Different Sets of Post-Embryonic Development Genes Are Conserved or Lost in Two Caryophyllales Species (Reaumuria soongorica and Agriophyllum squarrosum)

Pengshan Zhao1,2*, Jiwei Zhang1,2, Xin Zhao1,2, Guoxiong Chen1,2, Xiao-Fei Ma1,2

1 Key Laboratory of Stress Physiology and Ecology in Cold and Arid Regions, Gansu Province, Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou, P.R. China, 2 Shapotou Desert Research & Experiment Station, Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou, P.R. China

* zhaopengshan@lzb.ac.cn

Abstract

Reaumuria soongorica and sand rice (Agriophyllum squarrosum) belong to the clade of Caryophyllales and are widely distributed in the desert regions of north China. Both plants have evolved many specific traits and adaptation strategies to cope with recurring environmental threats. However, the genetic basis that underpins their unique traits and adaptation remains unknown. In this study, the transcriptome data of R. soongorica and sand rice were compared with three other species with previously sequenced genomes (Arabidopsis thaliana, Oryza sativa, and Beta vulgaris). Four different gene sets were identified, namely, the genes conserved in both species, those lost in both species, those conserved in R. soongorica only, and those conserved in sand rice only. Gene ontology showed that post-embryonic development genes (PEDGs) were enriched in all gene sets, and different sets of PEDGs were conserved or lost in both the R. soongorica and sand rice genomes. Expression profiles of Arabidopsis orthologs further provided some clues to the function of the species-specific conserved PEDGs. Such orthologs included LEAFY PETIOLE, which could be a candidate gene involved in the development of branch priority in sand rice.

Introduction

Reaumuria soongorica and sand rice (Agriophyllum squarrosum) belong to the clade of Caryophyllales and are widely distributed in the arid regions of north China [1–3]. R. soongorica (2n = 22; genome size = 778 Mb) is a perennial xeric shrub and a constructive, dominant species populating the zonal landscape in desert ecosystems [1,4,5]. During adaptation to recurring environmental threats and continuing desertification, R. soongorica has evolved many specific traits and physiological changes, such as its extremely thick cuticle, hollow stomata, the presence of a salt gland, and accumulation of some low-molecular-weight metabolites [1,4,6].
Another remarkable characteristic of *R. soongorica* is resurrection. *R. soongorica* can enter temporal dormancy when water is limited but resumes its original active functions when water becomes available [6].

Sand rice (2n = 18; genome size = 714–758 Mb) is branched later than *R. soongorica* within Caryophyllales and is a pioneer annual psammophyte endemic to the mobile and semi-mobile sand dunes, which differ from the habitat of *R. soongorica* (Fig 1A and 1B; [3,7]). Sand rice has evolved many strategies to adapt to sand dune surface environment, including rapid root growth after germination, long hypocotyl, and pronounced drought and heat tolerance [3,7]. In the seedling stage, the shoot growth of sand rice assumes a striking pattern [7]. Two lateral branches emerge first, while the main stem is inhibited; the main stem then develops later with the second pair of branches (Fig 1C). This special shoot architecture, called branch priority, is crucial to survival against violent wind damage [7].

*R. soongorica* and sand rice possess unique phenotypic features and ecological adaptations, rendering them as models to investigate the evolution of stress response strategies and the genetic basis of important traits essential to survival in the harsh environment of the desert ecosystem. The transcriptomes of *R. soongorica* and sand rice have been assembled using Illumina sequencing [1,3]. Sets of candidate genes related to abiotic stress events or tolerance have

---

**Fig 1. Habitat and shoot architecture.** Habitat (A and B) of *R. soongorica* and sand rice in China; (C) the branch priority of sand rice.

doi:10.1371/journal.pone.0148034.g001
been identified previously through comparisons with the expression profiles of the orthologs in *Arabidopsis thaliana*, as well as digital gene expression profiling [3,4]. However, many of the fundamental questions, including those on speciation and the genetic basis for unique traits, remain open for study. Genome structure and evolution are crucial for plant phenotypic diversity and speciation [8,9]. Characterization of the orthologous gene composition among different species is a powerful strategy in analyzing gene conservation and loss during speciation and adaption to the habitat [10–14]. In the present study, gene conservation and loss in *R. soongorica* and sand rice were unraveled by comparing their proteins with those of three other sequenced plants: *A. thaliana*, *Oryza sativa* (rice), and *Beta vulgaris* (sugar beet). Gene ontology (GO) showed that post-embryonic development genes (PEDGs) were enriched in all four gene sets. The expression profiles of the *Arabidopsis* orthologs were further acquired to gain more insight into the function of the species-specific PEDGs.

