The 6th International Conference on Biochemistry and Molecular Biology

Rice lipoxygenase: their sequence analysis and putative roles

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Abstract

Plant lipoxygenase (LOX) has been paid much attention on the role in plant defense against stresses. However, little information on the role of rice LOX has been known. Available rice genome databases have provided opportunity to survey LOX genes in rice and suggest putative role(s) of rice LOXs, using characterized LOXs from other plants as references. Genome sequence analysis of *japonica* rice has revealed 13 LOX genes that distribute in chromosomes 2, 3, 4, 5, 8, 11 and 12, resemble to that of *indica* rice. Percentage similarity of deduced amino acid sequences of OsJLOX1 – 13, from *japonica* rice, is in range of 28.4 – 88.1%, while OsILOX1 – 13, from *indica* rice, is in range of 26.6 – 89.8%. In addition, each LOX with the same number shares similarity in range of 91.2 – 100%. A phylogenetic tree of rice LOX homologues and related proteins from other species was constructed and resulted in 3 clades. Clade I composed of 6 rice LOXs numbers 3, 4, 5, 6, 8 and 11, which may be related to plant defense against pathogen and quality of rice seed. Clade II consisted of 2 rice LOXs, numbers 2 and 7, which probably involve in plant development rather than plant defense. Clade III composed of 5 rice LOXs, numbers 1, 9, 10, 12 and 13, which possibly involve in plant defense against biotic and abiotic stresses.

Introduction

Rice (*Oryza sativa*) is staple food crop for almost half of the world population[1]. More often that rice production is threatened by harsh environment and/or invasions of pathogens and pests, which lead to reduction of rice yield production. Although, plants evolved various defensive strategies to protect themselves against stresses, little information has been mentioned in rice.

Plant lipoxygenase (LOX) is known as one of the enzymes involved in lipoxygenase pathway that plays important role in plant defense[2]. LOX is the determining step for synthesis of jasmonic acid and methyl-jasmonate, which being induced during plant pathogen attack[2]. Besides, another role of LOX has been proposed on plant growth and development[3]. LOX has various isoforms that temporally and spatially expressed in various tissues of plants, such as seeds, germinating seedlings, other vegetative tissues and reproductive tissues[3,4]. In recent years, physiological roles of LOXs have been studied much in dicotyledonous plants, such as *Arabidopsis thaliana*, soybean and tomato[5–7]. Maize, a monocotyledonous plant, has been also received attention on the role of LOX in the plant biotic stresses[8,9]. However, rice is the least studied.

LOX is a family of non-heme iron containing enzyme that catalyzes insertion of oxygen into polyunsaturated fatty acid (PUFAs)[10,11]. LOX structure is a monomeric protein that consists of β-barrel and α-helice domains. β-barrel domain locates in amino-terminus, which

function could be involved in membrane or substrate binding[12–14]. α-helice locates in carboxy-terminus, which is the catalytic site of the enzyme containing one iron atom per protein molecule[10]. The LOX pathway is initiated by oxygenation of linoleic or linolenic acids at C9 or C13 positions, which results in highly reactive 9- or 13-hydroperoxide products[15]. In fact, further conversions of hydroperoxides to other end products that specific for growth and development, and defense response to pathogen attack[16,17], such as jasmonic acid, methyl jasmonate, traumatin or volatile aldehydes[18,19], are depended on different isoforms of LOXs. To understand the role of LOXs in rice, a sequence comparison approach has been used in this work. Available rice genome databases were searched for LOXs in 2 rice cultivars, *japonica* and *indica*. Analysis of putative roles of rice LOXs was made by phylogenetic relationship among characterized LOXs from other plants.

