Genome-wide in silico identification of phospholipase D (PLD) gene family from Corchorus capsularis and Corchorus olitorius: reveals their responses to plant stress

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Abstract

**Background:** Plant grows in nature facing various types of abiotic stresses for their normal growth and development. During abiotic stress, plants evolve different types of mechanisms to survive in a hostile environment. Phospholipase D (PLD) plays important role in the regulation of diverse cellular processes including stress responses in plants. Member of PLD genes are well studied in different model plants; however, their functions in the jute are not clear yet.

**Result:** In the present study, a total of 12 and 11 PLD genes were identified in the genome of *C. capsularis* and *C. olitorius*, respectively. The presence of the two conserved HKD motifs in PLD genes except for *CoPLDδ-*2 in jute suggests their strong lipase activity. Twenty different motifs were found in the identified PLD genes, and PLD-β1, PLD-γ1, and all members of PLD-δ1 of both jute species contained the highest number of motifs. Phylogenetic analysis showed the close evolutionary relationship among the five groups of jute PLD proteins along with the PLD proteins from *Arabidopsis*. Tissue-specific expression pattern of PLDα1-2, PLD-α2, PLDβ1, PLDγ1, and PLDδ1 of two jute species suggested their involvement in plant growth and development. However, the expression pattern of PLDα1-2, PLDα1-3, PLDδ1, and PLDδ3 indicated their association during waterlogging stress. In addition, PLD-α2, PLDβ1, and PLDδ2 seemed to be involved in drought stress as well as salinity stress.

**Conclusion:** This genome-wide identification of jute PLD genes from *C. capsularis* and *C. olitorius* will help to further functional characterization of the PLD genes for developing stress-tolerant jute variety.

**Keywords:** Phospholipase D, Jute, Plant growth, Gene expression and abiotic stress

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**Background**

Plants grow in nature where they are constantly facing abiotic and biotic stresses during their growth and development. They need to adjust themselves in nature by adopting the surrounding changes for their survival and it is also crucial to prevent cellular damage [1]. Environmental stresses (abiotic stress) in plants are minimized by several mechanisms including lipid signaling pathway and higher plants respond instantly to overcome the abiotic stresses by the modifications in their cellular process [2, 3]. Phospholipids are secondary messenger in lipid signaling pathway, produced immediately and transiently response in various stresses by the activation of phospholipases or lipid kinases [4].

Phospholipase D (PLD) proteins are member of the lipid signaling pathway that hydrolyzes the bonds of phospholipids for generating the phosphatidic acids (PA) with a free head group choline [5–7]. All eukaryotic PLDs were categorized into three subfamilies (C2-PLD, PX-PH-PLD, and SP-PLD) where C2-PLD subfamily...
regulates Ca$^{2+}$-dependent while both PX (phox cen-
sequence) and PH (pleckstrin homology) control Ca$^{2+}$-
independent activity [8, 9]. In addition, members of the
SP-PLD subfamily contain a signal peptide in its N-
terminus [10]. Biochemical studies identified an N-
terminal phospholipid-binding sequence and two catalytic
HKD (HxKxxxxD) motifs for lipase activity in the mem-
bers of PLDs of all eukaryotic organisms [11].

PLDs have been shown to involve in plant growth and
developmental processes under both abiotic and biotic
stress [12, 13]. In Arabidopsis, PLDα1 has been shown
responsible for PLD activity which stimulated accumu-
lation of ABA and JA in wounding of plants, and also
involved in stomatal closure during drought stress [14,
15]. In Oryza sativa, PLDβ1 gene was reported to be
responsible for seed germination by stimulating ABA
signaling pathway as well as protect plant from micro-
bial attack [16]. The first complementary DNA (cDNA)
of PLD was cloned in 1994 from castor bean; since then,
many PLD proteins were identified from different plants
[17]. Recent advances in genome sequencing facility have
given an opportunity to dissect the member of PLD genes
at the genomic level from any organism. However, the
PLD protein family of many organisms including jute has
not been studied yet.