**Materials and Methods**

**Orthologous gene clusters**

The protein sequences of *A. thaliana* and rice were downloaded from the TAIR10 release (www.arabidopsis.org) and Rice Genome Annotation Project (http://rice.plantbiology.msu.edu/). Information on sugar beet proteins was obtained from Dohm et al. [15] (http://bvseq.molgen.mpg.de/Genome/Download/RefBeet-1.1/). For *R. soongorica* and sand rice, unasigned from our two previous publications [1,3] were downloaded and the ORFs were analyzed using the Getorf program from both sides to obtain the protein sequence (http://emboss.sourceforge.net/apps/cvs/emboss/apps/getorf.html). Orthologous gene clusters were constructed according to the method of Golicz et al. [11]. In brief, the genes conserved among the five species (*A. thaliana*, *O. sativa*, *B. vulgaris*, *R. soongorica*, and *A. squarrosum*) were screened by obtaining the reciprocal best hit (RBH, Blastp program with an e-value < 1e-5) between *Arabidopsis* genes and each gene of the four other species. Orthologous genes were assigned into four types of Clusters, particularly, from 2 to 5, and each sub-cluster contained at least an *Arabidopsis* gene and one gene from the remaining species.

**Analysis of gene conservation and loss in *R. soongorica* and sand rice**

*B. vulgaris* is phylogenetically close to *R. soongorica* and sand rice within the Caryophyllales family [3]. To be strict, only the sub-clusters comprising at least three genes (one *Arabidopsis* gene, one rice ortholog, and one sugar beet gene) were used to identify the conserved and lost genes in *R. soongorica* and sand rice. In particular, 1,113 and 1,666 sub-clusters included the rice and sugar beet genes, respectively, in Cluster3. Only 560 overlapping sub-clusters included both rice and sugar beet genes.

**GO annotation**

The representative *Arabidopsis* gene in each identified sub-cluster was subjected to GO annotation using AgriGO with default setting [16]. The GO type was Plant GO slim. GO enrichment was analyzed using the hypergeometric test and corrected by Yekutieli (FDR under dependency). The enrichment thresholds of FDR were less than 0.01 in gene sets conserved and lost in *R. soongorica* and sand rice and those conserved only in *R. soongorica*. For sand rice-specific conserved gene set, the threshold of FDR was less than 0.05. The pairwise comparisons in different gene sets were done using the Student’s t-test.
Expression profile analysis
The Affymetrix GeneChip array data of global gene expression profiles during Arabidopsis seed development were downloaded from the NCBI GEO database (GSE680; [17]). The raw data were standardized by RMA with Genespring software (version 12.5, Agilent). Heat maps for the different sets of PEDGs were generated using Multi-Experiment viewer software (MeV, version 4.8.1) with unsupervised hierarchical clustering analysis.

Results
Identification of the genes conserved or lost in R. soongorica and sand rice
Four types of Clusters (2–5) were constructed, and a total of 16,416 sub-clusters were identified (Fig 2). In Cluster2, each sub-cluster contained only two genes: one from Arabidopsis and another from the remaining four species. To be strict and logical, Cluster2 was not included in the screening of conserved and lost genes. Sugar beet is a representative species of the Caryophyllales family, and it has emerged after R. soongorica but before sand rice speciation [3,15]. The recently assembled genome of sugar beet could shed more light on the genome evolution of R. soongorica and sand rice. The sub-clusters comprising at least three genes from Arabidopsis, rice, and sugar beet were then analyzed. In Cluster5, all sub-clusters (5,441) included five genes, representing one ortholog from each five species. In Cluster3, 1,113 and 1,666 sub-clusters contained one rice ortholog and one sugar beet gene, respectively. The number of shared sub-clusters containing both rice and sugar beet genes was 560. Therefore, 5,441 genes were conserved and 560 genes were lost in both R. soongorica and sand rice, as compared with the three remaining species (A. thaliana, O. sativa, and B. vulgaris).

In Cluster4, each sub-cluster contained four genes from four different species (Fig 2). Among these sub-clusters, 2,935 and 3,688 included the rice and sugar beet orthologous genes, respectively. A total of 2,635 shared sub-clusters were found to contain only one ortholog from R. soongorica or sand rice. Detailed analysis identified the sets of species-specific conserved and lost genes. A total of 1912 genes were conserved in R. soongorica but lost in sand rice, whereas 723 genes were conserved in sand rice but lost in R. soongorica.