Methodology

Sequences were generally collected from 3 databases. LOX loci, nucleotide sequences of genomic DNA, mRNA and amino acid sequences of LOXs in *japonica* rice, mainly from Nipponbarre cultivar, were provided by http://www.ncbi.nlm.nih.gov/gene, the Entrez Gene website. However, information of *indica* LOX (mainly from 93-11 cultivar) was not able to obtained directly from one database. Amino acid and mRNA sequences of OsILOXs were collected from BGI-RIS, and subsequently blasted using BLASTP in NCBI to identify whether the sequences were LOX proteins. BLASTN was used to search for genomic DNAs of OsILOXs and chromosomal loci in GRAMENE databases. Amino acid and spliced mRNA sequences of *indica* rice were collected from http://rise.genomics.org.cn/, website of the Beijing Genomics Institute-Rice Information System (BGI-RIS). LOX loci, genomic DNA sequences of *indica* rice were available in http://www.gramene.org, website of GRAMENE database. Amino acid sequences of LOXs from tomato (*Solanum lycopersicum*), soybean (*Glycine max*) and maize (*Zea mays*) were collected from The National Center for Biotechnology Information (NCBI database) and Entrez Gene. Amino acid sequences of LOXs from *Arabidopsis thaliana* were obtained from The Arabidopsis Information Resources (TAIR). Analysis of sequences used BLASTN and BLASTP that available in NCBI. ClustalW, based on http://www.genome.jp/tools-bin/clustalw, was used for sequence alignment. Phylogenetic analysis using phylogenetic tree that was constructed by bootstrap (1000 replicates), Neighbor-joining (NJ) using MEGA 6.0[20], after multiple sequence alignment using ClustalW[21].

Results and Discussion

Complete sequences of LOX genes in *japonica* (cultivar Nipponbarre) and *indica* (cultivar 93-11) rice have been collected from various databases, which are termed OsJLOX and OsILOX, respectively. Gene ID, chromosome number, gene position, exon number and sizes of genomic DNA and protein are shown in Table 1.

This work found 13 DNA sequences of LOX genes from 2 cultivars of rice, *japonica*, and *indica*, which OsJLOX and OsILOX, are numbered in sequence accordingly (Table 1). Each of LOX gene from both cultivars, with the same number, shares percentage of similarity of deduced amino acid sequences at 91.2 – 100%. LOX genes in *japonica* and *indica* rice also locate at the same chromosome numbers 2, 3, 4, 5, 8, 11 and 12. However, position and length of each gene were different (Table 1). In order to analyze the redundancy of LOXs in this study, amino acid sequences of OsJLOXs and OsILOXs were aligned to analyze the similarity scores of LOXs. As shown in Table 2, OsJLOXs showed similarity in range of 28.4 – 88.1%. Likewise, OsILOXs showed similarity in range of 26.6 – 89.8% (Table 3). Although, recent work of Agrawal et al. (2004) reported 16 LOXs found in *japonica* rice database[2], some sequences were redundant. Sequence comparison of Agrawal's LOXs to the rice LOXs in this work showed their similarity to only 9 sequences of current study (LOX1, 2, 3, 5, 6, 8, 10, 11 and 12). LOX4, 7, 9, and 13 of this work have missed in previous study. The number of rice LOXs could be

different when leaves of *indica* rice, cultivar Pusa Basmati 1, was challenged with blast fungus (*Magnaporthe grisea*), which 12 LOX genes were expressed[22]. In addition, 3 LOX proteins were purified from seed and seedling of *japonica* rice[23,24]. It is noted that the system to sequence LOX numbers is remained unstable. Therefore, it is unable to refer LOXs in this study to other work.

Roles of rice LOXs have been previously reported based on sequence comparison of rice LOXs to characterized ones from *Arabidopsis thaliana*, barley (*Hordeum vulgare*), tomato (*Solanum lycopersicum*), potato (*Solanum tuberosum*) and maize (*Zea mays*)[2]. Seven OsLOXs are likely to be associated to fatty acid synthesis as reported by Agrawal and colleagues and corresponded to OsLOX numbers 1, 2, 5, 8, 10, 11 and 12 in this work[2]. LOX2 from Huang and colleagues has been proved for seed longevity in Nipponbare and a Chinese rice cultivar using transgenic approach[25]. The LOX2 shows 100% similarity to OsJLOX6 and OsILOX6. This suggested that OsJLOX6 and OsILOX6 would be involved in seed longevity. In fact, three LOXs have been purified from rice seed and seedling[23,24], to which LOX3 is suggested its role on insect attraction and seed rancidity[26,27]. Fortunately, amino acid sequences of these 3 LOXs have never been reported.