Jute is an important natural phloem fiber producing
plant with its vegetable properties [18], and contributes
the national economy of Bangladesh by earning foreign
currency [19, 20]. The quality of jute fiber produced from
Bangladesh is incomparable and very much differ from
synthetics [21–23]. However, jute production is ham-
pered due to both biotic and abiotic stresses through-
out its growing season [24]. Among abiotic stress, water
deficiency, water-logging condition, and salinity stress
are noticeable for hampering jute yield [25–27]. How-
ever, yield loss of jute can be overcome through several
way including searching of germplasms and develop-
ing new variety through transgenic and genome editing
approaches. Therefore, characterization of the genes
associated with stress responses in both jute species can
be helpful for future breeding programs to improve the
traits of jute.

Recent decoding of draft genome sequences of both
jute species [28] has opened an opportunity to identify
the PLD genes from jute. The present work was focused
to identify the PLD genes through bioinformatics analy-
sis to understand their relationship with other reported
PLDs leading to stress-tolerant variety development.

Materials and methods
Identification of PLD genes from two jute species
For identifying PLD genes from both Corchorus capsu-
laris and Corchorus olitorius genomes, genomic data
of two jute species were downloaded from the National
Center for Biotechnology Information (NCBI) database
(PRJNA215141 and PRJNA215142). Reference protein
sequences of PLD genes from the model plant Arabi-
dopsis and rice along with other plants (cotton, grape,
and poplus) were downloaded from the TAIR (http://
www.arabidopsis.org), PlantGDB (http://www.plant
pdb.org/OsGDB/), Cottongen (https://www.cottongen.
org/), and grape database (http://genomes.cribi.unipd.it/
grape/). BLAST tool was carried out for the detection of
PLD homologous genes in both jute species. The E value
threshold was selected at 10$^{-10}$ for this analysis. All puta-
tive PLD genes were manually confirmed by the presence
of HKD domain responsible for the hydrolysis activity
through multiple sequence alignment (https://www.ebi.
ac.uk/Tools/msa/clustalo/).

Analysis of gene structure, domain, motifs, localization,
and physiochemical properties
Exon and intron structures of PLD genes of both jute
species were determined with the help of online software
Gene Structure Display Server 2.0 (GSDS 2.0) (http://
gds.cbi.pku.edu.cn/) through the information of general
feature format (GFF). WoLF PSORT, an online-based
platform, was used to predict the probable localization
of PLD genes in both jute species [29]. Different phys-
ical and chemical assessment and related indexes like
theoretical isoelectric point (pl), molecular formula, ali-
phatic index, stability index, and grand average of hydro-
pathicity (GRAVY) were asssed with the ProtParam tools
(https://web.expasy.org/protparam/) [30, 31].

Phylogenetic analysis
ClustalW2 software was used to align the selected pro-
tein sequences for phylogenetic analysis of PLD proteins
from two jute species, Arabidopsis, three cotton species,
grape, Medicago, poplus, and peach. With the aligned
protein file, a phylogenetic tree was constructed with
MEGA X and neighbor-joining method was used for the
phylogenetic tree [32, 33] inferred from 1000 bootstrap
replicates with other default parameter.

Expression analysis of PLD genes
Publically available transcriptome data were down-
loaded from sequence read archive (SRA) and used for
the expression pattern analysis of PLD genes of two jute
species (C. capsularis and C. olitorius). For expression
profiling of drought stress and salinity stress condition,
data were downloaded from the project PRJNA378897,
SRP116874, and SRP116874, respectively [27, 34, 35].
Data of waterlogging stress were collected form the acce-
ssion number SRP049494, produced by our group
earlier. Expression pattern of both jute species were
compared by aligning the RNA-Seq reads with reference genomes of jute and then the transcript abundances were measured using the cufflinks v2.2.1 package, visualized by R libraries [36].