Characteristics of the different sets of conserved and lost genes
The protein length, protein identities with the Arabidopsis orthologs, and transcript GC contents of the genes in each conserved or lost sub-cluster were characterized in detail (Figs 3 and 4). For the 5,441 genes conserved in both R. soongorica and sand rice, the protein lengths in R. soongorica and sand rice were significantly shorter than those in Arabidopsis and sugar beet (Fig 3). Unexpectedly, the average protein sequence identity with the Arabidopsis orthologous protein was 63.45% in sand rice, which was even lower than that in rice. The mean GC content of the rice transcripts (54.61%) was the highest among the five species. Although the GC ratios ranged from 43.46% to 44.88%, pairwise tests showed marked differences among the remaining four species ($p < 0.01, S1 Table$). For the 560 genes lost in both R. soongorica and sand rice, similar patterns were found in the protein identities and GC contents, although only the proteins from three species were included in each sub-cluster of this set (Fig 3). The protein lengths of the 560 genes from Arabidopsis, rice, and sugar beet were relatively similar ($p > 0.05$), which differed from the situation in the gene set conserved in both R. soongorica and sand rice.

In the species-specific conserved or lost gene sets (Fig 4), the protein lengths in R. soongorica ($p < 0.01$) and sand rice ($p < 0.05$) were shorter compared with those in the other three species.
The protein identities of *R. soongorica* and sand rice with *Arabidopsis* proteins showed no difference from that of sugar beet in the 1912 (*p* = 0.23) and 723 gene sets (*p* = 0.41), respectively, which were consistent with their phylogenetic relationship [3]. The GC contents resembled the results of 5441 and 560 gene sets, except for the comparison between the *R. soongorica* and *Arabidopsis* genes in the 1912 gene set (*p* = 0.26).

![Gene conservation and loss in two desert plants](https://example.com/fig2)

**Fig 2.** Genes conserved and lost in *R. soongorica* and sand rice. (A) Four kinds of Clusters with different numbers of orthologs are showed. In particular, 4470 sub-clusters were assigned into Cluster2, of which 888 sub-clusters contained the *A. thaliana* and *O. sativa* genes; (B-C) A total of 5,441 genes were conserved and 560 genes were lost in both *R. soongorica* and sand rice. Meanwhile, 1912 genes were conserved in *R. soongorica* but lost in sand rice, whereas 723 genes were conserved in sand rice but lost in *R. soongorica*.

![Gene characteristics](https://example.com/fig3)

**Fig 3.** Characteristics of the conserved (5441 genes) and lost (560 genes) gene sets common to both *R. soongorica* and sand rice. At, *A. thaliana*; Os, *O. sativa*; Bv, *B. vulgaris*; Rs, *R. soongorica*; As, *A. squarrosum*. 

![Gene characteristics](https://example.com/fig3)
GO annotations of the different sets of conserved and lost genes

To gain more insight into the functions of the genes clustered in the different sets, the representative Arabidopsis ortholog in each sub-cluster was subjected to GO term enrichment using the AgriGO program [16]. A total of 91 GO terms were strongly enriched among all gene sets. In the gene set conserved in both R. soongorica and sand rice, 37 terms were overrepresented in biological process, 12 in molecular functions, and 36 in cellular component categories \( (p < 0.01) \). The GO categories “post-embryonic development”, “catalytic activity”, and “intracellular” were the most enriched (Fig 5A and S1 Fig). By narrowing the GO enrichment terms into the biological process category, “post-embryonic development” was identified to be shared among common and species-specific conserved and lost gene sets (Figs 5 and 6). These results demonstrated that the different sets of genes involved in post-embryonic development were conserved during the speciation and adaptation of R. soongorica and sand rice.

Expression profiles of Arabidopsis post-embryonic development orthologs during seed development

In this study, 287 common conserved, 26 common lost, 70 R. soongorica-, and 40 sand rice-specific conserved PEDGs were identified (S2 Table). To gain further insight into their expression profiles during seed development, GEO data GSE680 [17] were reanalyzed using GeneSpring software and hierarchical clustering of gene expression signal intensities was conducted to generate a heat map. We opted to focus on the unique phenotypic feature, so only the species-specific conserved and lost genes were illustrated, whereas the expression profiles of the common conserved and lost PEDGs are shown in S2 and S3 Figs. A total of 64 out of 70 R. soongorica-specific conserved PEDGs were found with specific probes in GSE680. Twenty-eight genes (i.e., TITAN 9 [TTN9], ARGONAUTE 1 [AGO1], and TERMINAL FLOWER 2 [TFL2]) showed high expression in the early stages of seed development, such as in the

Fig 4. Characteristics of the species-specific conserved and lost gene sets. A total of 1912 genes were conserved in R. soongorica but lost in sand rice, whereas 723 genes were conserved in sand rice but lost in R. soongorica.