To further suggest putative roles of OsJLOXs and OsILOXs in this study, their amino acid sequences were aligned with characterized LOXs, which were 6 LOXs from tomato (*Solanum lycopersicum*), 3 LOXs from soybean (*Glycine max*), 13 LOXs from maize (*Zea mays*) and 6 LOXs from *Arabidopsis thaliana*. Subsequently, construction of a phylogenetic tree among OsLOXs and characterized LOXs from other plants was made using bootstrap (1000 replicates), Neighbor-joining (NJ) via MEGA 6.0 (Figure 1). Three clades were resulted and roles of OsLOXs have been suggested.

Clade I composes of 6 OsJLOXs and 6 OsILOXs, numbers 3, 4, 5, 6, 8 and 11, which includes AtLOX1, AtLOX5, TomloxA, TomloxB, TomloxE, GmLOX1, GmLOX2, GmLOX3, ZmLOX1, ZmLOX2, ZmLOX3, ZmLOX4, ZmLOX5, ZmLOX6 and ZmLOX12. AtLOX1 and AtLOX5 are detected in cytoplasm and responsible for lipid peroxidation[28], lateral root formation[29] and defense response against bacteria and wounding by producing abscisic acid and jasmonic acid[6,30]. In addition, TomloxA is highly expressed in germinating seeds as well as in ripening fruit. TomloxB is fruit specific and highly detected in ripening fruit[31]. TomloxE, based on RNAi transformant, is associated to oxidation of α-linoleic acid and linolenic acid that leads to poor nutritional quality of tomato[32]. ZmLOX1 is responsible to jasmonate biosynthesis burst during wounding[33]. ZmLOX2 may play role in biotic stress, in which expression is down regulated in a maize line that resistant to *Aspergillus flavus*[8]. Transgenic ZmLOX3 suggests its role as a root-specific suppressor to root growth during nematode attack, while ZmLOX4 and ZmLOX5 are induced by virulent and avirulent strains of fungal leaf pathogen, *Cochliobolus carbonum*[34,35]. In addition, ZmLOX6 is induced by jasmonic acid, but suppressed by abscisic acid, salicylic acid and ethylene. However, ZmLOX6 is not response to wounding or insects, while ZmLOX12 is strongly induced in response to *Fusarium verticillioides* infection[34,36]. This suggests that members of OsLOXs in clade 1 may be related to plant defense against pathogen and quality of rice seed.

Clade II contains 2 OsJLOXs and 2 OsILOXs, numbers 2 and 7, including AtLOX3, AtLOX4, AtLOX6, TomloxD, ZmLOX7, ZmLOX8 and ZmLOX9. AtLOX3, AtLOX4 and AtLOX6 are found in chloroplast and responsible for lipid peroxidation[28], growth[37], anther development[4] and response to wounding[38]. Transgenic TomloxD plant increases jasmonic acid accumulation by catalytic conversion of α-linoleic acid to (13S)-hydroperoxy octadecatrienic acid (13-HPOT), jasmonic acid precursor. The transgenic tomato is also tolerant to *Cladosporium fulvum* and high-temperature stress[7]. In addition, overexpressed TomloxD plant also elevates wound-induced jasmonic acid biosynthesis and increased of wound-responsive genes, thereby enhances resistance to insect herbivore attack and necrotrophic pathogen infection[7]. ZmLOX8 is required for jasmonic acid-mediated tassel development, to which

ZmLOX8 may provide substrate for wound-induced jasmonic acid biosynthesis[9]. ZmLOX7 is not response to either basal or wound-induced jasmonic acid in leaf[9]. ZmLOX9 is not response to both atoxigenic and toxigenic *Aspergillus flavus*[8]. Most roles in characterized LOXs from maize suggests putative role of OsLOXs on plant development more than plant stress from pathogen.