Results

Identification of PLD genes from two jute species (C. capsularis and C. olitorius) and conservation of HKD domain

To identify the PLD genes from two jute species, protein sequences of PLD genes from Arabidopsis, cotton, grape, poplus, and rice were employed as query, and found 12 and 11 PLD genes in C. capsularis and C. olitorius, respectively (Table 1). Based on the nomenclature instruction for plants, Cc and Co symbols were used for C. capsularis and C. olitorius, respectively. Depending on the amino acid sequence homology with Arabidopsis, PLD genes of both jute species were divided in five groups namely alpha (α), beta (β), gamma (γ), delta (δ), and zeta (ζ). Both jute species had the similar number of PLD genes in different groups except the zeta (ζ). Analysis also revealed that C. olitorius genome have one zeta (ζ) containing PLD genes, whereas C. capsularis have two members of zeta (ζ) containing PLD genes (Table 1).

Next, the presence of two HKD domains was analyzed through the amino acid sequence of PLD genes. Analysis of protein sequence found higher conservation of two HKD (HxKxxxxD) domains in all PLD genes of both jute species except CoPLDδ-2 (Fig. 1). CoPLDδ-2 had only one HKD domain in its protein sequence; however, HKD domains were located far away from each other.

Structure analysis of PLD genes in jute species

Structure analysis of PLD genes found that PLD-ζ1 contained the highest number of exon (20) and intron (19) in both jute species; however, this PLD-ζ1 gene did not have the higher protein length (Table 1 and Fig. 2). The analysis also observed that CoPLD-α1-3 from the C. olitorius had the lower number of exon (2) and intron (1) but not having the lower gene length. In case of gene length, CcPLD-β1 was the longest gene length having 10 exons and 9 introns followed by the CoPLD-β1. On the other hand, both CoPLD-α4 and CcPLD-α4 had the lower gene length (Table 1). Subcellular analysis revealed that most of the PLD proteins were found in the cytoplasm (61%) followed by endoplasmic reticulum (35%) (Table 1). However, CcPLD-β1 and Co PLD-β1 solely seemed to be localized in the nucleus.

| Gene Name | Gene ID       | Protein length | Nucleotide length | Number of exon | Number of intron | Subcellular localization |
|-----------|---------------|----------------|-------------------|----------------|-------------------|--------------------------|
| CcPLD-α1-1 | CCACVL1_12572 | 812            | 2436              | 3              | 2                 | Endoplasmic               |
| CcPLD-α1-2 | CCACVL1_23328 | 821            | 2463              | 4              | 3                 | Endoplasmic               |
| CcPLD-α1-3 | CCACVL1_23327 | 824            | 2472              | 3              | 2                 | Endoplasmic               |
| CcPLD-α2   | CCACVL1_27885 | 809            | 2427              | 4              | 3                 | Endoplasmic               |
| CcPLD-α4   | CCACVL1_18644 | 774            | 2322              | 4              | 3                 | Endoplasmic               |
| CcPLD-β1   | CCACVL1_14191 | 1129           | 3387              | 9              | 9                 | Cytoplasm                 |
| CcPLD-β1   | CCACVL1_07714 | 852            | 2556              | 9              | 8                 | Cytoplasm                 |
| CcPLD-β1   | CCACVL1_27035 | 818            | 2454              | 9              | 8                 | Cytoplasm                 |
| CcPLD-β2   | CCACVL1_09123 | 845            | 2535              | 10             | 9                 | Cytoplasm                 |
| CcPLD-β3   | CCACVL1_16893 | 847            | 2541              | 10             | 9                 | Cytoplasm                 |
| CcPLD-ζ1   | CCACVL1_02467 | 1077           | 3231              | 20             | 19                | Cytoplasm                 |
| CcPLD-ζ2   | CCACVL1_28516 | 1097           | 3291              | 18             | 17                | Cytoplasm                 |
| CoPLD-α1-1 | COLO4_35115   | 812            | 2436              | 3              | 2                 | Endoplasmic               |
| CoPLD-α1-2 | COLO4_18852   | 821            | 2463              | 4              | 3                 | Endoplasmic               |
| CoPLD-α1-3 | COLO4_18851   | 777            | 2331              | 2              | 1                 | Endoplasmic               |
| CoPLD-α2   | COLO4_12949   | 809            | 2427              | 3              | 2                 | Endoplasmic               |
| CoPLD-α4   | COLO4_30647   | 773            | 2319              | 4              | 3                 | Endoplasmic               |
| CoPLD-β1   | COLO4_12643   | 1124           | 3372              | 10             | 9                 | Cytoplasm                 |
| CoPLD-γ1   | COLO4_23790   | 852            | 2556              | 9              | 8                 | Cytoplasm                 |
| CoPLD-δ1   | COLO4_22499   | 857            | 2571              | 10             | 9                 | Cytoplasm                 |
| CoPLD-δ2   | COLO4_26079   | 806            | 2418              | 10             | 9                 | Cytoplasm                 |
| CoPLD-δ3   | COLO4_11759   | 847            | 2541              | 10             | 9                 | Cytoplasm                 |
| CoPLD-ζ1   | COLO4_03795   | 1078           | 3234              | 20             | 19                | Cytoplasm                 |
from motif analysis revealed that jute PLD genes contained twenty different motifs in their gene sequences (Fig. 3). The analysis detected the PLD-β1, PLD-γ1 of both jute species and CoPLD-δ1 of C. olitorius contained all motifs in their amino acid sequences; however, motif 8 was duplicated in CoPLD-β1 exceptionally. It was also observed that PLD-α1-1, PLD-α1-2, PLD-α1-3, and PLDα2 had the second highest number of motifs and all members of those genes did not contain the motif number 19 in both jute species. In addition, lowest number of motifs (9 motifs) was found in PLD-ζ1 in both jute species (Fig. 3).

