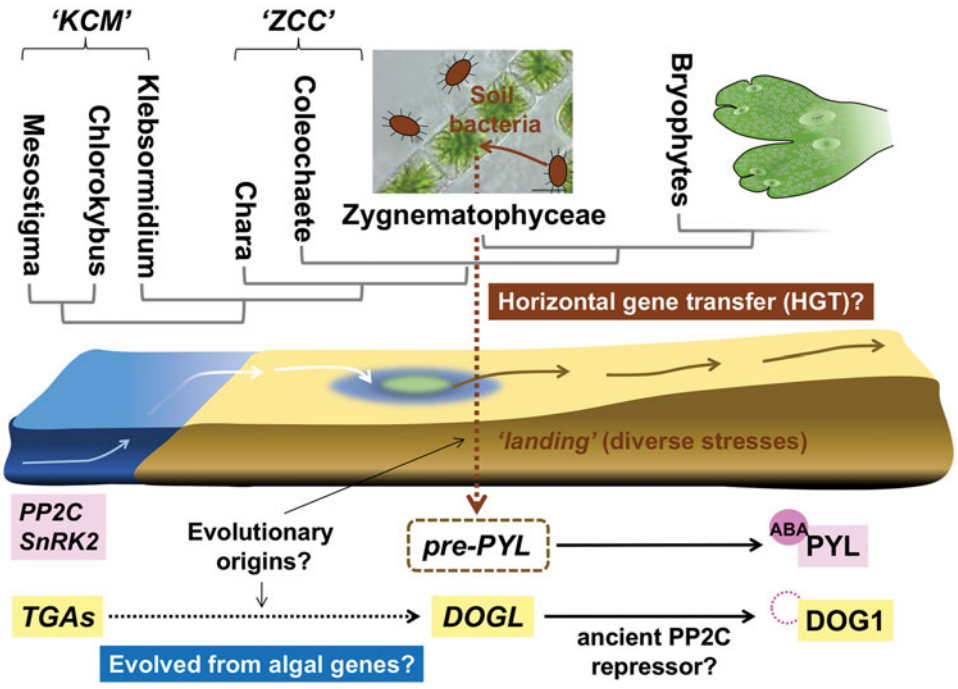


Fig. 5. Proposed distinct evolutionary origins of the two PP2C repressors *DOG1* and *pre-PYL*. The ancestral ABA receptor *pre-PYL* and ancestral *DOGL* seem to have emerged at the similar timings. This is the time when plants were 'landing' from water, exposing themselves to diverse stresses (de Vries and Archibald, 2018; Cheng et al., 2019). The window of terrestrial adaptation of plants is where we can start to find *pre-PYL* and *DOGL*. *pre-PYL* later became an ABA receptor (Sun et al., 2019), which is an ABA-dependent PP2C repressor, while *DOGL* evolved to *DOG1*, an ABA-independent PP2C repressor. *Pre-PYL* and *DOGL* emerged at similar timings; however, their evolutionary origins seem to be distinct. It has been proposed that *pre-PYL* originated in soil bacteria and were brought into plants through horizontal gene transfer (Cheng et al., 2019). By contrast, our analysis suggests that *DOGLs* have evolved from *TGAs* (Sall et al., 2019; Nishiyama et al., 2021; and this study), which we can find in *Klebsormidium* and *Mesostigma*, more ancestral algae than *Zygnema*. *Klebsormidium* has *PP2C* and *SnRK2* already (Hori et al., 2014; Shinozawa et al., 2019), and *Mesostigma* has *SnRK2* (de Vries et al., 2018). An outstanding question is: When did DOGL become a PP2C repressor? *KCM*: *Klebsormidium*, *Chlorokybus* and *Mesostigma*; PP2C, protein phosphatase 2C; pre-PYL, pre-PYRABACTIN RESISTANCE 1-LIKE; SnRK, SNF1-related protein kinase; *TGA*, *TGACG motif-binding transcription factor*; *ZCC*, *Zygnematophyceae*, *Coleochaete* and *Chara*. Photo (*Zygnema*): Feng et al. (2021), CC BY.

chemically induced expression of *Nymphaea DOGL4* in *Arabidopsis* seeds might upregulate seed storage protein, oleosin and *LEA* genes.

Instead of expressing the ancient genes in *Arabidopsis*, equally or even more exciting is to introduce the modern seed genes to basal angiosperms. Functional genomics using *Amborella* may not be practical; however, it has been proposed that *Nymphaea thermarum*, a smallest water lily, could be used as a model system for basal angiosperms (Povilus et al., 2015). Successful transformation of another *Nymphaea* species with *Agrobacterium* has also been reported (Yu et al., 2018). Therefore, it is feasible to test how the modern seed genes of eudicots and monocots affect the biology of early diverging angiosperms. These 'back-to-the-future' experiments are anticipated to produce very interesting results, possibly reconstituting key evolutionary events that might have happened during the history of seed plants.