Clade III, composes of 5 OsJLOXs and 5 OsILOXs, numbers 1, 9, 10, 12 and 13, including AtLOX2, TomloxC, TomloxF, ZmLOX10, ZmLOX11 and ZmLOX13. The rice LOXs in this clade are similar to AtLOX2 that is found in chloroplast and responsible for jasmonic acid and salicylic acid accumulations[39], green leaf volatile[40] and wounding[41]. In addition, this clade also composes of TomloxC that associates to flavor volatiles in both fruits and leaves, to which unrelated to bacterial attack[42]. TomloxF expression is stimulated by non-pathogenic rhizobacteria *Pseudomonas putida* BTP1[43]. ZmLOX10 is preferentially expressed in leaves and induced in response to wounding, cold stress, defense-related hormones jasmonic acid, salicylic acid and abscisic acid, and avirulent strain of *Cochliobolus carbonum*, which suggests a role in maize adaptation to abiotic stresses and defense response against pathogens and pests[17]. ZmLOX11 was highly expressed in silks and induced in leaves only by abscisic acid[17]. ZmLOX13 is response to *Aspergillus flavus*[8]. This suggests the role of OsLOXs might involve in protection of rice against biotic and abiotic stresses.

Conclusion

Thirteen sequences of genes and proteins of lipoxygenase from *japonica* and *indica* were fetched from databases in order to analyzed putative functions of rice lipoxygenase. Both rice cultivars shared similar genes of lipoxygenases. Their putative roles were classified into 3 groups according to 3 clades of a phylogenetic tree, which was compiled with 28 known lipoxygenases from *Arabidopsis*, tomato, soybean and maize. Most of them might be involved in rice development, defense mechanism and production of volatile compounds, which are waited to be proven.