Physical and molecular characteristics of PLD genes

Different physical and molecular characteristics of PLD proteins were summarized in Table 2. Analysis found variation in theoretical isoelectric point (pl) ranged from 5.4–8.4 and 5.4–8.38 in C. capsularis and C. olitorius, respectively which was below 7.0 in most PLD proteins. These results clearly indicated that PLD proteins were slightly acidic to marginally basic. Next, the aliphatic index was measured which help to predict the thermal stability of the protein. The analysis found the higher aliphatic index of PLD proteins ranging from 71 to 87 in both jute species (Table 2). From this result, it can be predicted that PLD proteins are highly thermally...
stable. Half of the CcPLD and CoPLD proteins had values less than 40 in the instability index, suggesting their stability in nature. In addition, all the members of PLD protein in both jute species seemed to be hydrophilic as the contained negative value in GRAVY test (Table 2). Molecular weight analysis found the variation in PLD proteins varying from 88 to 122 kDa where higher weight was observed in PLD-β1 and PLD-ζ1 in both jute species. However, the lower molecular weight was found in PLD-α4 in both species and PLD-α1-3 in C. olitorius species (Table 2).

Phylogenetic analysis of PLD proteins of two jute species

By using the amino acid sequence of PLD proteins from two jute species as well as other some plants, a phylogenetic tree was constructed to understand the evolutionary history of the PLD proteins. The phylogenetic tree revealed that 12 CcPLD and 11 CoPLD (five groups) proteins are clustered into five different clades along with the Arabidopsis 12 AtPLD proteins (Fig. 4). Among the different clades, the α type of jute species created the largest clade having 53 members. However, epsilon (ε) isoform of cotton species was found phylogenetically related with alpha (α) isoform of both jute species as well as Arabidopsis. The second largest clade was with the member of PLDδ constituted with 38 members of different plant species (Fig. 4). It was also found that PLDβ and PLDγ of both jute species were phylogenetically closely related as they were under the same clade in the phylogenetic tree (Fig. 4). This might have resulted for the presence of similar motifs in the amino acid sequence and it was observed in the presence of motifs (Fig. 3). From the phylogenetic tree, it was also observed that jute species and Arabidopsis proteins do not contain the isoform phi (φ); however, grape, peach, Medicago truncaluta, and cotton species had this PLD isoform (Fig. 4). Members of PLDδ proteins from Arabidopsis and jute species were found to be closely related with PLDβ and PLDγ. However, PLDζ proteins are far away from the rest clades in evolutionary distance, suggesting their sequence characteristics might be varied from the other member of PLD proteins in jute species.