doi:10.1371/journal.pone.0148034.g004
unfertilized ovules and seeds containing zygotes (24-Hr Seed), and they were down-regulated in the seedling, rosette leaf, and stem (Fig 7). STEROL METHYLTRANSFERASE 1 (SMT1), FERRITIN 4 (ATFER4), VERNALIZATION INSENSITIVE 3-LIKE 1 (VEL1), ASPARTATE AMINOTRANSFERASE (AAT), EMBRYONIC FACTOR 1 (FAC1), ASCORBATE PEROXIDASE 1 (APX1), and AT2G44060 showed reduced expression levels, whereas RADICAL-INDUCED CELL DEATH 1 (RCD1), CULLIN 1 (ATCUL1), small ubiquitin-related modifier (SUMO) E3 ligase SIZ1 exhibited high expression levels in post mature green seed. In particular, SEPALLATA 3 (SEP3) was up-regulated in the floral bud, ovule, zygote, globular stage and
cotyledon stage seed. **ARABIDOPSIS THALIANA SEED GENE 1 (ATS1)** only exhibited high expression levels in mature and post mature green seed.

For the 40 sand rice-specific conserved PEDGs, 36 genes with corresponding probes were extracted; the resulting heat map exhibited a diverse expression pattern (Fig 8). Four genes (\texttt{AT1G32560}, \texttt{1-CYSTEINE PEROXIREDOXIN 1 [ATPER1]}, \texttt{AT3G22490}, \texttt{EARLY METHIONINE-LABELLED 6 [EM6/GEA6]}) showed high expression levels in mature and post mature green seeds but little signals in other tissues. These findings were consistent with their function as late embryogenesis abundant proteins (LEAs), except for \texttt{ATPER1}. \texttt{ATMYB5}, which is involved in seed coat formation, mucilage synthesis, and trichome branching [18], showed high expression from the zygote to the post mature green seed. Our unpublished data showed that branch formation was initiated in three-day-old sand rice seedlings. Therefore, the expression profile in three-day-old seedling after imbibition should provide some clues to the genetic base of branch priority. In 36 sand rice PEDGs, **TOO MANY MOUTHS (TMM)**, **LEAFY PETIOLE (LEP)**, **EMBRYO DEFECTIVE 1865 (EMB1865)**, **PHYTOCHROME INTERACTING FACTOR 3-LIKE 5 (PIL5)** exhibited high expression levels, whereas **DICER-LIKE 4 (DCL4)** exhibited low expression levels in seedlings.

**Discussion**

Caryophyllales species comprise approximately 6% diversity of the angiosperm species, and they are known for their extraordinary variety in growth forms and ecological adaptations [19]. \textit{R. soongorica} and sand rice are located at different niches and show repeated adaptation to recurring or multiple environmental stresses in the desert ecosystem. Combined with unique phenotypic features, these two species under the order of Caryophyllales are noteworthy and merit the investigation of their gene and genome evolution. The published transcriptomes of \textit{R. soongorica} and sand rice paved the way for genome-wide evolution analysis [1,3]. In the present report, gene conservation and loss were dissected by comparisons with the well-annotated **Arabidopsis** genome, and the monocot species \textit{O. sativa} was also included to strictly cluster orthologous genes. Moreover, only the sub-cluster that contained the \textit{B. vulgaris} ortholog was used to identify the conserved or lost genes because of its phylogenetic relationships with \textit{R. soongorica} and sand rice [3]. Notably, the newly evolved genes fall out of the scope of the approach used in this report.
GC content is suggested to play a crucial role in genome function and species ecology [20]. Studies on the genomic composition, especially for non-model plants, which accounts for a large proportion of angiosperm, will enable us to deepen the existing knowledge on the relationship between genomic architecture and organization and adaptations to different...
An extensive survey of genomic composition across 239 monocot species demonstrated a strong association between variations in GC content and ecological relevance. Higher GC content is significantly associated with ecological distribution and increased tolerance to temperature extremes in monocot species. In our four conserved and lost gene sets, the GC contents of the rice genes were obviously higher than those of the genes from the other species. This finding was consistent with previous finding that of the Poaceae species, which hold the highest GC contents among land plants. However, a similar association between GC content and climate variations was not found in this study. The GC contents of the *R. soongorica* and sand rice genes clustered in our sets were even lower than those of the *Arabidopsis* genes. This result was due to at least two reasons. First, transcriptome data were used, from which unigenes could be partially assembled. As shown in Figs 3 and 4, the protein lengths of the *R. soongorica* and sand rice genes were significantly lower than those of the *Arabidopsis* genes. An extensive survey of genomic composition across 239 monocot species demonstrated a strong association between variations in GC content and ecological relevance. Higher GC content is significantly associated with ecological distribution and increased tolerance to temperature extremes in monocot species. In our four conserved and lost gene sets, the GC contents of the rice genes were obviously higher than those of the genes from the other species. This finding was consistent with previous finding that of the Poaceae species, which hold the highest GC contents among land plants. However, a similar association between GC content and climate variations was not found in this study. The GC contents of the *R. soongorica* and sand rice genes clustered in our sets were even lower than those of the *Arabidopsis* genes. This result was due to at least two reasons. First, transcriptome data were used, from which unigenes could be partially assembled. As shown in Figs 3 and 4, the protein lengths of the *R. soongorica* and sand rice genes were significantly lower than those of the *Arabidopsis* genes.
shorter than those of the other three plants with sequenced genomes. Constructing draft genomes for these two species in the future would resolve this issue precisely. Second, the possibility that a different association exists in dicots cannot be ruled out. A large-scale survey of GC content across a vast majority of dicot species is necessary to test the relationship between genomic composition and ecological adaptations to various environments.