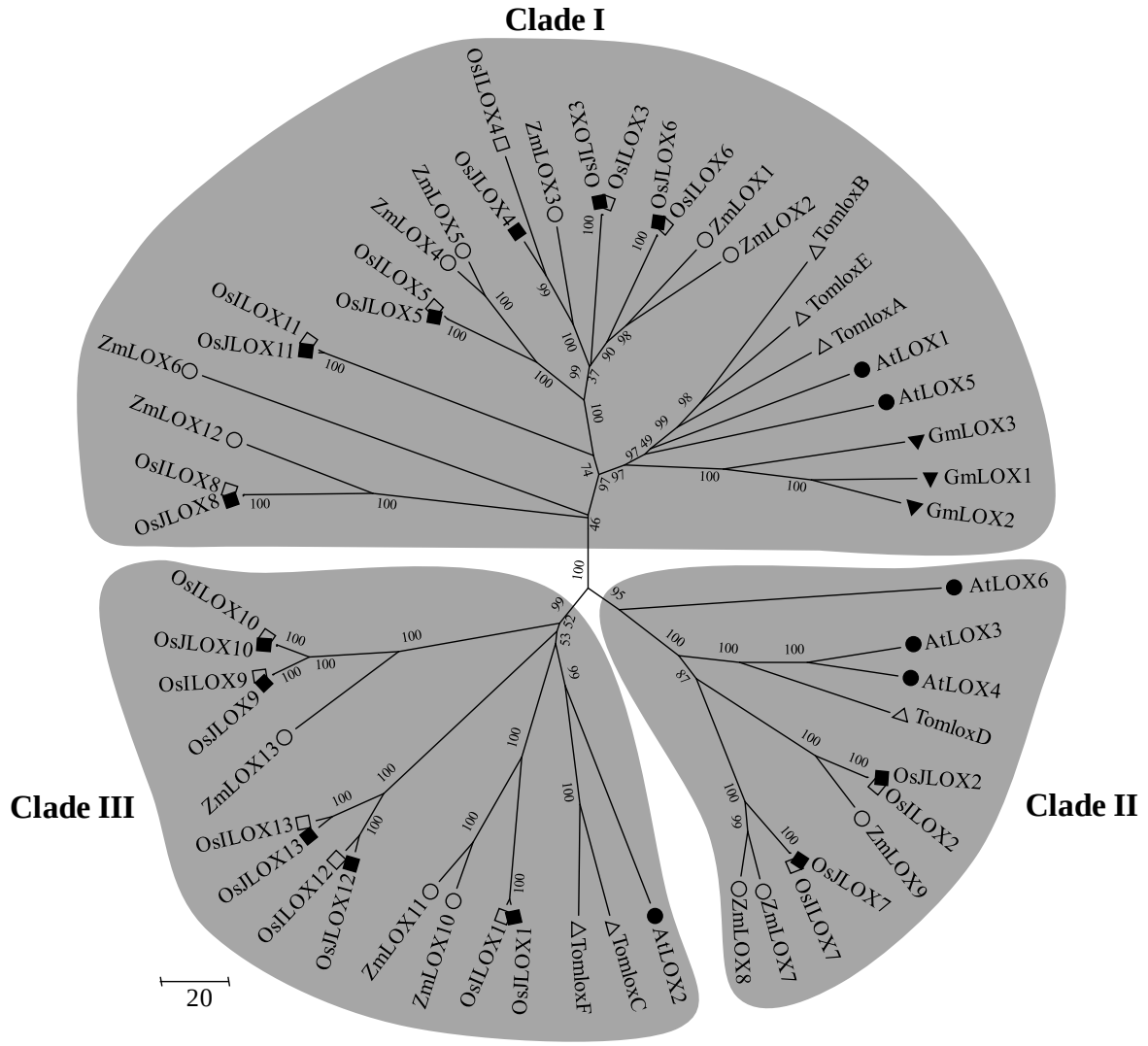

Figure 1. A phylogenetic tree of rice lipoxygenase homologs (OsJLOXs and OsILOXs) and related proteins from other plant species. Tomato (Tomlox Δ), soybean (GmLOX ▼), *Arabidopsis* (AtLOX ●), maize (ZmLOX o) and rice (OsJLOX: *japonica* ■ and OsILOX: *indica* □). OsJLOXs and OsILOXs were aligned by ClustalW. The tree was constructed by bootstrap 1000 replicates, the Neighbor-joining (NJ) phylogenic inference using MEGA 6.0.

Table 1. Data and similarity score of LOXs between *japonica* and *indica* rice

japonica (cv. Nipponbare) Entrez gene of NCBI							*indica* (cv. 93-11) RIS and GRAMENE database							similarity score of protein
Name	gene ID	Chr	Position	exon number	DNA (bp)	Protein (residues)	Name	gene ID	Chr	Position	exon number	DNA (bp)	Protein (residues)	
OsJLOX1	LOC4328603	2	5276619..5282835	6	6217	926	OsILOX1	BGIOSGA006958	2	6134538-6140071	7	5534	893	98.7
OsJLOX2	LOC4331824	3	4187035..4193536	9	6502	918	OsILOX2	BGIOSGA011980	3	4592404-4598138	9	5735	905	99.6
OsJLOX3	LOC4333818	3	28049586..28053733	9	4148	863	OsILOX3	BGIOSGA013391	3	32162686-32166430	9	3745	863	99.9
OsJLOX4	LOC4333821	3	28089922..28094638	9	4741	866	OsILOX4	BGIOSGA013392	3	32226968-32231396	9	4429	856	91.2
OsJLOX5	LOC4333823	3	28106903..28113288	9	6386	877	OsILOX5	BGIOSGA013393	3	32249367-32255214	9	5848	877	99.9
OsJLOX6	LOC4334049	3	30315455..30318972	4	3518	870	OsILOX6	BGIOSGA013525	3	34517965-34521153	4	3189	870	99.9
OsJLOX7	LOC9267158	4	22304760..22309325	7	4566	922	OsILOX7	BGIOSGA016491	4	20508218-20512247	7	4030	870	99.6
OsJLOX8	LOC4338358	5	13734211..13740531	9	6321	847	OsILOX8	BGIOSGA019579	5	14727241-14732440	9	5200	846	99.1
OsJLOX9	LOC4345993	8	25216456..25224219	6	7764	924	OsILOX9	BGIOSGA028967	8	26833978-26844855	12	10878	1498	99.8
OsJLOX10	LOC4345994	8	25240904..25250040	6	9137	941	OsILOX10	BGIOSGA028970	8	26892324-26902570	6	10247	852	100.0
OsJLOX11	LOC4350766	11	21675027..21684597	3	9571	868	OsILOX11	BGIOSGA035483	11	18322795-18326064	3	3270	707	99.4
OsJLOX12	LOC4352505	12	22854745..22860205	8	5461	922	OsILOX12	BGIOSGA036014	12	18367286-18372540	8	5255	918	95.8
OsJLOX13	LOC4352509	12	22920092..22936843	9	16752	853	OsILOX13	BGIOSGA037589	12	18424656-18434305	7	9650	747	91.4