Expression analysis of jute PLD genes

To investigate the probable functions of PLD genes of both jute species expression results from tissues, drought condition, salinity, and waterlogging conditions were analyzed.
In tissue-specific expression profiling, PLDα1-1 highly upregulated only in seedling stage in both jute species compared to the other tissues (Fig. 5A). In addition, CoPLDβ1 alone highly upregulated in seedling stage than the other PLD genes in two jute species. These results suggested the stage-specific function in jute plant. The analysis also observed higher expression of CoPLDα1-3 and CcPLDα1-3 in fiber cells than the remaining tissues. This result may indicate the specific function of PLDα1-3 during fiber cell formation. Whereas CoPLD-α2 and CcPLD-ζ1 showed higher expression patterns in stem cell compared to the other tissues (Fig. 5A). It was also observed that most PLD genes were upregulated in all tissues; however, downregulation was found in leaf and fiber cells. In addition, CcPLD-β3 showed upregulated expression during the flowering and fruiting stage indicated the importance of this gene for flowering and fruiting for jute.

Under waterlogging condition, expression pattern of three PLD genes of *C. capsularis* (CcPLDα1-1, CcPLD-α4, and CcPLD-ζ1) gradually increased with the increase of waterlogging periods (Fig. 5B). This result may indicate the involvement of these three PLD genes during waterlogging stress. In case of *C. olitorius*, CoPLD-ζ1 showed an increasing expression pattern up to 8 h of waterlogging condition indicating the importance of this gene during early waterlogging condition. Analysis also found that PLD genes of *C. capsularis* more or less upregulated under waterlogging stress compare to the PLD genes of *C. olitorius*. This result indicated the reasons of being waterlogging tolerance ability of *C. capsularis* than the *C. olitorius* (Fig. 5B).
In case of *C. capsularis* salt-sensitive variety, *CcPLDα1*-*2*, *CcPLDα1*-*3*, *CcPLDα2*, *CcPLDβ1*, *CcPLDδ2* were highly unregulated and *CcPLDα1*-*1*, *CcPLDα4*, *CcPLDγ1*, *CcPLDδ1* were downregulated under salt stress condition compared to the control in root (Fig. 5C).

Three PLD genes (*CoPLDα2*, *CoPLDβ1*, and *CoPLD-ζ1*) were upregulated in root sample of *C. olitorius*. In addition, *CoPLDα1*-*1* was found highly downregulated in root samples in the same jute species. However, expression of PLD genes in salt stressed leaves was not comparable compare to the root sample. Expression pattern of PLD genes in salt-tolerant *C. olitorius* jute was also analyzed. Comparative higher and upregulated expression of PLD genes was observed in in root than the samples of leaves (Fig. 5C right panel).

Expression analysis of PLD genes under drought condition revealed that PLDα1-1, PLDα1-3, and PLD-ζ1 was down regulated in *C. olitorius*, whereas highly upregulated in *C. capsularis* compared to the control condition (Fig. 5D). On the other hand, PLDβ1, PLDγ1, and PLDδ1 showed upregulated expression in *C. olitorius*; however, comparatively lower and downregulated expression in *C. capsularis*. PLDα1-2 showed higher downregulation in both jute species under the same stress condition. Form the above result, it can be predicted that not all but some of the PLD genes might play an important role during drought stress condition.

**Discussion**

Plant evolves a number of mechanisms to protect themselves against various environmental stresses for their survival. Phospholipase D (PLD) is a member of phospholipase superfamily which is involved to protect plants from external stresses [37]. PLD gene family of plant play an important role during various stresses such as cold, drought, and salt conditions as well as involved in programmed cell death [16]. However, the member of plant PLDs are more complex than the other organism containing different types of enzymes with noticeable structural, biochemical and regulatory properties.