Desiccation tolerance in vegetative tissues of resurrection plants also occurs in pollen grains and orthodox seeds, but not in recalcitrant seeds, which exhibit sensitivity to water loss and only can survive for a short period [21–24]. Large scale transcriptome profiling of dehydration and rehydration tissues of different resurrection plants has shown that many core dehydration-related genes are shared with the orthodox seeds, but their expression patterns are differed from those in the desiccation-sensitive species, namely the recalcitrant seeds [21,25–30]. A recent genomic analysis of a resurrection plant Boea hygrometrica did not identify any genome structure specific for desiccation tolerance [30]. This evidence further supports the statement that vegetative desiccation tolerance employs the preexisting genetic elements but alters their expression patterns to provide more effective protection in resurrection plants [21,29,30]. In the present study, 5441 genes were shared among resurrection plant R. soongorica and other four species (Fig 2). GO annotation revealed that 37 biological process terms were overrepresented (p < 0.01; Fig 5). Some GO terms, such as photosynthesis, carbohydrate metabolic process, nitrogen metabolic, lipid metabolic, and response to stress, were also enriched in published transcriptomes of resurrection plants [21,27,29,30]. Eleven GO terms were overlapped with the desiccation tolerance associated transcriptome in Arabidopsis seeds [26]. Moreover, we found that 168 R. soongorica transcripts out of 5441 genes show differential expression patterns in drought-treated transcriptome [4]. These results demonstrated that desiccation tolerance mechanisms similar to those of resurrection plants and seeds are employed by R. soongorica and sand rice to survival against water shortage in desert ecosystems.

In all four gene sets, the biological process term “post-embryonic development” was overrepresented (p < 0.01; Figs 5 and 6). A total of 264 common conserved, 24 common lost, 64 R. soongorica-, and 36 sand rice-specific conserved PEDGs were found, of which each Arabidopsis ortholog has a specific ATH1 probe. A diverse expression pattern was found in all four Arabidopsis PEDG sets during seed development (Figs 7 and 8 and S2 Fig). By re-analyzing the cellular localization and molecular function of species-specific PEDGs, we found that the R. soongorica genes were mostly located in the nucleus (p = 3e-06) and cytosol (p = 6e-05) and functioned through protein binding (p = 3.5e-15). By contrast, the sand rice genes were enriched in the nucleus (p = 0.00097) and involved in DNA binding (p = 1.2e-06). Out of 64 R. soongorica-specific conserved PEDGs, three well-known genes showed high expression levels in post mature green seed (Fig 7). RCD1 contains a poly(ADP-ribose) polymerase domain and a WWE protein-protein interaction domain and is involved in abscisic acid (ABA), ethylene, and jasmonate signaling and the regulation of many stress-responsive genes [31–33]. ATCUL1 is an essential component of ubiquitin ligase complex in mediating protein degradation and plays a critical role in diverse cellular processes [34–39]. In Arabidopsis, SIZ1 mediated SUMO modification is involved in the regulation of several stress response, such as ABA signaling, phosphate deficiency response, and drought tolerance [40–42]. These results indicated that the core genetic modules implicated in environmental adaptation are conserved during the speciation and evolution of R. soongorica.

Dehydration-induced accumulation of LEA transcripts and proteins is a shared response in desiccation tolerance and desiccation sensitive plants [21,23,24,43]. Among the 36 sand rice-specific conserved PEDGs (Fig 8), three LEA genes exhibited high expression levels in mature and post mature green seeds. These results lead to the hypothesis that some LEA genes are specifically selected to mediate the acquisition of vegetative dehydration tolerance in sand rice.
Five PEDG genes (TMM, LEP, EMB1865, PIL5, and DCL4) showed evidently up- or down-regulated patterns in the seedling than in the other stages. In Arabidopsis, LEP mutation results in loss of leaf petiole and aberrant inflorescence branching and silique shape [44,45]. Thus, LEP should be considered as a possible candidate gene involved in the regulation of branch priority in sand rice. The detection of its expression profiles during seed development and germination may provide more evidence for its precise function. Meanwhile, DCL4 is essential for small RNA processing [46], and it is down-regulated in seedlings. Although no direct evidence is available on the involvement of DCL4 in Arabidopsis branching, the role of small RNA should be considered when elucidating the genetic base of branch priority.