Beside the evolution of the molecular mechanisms of seed maturation programmes, important evolutionary questions associated with seed formation, such as the origin and evolution of the endosperm, can also be investigated by the back-to-the-future experiments. For example, *Amborella* seeds have a well-developed triploid endosperm (Fogliani et al., 2017), while seeds of some *Nymphaea* species develop only a minute diploid endosperm, with a perisperm being the major storage tissue (Povilus et al., 2015). The *Arabidopsis* genes that have been identified for their function in nucellus (i.e. perisperm) development or degeneration (e.g. *TRANSPARENT TESTA16*; Xu et al., 2016) can be expressed in *Nymphaea* species. Their expression could alter the fate (expansion or degeneration) of the nucellus, hence the ratio of perisperm and endosperm volume in mature *Nymphaea* seeds, addressing important questions about a possible evolutionary transition of the replacement of the perisperm by the endosperm. Outcomes of those approaches could provide a convincing experimental proof for evolution, which is normally very difficult to acquire. Thus, phylogenomic studies of seeds can efficiently be integrated with experimental biology and could contribute back to the field of evolutionary biology.

Prospects

Phylogenomics offers promising tools to advance our understanding of seeds in both mechanistic and evolutionary aspects. Its contribution might not be limited to basic seed biology but could enhance applied aspects of seed science, possibly leading to technology development. Evolutionary pressure has selected seed traits advantageous for their adaptation and survival under natural conditions. By contrast, agriculture often takes advantage of seed traits that are not necessarily useful for plant survival or that are even against evolutionary pressure. A good example is a non-shattering (grain retention) phenotype, which blocks seed dispersal. From this point of view, some of the ancient seed traits might be useful for agriculture.

In the basal angiosperm *Hydatella inconspicua* (*Nymphaeales*) seeds that contain a perisperm as the major storage tissue, the

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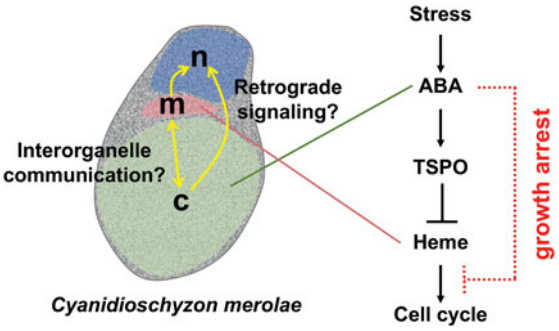


Fig. 6. Possible roots of dormancy-like ABA-induced growth arrest in the unicellular red alga. The ancient red alga *C. merolae* contains the nucleus (n), one mitochondrion (m) and one chloroplast (c). In this species, stress-induced ABA causes growth arrest of the cell by scavenging haeme, another signalling molecule, with tryptophan-rich sensory protein O (TSPO) (Kobayashi et al., 2016). ABA and haeme, which are probably produced by chloroplast and mitochondrion, respectively, are thought to be involved in interorganelle communication (Kobayashi et al., 2016) and possibly in retrograde signalling also. Intracellular signalling in the seed cells is also emerging as the key element of the germination and dormancy mechanisms (Nonogaki, 2019).

accumulation of starch in the perisperm is initiated even before fertilization, which is a gymnosperm tendency (Friedman, 2008). This ancient trait in early diverging angiosperms is probably wasteful in terms of resource allocation within a maternal plant and has been suppressed by evolutionary pressure, so that only successfully fertilized ovules are nourished as observed in the endosperm of many angiosperm species (Friedman, 2008). However, this fertilization-independent reserve accumulation might be useful for crop modification. If perisperm or endosperm development can be induced without fertilization in grain crops, especially when it is pre-programmed in a spontaneous manner (with a fertility restoration programme), more efficient and sustainable grain production can be established. Recurring issues of reduced yield of grain crops under heat and drought conditions, which are caused by unsuccessful fertilization due to those stresses, can be addressed by this approach bypassing the stress-sensitive stage.

Fertilization-independent embryo formation could also be possible if the origin, evolution and core mechanisms of apomixis are fully understood. There was an encouraging development in rice apomixis research recently (Khanday and Sundaresan, 2021). It might be sooner than we think when seed cloning of F-1 hybrid vegetables will also become possible, which could drastically change the architecture of global seed business. A better understanding of nucellus development, including its interaction with the integuments, might allow us to freely modify testa properties as well. For instance, if we could induce water- and gas-impermeable integuments (i.e. testa) typical of hard seeds, it will change common practice of seed storage and supply, because hard seeds could maintain their longevity without requiring specific warehouses or shipping packages while their germination can be induced by relatively simple scarification just before imbibition. Thus, more understanding of the evolution of developmental programmes of seed parts (testa, perisperm, endosperm and embryo) will offer opportunities of crop modification and seed business also.

While evolutionary studies are focused on past events, they could provide forward-looking perspectives for research and innovative ideas for technology development. Plants and seeds have performed a myriad of experiments over the course of evolution, probably with numerous failures from a fitness point of view, some of which can be revitalized for applied purposes as discussed above. Many of the experimental records of plants have probably been written in their genomes, including the ancient mechanisms, which might still be present in the genome but are just silenced. Those lost traits can be retrieved from plant genomes. Therefore, we should maximize the utility of plant genomes for future seed research and technology development. The potential of seed science is not limited to agricultural and pharmaceutical applications. Recently, 'seed-inspired microfliers', which can be equipped with electronic device to monitor environmental conditions, have been developed (Kim et al., 2021). Thus, seeds have unlimited potential and are the 'natural capital' (Mattana et al., 2021) for the 21st century.

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Conflicts of interest. None declared.

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