Number of PLD genes in different plants are not consistent as various reports showed the variation of PLD gene member in different plants [38–42]. Member of PLD gene family has a unique feature of having two HKD (HxKxxxxD) domains far away from each other, however, interact with each other for promoting lipase activity [12]. In this study, a total of 12 and 11 PLD genes were identified from two jute species *C. capsularis* and *C. olitorius*, respectively, through the bioinformatic analysis (Table 1). The amino acid analysis identified

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**Table 2** List of identified PLD genes along with several physical and chemical properties

| Gene Name   | Gene ID       | Theoretical PI | Aromatic index | Instability index | GRAVY  | Molecular weight (da) |
|-------------|---------------|----------------|----------------|--------------------|--------|-----------------------|
| CcPLD-α1-1  | CCACVL1_12572 | 6.24           | 84.86          | 41.36              | -0.371 | 92,802.87             |
| CcPLD-α1-2  | CCACVL1_23328 | 6.41           | 84.08          | 39.33              | -0.396 | 93,082.90             |
| CcPLD-α1-3  | CCACVL1_23327 | 6.08           | 85.44          | 41.29              | -0.459 | 93,957.79             |
| CcPLD-α2    | CCACVL1_27885 | 5.40           | 80.27          | 40.56              | -0.43  | 91,949.97             |
| CcPLD-δ4    | CCACVL1_18644 | 6.89           | 77.86          | 40.52              | -0.439 | 88,663.17             |
| CcPLD-β1    | CCACVL1_14191 | 6.75           | 71.09          | 47.7               | -0.514 | 126,114.87            |
| CcPLD-γ1    | CCACVL1_07714 | 8.64           | 83.51          | 38.63              | -0.374 | 96,031.70             |
| CcPLD-δ1    | CCACVL1_27035 | 6.50           | 80.81          | 32.5               | -0.465 | 93,172.15             |
| CcPLD-δ2    | CCACVL1_09123 | 6.53           | 79.59          | 37.47              | -0.344 | 96,162.48             |
| CcPLD-δ3    | CCACVL1_16893 | 6.52           | 81.48          | 35.68              | -0.377 | 95,999.25             |
| CcPLD-α1-1  | CCACVL1_02467 | 5.91           | 83.83          | 43.62              | -0.388 | 122,332.91            |
| CcPLD-α2    | CCACVL1_27856 | 6.49           | 81.07          | 50.26              | -0.402 | 124,644.60            |
| CoPLD-α1-1  | COLO4_35115   | 6.19           | 84.38          | 41.54              | -0.388 | 92,985.85             |
| CoPLD-α1-2  | COLO4_18852   | 6.27           | 84.19          | 39.11              | -0.386 | 92,972.74             |
| CoPLD-α1-3  | COLO4_18851   | 5.95           | 87.09          | 43.23              | -0.415 | 88,328.57             |
| CoPLD-α2    | COLO4_12949   | 5.43           | 80.26          | 39.5               | -0.436 | 91,937.89             |
| CoPLD-α1-2  | COLO4_30647   | 6.92           | 77.96          | 40.5               | -0.419 | 88,664.18             |
| CoPLD-β1    | COLO4_12643   | 6.92           | 71.23          | 48.04              | -0.481 | 125,576.58            |
| CoPLD-γ1    | COLO4_23790   | 8.38           | 83.29          | 36.33              | -0.374 | 95,903.46             |
| CoPLD-δ1    | COLO4_22499   | 6.64           | 79.75          | 32.54              | -0.456 | 97,286.87             |
| CoPLD-δ2    | COLO4_26079   | 6.38           | 79.7           | 37.98              | -0.372 | 91,822.46             |
| CoPLD-δ3    | COLO4_11759   | 6.50           | 81.13          | 35.38              | -0.364 | 95,826.05             |
| CoPLD-ζ1    | COLO4_03795   | 5.93           | 82.94          | 44.04              | -0.406 | 122,480.92            |
the conservation of two HKD domains in all jute PLD genes except CoPLDδ2 (Fig. 1). In addition, C. capsularis genome contained two PLD proteins having zeta isoform (CcPLDζ1 and CcPLDζ2), whereas C. olitorius genome contains single protein with zeta isoforms (CoPLDζ1) (Table 1). Sequence alignment found high sequence similarity between CcPLDζ1 and CoPLDζ1 (Data not shown); however, CcPLDξ2 sequence showed insertion of partial amino acid resulting in more protein length than the CcPLDξ1 and CoPLDξ1 (Table 1).