Supporting Information

S1 Fig. GO annotation of the 5441 conserved genes common to both R. soongorica and sand rice.
(TIF)

S2 Fig. Expression profiles of the common conserved Arabidopsis PEDG orthologs during seed development. A total of 287 PEDGs were identified to be conserved to both R. soongorica and sand rice. A total of 264 corresponding Arabidopsis genes showed specific probe on the microarray.
(TIF)

S3 Fig. Expression profiles of the common lost Arabidopsis PEDG orthologs during seed development. A total of 26 PEDGs were identified to be lost to both R. soongorica and sand rice. A total of 24 corresponding Arabidopsis genes showed specific probe on the microarray.
(TIF)

S1 Table. Detailed p values of the pairwise t test.
(DOCX)

S2 Table. Lists of PEDGs in four different gene sets.
(XLSX)

Acknowledgments
We thank Prof. Yubin Liu for her kind offer of drought transcriptome dataset of R. soongorica.

Author Contributions
Conceived and designed the experiments: PZ. Performed the experiments: PZ JZ. Analyzed the data: PZ. Contributed reagents/materials/analysis tools: JZ XZ GC XFM. Wrote the paper: PZ. Revised the manuscript: PZ GC. Wild survey: PZ JZ XZ GC XFM.

References
1. Shi Y, Yan X, Zhao P, Yin H, Zhao X, Xiao H, et al. Transcriptomic Analysis of a Tertiary Relict Plant, Extreme Xerophyte Reaumuria soongorica to Identify Genes Related to Drought Adaptation. Plos One. 2013; 8: e63993. doi: 10.1371/journal.pone.0063993 PMID: 23717523

2. Yin H, Yan X, Shi Y, Qian C, Li Z, Zhang W, et al. The role of East Asian monsoon system in shaping population divergence and dynamics of a constructive desert shrub Reaumuria soongarica. Sci Rep-UK. 2015; 5: 15823.

3. Zhao P, Capella-Gutierrez S, Shi Y, Zhao X, Chen G, Gabaldon T, et al. Transcriptomic analysis of a psammophyte food crop, sand rice (Agriophyllum squarrosum) and identification of candidate genes essential for sand dune adaptation. BMC Genomics. 2014; 15: 872. doi: 10.1186/1471-2164-15-872 PMID: 25287394
4. Liu Y, Liu M, Li X, Cao B, Ma X. Identification of differentially expressed genes in leaf of Reaumuria soongorica under PEG-induced drought stress by digital gene expression profiling. PLoS One. 2014; 9: e94277. doi: 10.1371/journal.pone.0094277 PMID: 24736242

5. Wang X, Zhang T, Wen Z, Xiao H, Yang Z, Chen G, et al. The chromosome number, karyotype and genome size of the desert plant diploid Reaumuria soongorica (Pall.) Maxim. Plant Cell Rep. 2011; 30: 955–964. doi: 10.1007/s00238-011-1020-3 PMID: 21327391

6. Liu YB, Wang G, Liu J, Zhao X, Tan HJ, Li XR. Anatomical, morphological and metabolic acclimation in the resurrection plant Reaumuria soongorica during dehydration and rehydration. J Arid Environ. 2007; 70: 183–194.

7. Chen G, Zhao J, Zhao X, Zhao P, Duan R, Nevo E, et al. A psammophyte Agriophyllum squarrosum (L.) Moq.: a potential food crop. Genet Res Crop Ev. 2014; 61: 669–676.

8. Amborella Genome P. The Amborella genome and the evolution of flowering plants. Science. 2013; 342: 1240899. doi: 10.1126/science.1240899 PMID: 24357323

9. Carretero-Paulet L, Chang TH, Librado P, Herrera-Estrella L, Rozas J, et al. Genome-wide survey of adaptive molecular evolution in the carnivorous plant Utricularia gibba. Genome Biol Evol. 2015; 7: 444–456. doi: 10.1093/gbe/evu288 PMID: 25577200

10. Davidson RM, Gowda M, Moghe G, Lin H, Vaillancourt B, Shiu SH, et al. Comparative transcriptomics of three Poaceae species reveals patterns of gene expression evolution. Plant J. 2012; 71: 492–502. doi: 10.1111/j.1365-313X.2012.05005.x PMID: 22443345

11. Golicz AA, Schliep M, Lee HT, Larkum AW, Dolferus R, Batley J, et al. Genome-wide survey of the seagrass Zostera muelleri suggests evolution of the ethylene signalling network. J Exp Bot. 2015; 66: 1489–1498. doi: 10.1093/jxb/eru510 PMID: 25563969

12. Ma T, Wang J, Zhou G, Yue Z, Hu Q, Chen Y, et al. Genomic insights into salt adaptation in a desert poplar. Nat Commun. 2013; 4: 2797. doi: 10.1038/ncomms3797 PMID: 24256998

13. Vigeland MD, Spannagl M, Asp T, Paina C, Rudi H, Rognli OA, et al. Evidence for adaptive evolution of low-temperature stress response genes in a Pooidae grass ancestor. New Phytol. 2013; 199: 1060–1068. doi: 10.1111/nph.12337 PMID: 23701123

14. Zhao Y, Tang L, Li Z, Jin J, Luo J, Gao G. Identification and analysis of unitary loss of long-established protein-coding genes in Poaceae shows evidences for biased gene loss and putatively functional transcription of relics. BMC Evol Biol. 2015; 15: 66. doi: 10.1186/s12862-015-0345-x PMID: 25927997

15. Dohm JC, Minoche AE, Holtgrawe D, Capella-Gutierrez S, Zakrzewski F, Tafer H, et al. The genome of the recently domesticated crop plant sugar beet (Beta vulgaris). Nature. 2014; 505: 546–549. doi: 10.1038/nature12817 PMID: 24352233

16. Du Z, Zhou X, Ling Y, Zhang Z, Su Z. agriGO: a GO analysis toolkit for the agricultural community. Nucleic Acids Res. 2010; 38: W64–W70. doi: 10.1093/nar/gkq130 PMID: 20435677

17. Le BH, Cheng C, Bui AQ, Wagmaister JA, Henry PF, Pelletier J, et al. Global analysis of gene activity during Arabidopsis seed development and identification of seed-specific transcription factors. Proc Natl Acad Sci U S A. 2010; 107: 8063–8070. doi: 10.1073/pnas.1003530107 PMID: 20385809

18. Li SF, Milliken ON, Pham H, Seyit R, Napoli R, Preston J, et al. The Arabidopsis MYB Transcription Factor Regulates Muclilage Synthesis, Seed Coat Development, and Trichome Morphogenesis. Plant Cell. 2009; 21: 72–89. doi: 10.1105/tpc.108.063503 PMID: 19136646

19. Yang Y, Moore MJ, Brockington SF, Solts DE, Wong GK, Carpenter EJ, et al. Dissecting Molecular Evolution in the Highly Diverse Plant Cland Caryophyllalles Using Transcriptome Sequencing. Mol Biol Evol. 2015; 32: 2001–2014. doi: 10.1093/molbev/msv081 PMID: 25837578

20. Smarda P, Bures P, Horova L, Leprince O, Buitink J. Desiccation tolerance: From genomics to the field. Plant Sci. 2010; 179: 554–564.

21. Gechev TS, Benina M, Obata T, Tohge T, Sujeeth N, Minkov I, et al. Molecular mechanisms of desiccation tolerance in the resurrection glacial relic Haberlea rhodopensis. Cell Mol Life Sci. 2013; 70: 689–709. doi: 10.1007/s00018-012-1155-6 PMID: 22996258
26. Maia J, Dekkers BJW, Provan NJ, Liljekvist W, Hilhorst HWM. The Re-Establishment of Desiccation Tolerance in Germinated Arabidopsis thaliana Seeds and Its Associated Transcriptome. Plos One. 2011; 6: e29123. doi: 10.1371/journal.pone.0029123 PMID: 22195004

27. Oliver MJ, Dowd SE, Zaragoza J, Maqut SA, Payton PR. The rehydration transcriptome of the desiccation-tolerant bryophyte Tortula ruralis: transcript classification and analysis. BMC Genomics. 2004; 5: 89. PMID: 15546846

28. Oliver MJ, Guo L, Alexander DC, Ryals JA, Wone BW, Cushman JC. Sister group contrast using untargeted global metabolomic analysis delineates the biochemical regulation underlying desiccation tolerance in Sporobolus stapfianus. Plant Cell. 2011; 23: 1231–1248. doi: 10.1105/tpc.110.082800 PMID: 21467579

29. Rodríguez MC, Edsgard D, Hussain SS, Alquezar D, Rasmussen M, Gilbert T, et al. Transcriptomes of the desiccation-tolerant resurrection plant Craterostigma plantagineum. Plant J. 2010; 63: 212–228. doi: 10.1111/j.1365-313X.2010.04243.x PMID: 20444235

30. Xiao L, Yang G, Zhang L, Yang X, Zhao S, Ji Z, et al. The resurrection genome of Boea hygrometrica: A blueprint for survival of dehydration. Proc Natl Acad Sci U S A. 2015; 112: 5833–5837. doi: 10.1073/pnas.1505811112 PMID: 25902549