Phylogenetic analysis is one of the amino acid sequence analyses which help to understand not only the relationship of the proteins but also help to predict their evolutionary history [43]. It was also reported that protein
Fig. 5 Expression profiling of the member of PLD gene from two jute species (C. capsularis and C. olitorius). Tissue-specific gene expression of PLD proteins in various developmental tissues (A), in waterlogging stress condition (B), in salinity stress condition (C), and drought stress condition (D). Here, WT, con, and St indicates waterlogging, control, and stress, respectively.
functions can be interpreted through the phylogenetic tree and a novel method is required for the genome level understanding [44]. The phylogenetic analysis found four clades for CcPLD and CoPLD proteins along with the Arabidopsis PLD proteins (Fig. 3). Based on sequence similarity, similar results were also reported from the previous studies on rice and Arabidopsis, suggesting the evolution of PLD proteins in different species [45]. It is very likely that PLD proteins in similar clade may have the similar functions and similar prediction was reported in Solea senegalensis proteins involved in immune system [46]. In addition, PLDζ proteins of both jute species along with Arabidopsis were found far away from the rest clades in the evolutionary distance indicating their similar evolution with the same function of PLDζ proteins with Arabidopsis [47].

PLD genes are abundant in plant species and significantly involved in salt tolerance [48]. PLDα1 has been previously reported to be highly expressed in different plant organs such as root, stem, leaf, hypocotyl, petal, anther, and fiber in canola [7]. In addition, PLDδ has been reported to play important role in freezing and salt tolerance as well as involved in stomatal closure [49–52]. In silico study on publicly available data, seedling, and stem tissues were more favored for the expression of PLD genes rather than leaf, fiber, flower, and fruit, indicating their involvement in the xylem formation [27, 34, 35]. Tissue-specific expression pattern of CcPLDα1-1, CoPLDα1-1, CcPLDα1-3, and CoPLDβ1 showed the importance of PLD genes in jute (Fig. 5A). In addition, CcPLDα1-1, CcPLDα4, and CcPLDγ1 highly upregulated under waterlogging condition (Fig. 5B) which may have an effect on better survivability at excess water conditions. Similarly, several other PLD genes specially CcPLDα1-1, CcPLDα1-2 CcPLDα2, and CcPLDδ2 were upregulated in C. capsularis than the C. olitorius under salt and drought stress condition, indicating their important role of PLD genes in C. capsularis abiotic stress tolerance. Similar hypothesis was also found from one research where C. capsularis was suggested to be more abiotic tolerance than the C. olitorius [53].

**Conclusion**

In this in silico study, we provided genome-wide identification and analysis of phospholipase D proteins for the first time in natural phloem fiber producing plant jute. A total of 12 and 11 PLD genes were identified from C. capsularis and C. olitorius, respectively. Gene structure and phylogenetic analysis showed that jute PLD genes were divided in five groups (α, β, γ, δ, and ζ). Moreover, the position of PLD proteins in the phylogenetic tree suggests a close evolutionary relationship between two jute species. Expression analysis revealed at least five PLD genes (PLDα1-2, PLD-α2, PLDβ1, PLDγ1, and PLDδ1) from both jute species have a significant role in jute growth and development. In addition, the expression pattern of PLDα1-2, PLDα1-3, PLD-α4, PLDδ1, and PLDδ3 suggesting their involvement during waterlogging stress condition. Moreover, only three genes (PLD-α2, PLDβ1, and PLDδ2) seemed to play an important role against drought and salinity stress conditions. These results give an important understanding for developing abiotic stress-resistant jute variety.
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