31. Ahlfors R, Lang S, Overmyer K, Jaspers P, Brosche M, Tuorainen A, et al. Arabidopsis RADICAL-INDUCED CELL DEATH1 belongs to the WWE protein-protein interaction domain protein family and modulates abscisic acid, ethylene, and methyl jasmonate responses. Plant Cell. 2004; 16: 1925–1937. PMID: 15208934

32. Teotia S, Lamb RS. The paralogous genes RADICAL-INDUCED CELL DEATH1 and SIMILAR TO RCD ONE1 have partially redundant functions during Arabidopsis development. Plant Physiol. 2009; 151: 180–198. doi: 10.1104/pp.109.142786 PMID: 19625634

33. Vainonen JP, Jaspers P, Wyczaczek M, Lamminmaki A, Reddy RA, Vahtera L, et al. RCD1-DREB2A interaction in leaf senescence and stress responses in Arabidopsis thaliana. Biochem J. 2012; 442: 573–581. doi: 10.1042/Bjc20111739 PMID: 22150398

34. Azevedo C, Sadanandom A, Kitagawa K, Freialdenhoven A, Shirasu K, Schulze-Lefert P. The RAR1 AP2 transcription factor, LEAFY PETIOLE, in gibberellin-induced germination is revealed by the misexpression of a homologous gene, SOB2/DRN-LIKE. Plant Cell. 2006; 18: 29–40. PMID: 16339853

35. Harmon F, Imaizumi T, Gray WM. CUL1 regulates TOC1 protein stability in the Arabidopsis circadian clock. Plant J. 2008; 55: 568–579. doi: 10.1111/j.1365-313X.2008.03527.x PMID: 18433436

36. Moon J, Zhao Y, Dai X, Zhang W, Gray WM, Huq E, et al. A new CULLIN 1 mutant has altered responses to hormones and light in Arabidopsis. Plant Physiol. 2007; 143: 684–696. PMID: 17158585

37. Xu LH, Liu FQ, Lechner E, Genschik P, Crosby WL, Ma H, et al. The SCFCO1 ubiquitin-ligase complexes are required for jasmonate response in Arabidopsis. Plant Cell. 2002; 14: 1919–1935. PMID: 12172031

38. Zhang Y, Xu W, Li Z, Deng XW, Wu W, Xue Y. F-Box Protein DOR Functions As a Novel Inhibitory Factor for Abscisic Acid-Induced Stomatal Closure under Drought Stress in Arabidopsis. Plant Physiol. 2008; 148: 2121–2133. doi: 10.1104/pp.108.126912 PMID: 18835996

39. Catala R, Ouyang J, Abreu IA, Hu Y, Seo H, Zhang X, et al. The Arabidopsis E3 SUMO ligase SIPI regulates plant growth and drought responses. Plant Cell. 2007; 19: 2952–2966. PMID: 17905899

40. Miura K, Lee J, Jin JB, Yoo CY, Miura T, Hasegawa PM. Sumoylation of ABI5 by the Arabidopsis SUMO E3 ligase SIPI negatively regulates abscisic acid signaling. Proc Natl Acad Sci U S A. 2009; 106: 5418–5423. doi: 10.1073/pnas.081088109 PMID: 19276109

41. Miura K, Rus A, Sharkhau A, Yokoi S, Karthikeyan AS, Rahghothinga KG, et al. The Arabidopsis SUMO E3 ligase SIPI controls phosphate deficiency responses. Proc Natl Acad Sci U S A. 2005; 102: 7760–7765. PMID: 15894620

42. Cushman JC, Bohnert HJ. Genomic approaches to plant stress tolerance. Curr Opin Plant Biol. 2000; 3: 117–124. PMID: 10712956

43. van der Graaff E, Den Dulk-Ras A, Hooiakos PJJ, Keller B. Activation tagging of the LEAFY PETIOLE gene affects leaf petiole development in Arabidopsis thaliana. Development. 2000; 127: 4971–4980. PMID: 11044410

44. Ward JM, Smith AM, Shah PK, Galanti SE, Yi HK, Demianski AJ, et al. A new role for the Arabidopsis AP2 transcription factor, LEAFY PETIOLE, in gibberellin-induced germination is revealed by the misexpression of a homologous gene, SOB2/DRN-LIKE. Plant Cell. 2006; 18: 29–39. PMID: 16339853

45. Parent J-S, Bouteiller N, Elmayan T, Vaucheret H. Respective contributions of Arabidopsis DCL2 and DCL4 to RNA silencing. Plant J. 2015; 81: 223–232. doi: 10.1111/tpj.12720 PMID: 25376953