Table 2. Similarity score of amino acid sequence in *japonica* rice

	OsJLOX1	OsJLOX2	OsJLOX3	OsJLOX4	OsJLOX5	OsJLOX6	OsJLOX7	OsJLOX8	OsJLOX9	OsJLOX10	OsJLOX11	OsJLOX12	OsJLOX13
OsJLOX1	100.0	40.3	28.4	36.3	29.1	30.9	41.2	33.1	49.2	44.9	44.9	45.3	48.9
OsJLOX2		100.0	36.6	38.6	36.8	37.1	64.3	35.8	38.8	40.0	33.5	35.8	38.0
OsJLOX3			100.0	73.2	65.0	73.2	38.9	42.5	35.7	35.5	52.5	34.3	34.2
OsJLOX4				100.0	67.7	76.9	38.6	42.5	37.1	37.1	54.0	34.4	33.8
OsJLOX5					100.0	64.8	36.7	41.9	36.4	37.1	50.0	33.5	33.4
OsJLOX6						100.0	38.2	37.5	36.6	36.1	53.5	29.0	30.4
OsJLOX7							100.0	36.7	40.3	39.3	32.9	36.1	37.9
OsJLOX8								100.0	35.1	35.5	40.0	33.8	31.3
OsJLOX9									100.0	88.1	30.2	43.1	38.9
OsJLOX10										100.0	33.2	42.8	38.7
OsJLOX11											100.0	33.3	32.1
OsJLOX12												100.0	83.6
OsJLOX13													100.0

Table 3. Similarity score of amino acid sequence in *indica* rice

	OsILOX1	OsILOX2	OsILOX3	OsILOX4	OsILOX5	OsILOX6	OsILOX7	OsILOX8	OsILOX9	OsILOX10	OsILOX11	OsILOX12	OsILOX13
OsILOX1	100.0	39.2	28.9	28.6	29.2	31.6	39.5	32.0	39.1	46.2	31.3	44.6	49.7
OsILOX2		100.0	35.8	36.3	36.0	36.6	63.5	35.7	37.6	37.7	31.0	34.9	36.7
OsILOX3			100.0	66.5	64.9	73.5	38.2	42.1	35.5	35.8	53.7	29.2	30.4
OsILOX4				100.0	61.6	71.7	36.1	37.2	33.2	33.9	48.8	30.1	26.6
OsILOX5					100.0	64.8	35.9	41.6	35.2	37.8	51.1	33.0	28.8
OsILOX6						100.0	37.5	37.5	34.9	36.9	49.9	28.4	29.2
OsILOX7							100.0	34.9	40.6	40.6	29.6	35.5	36.8
OsILOX8								100.0	29.7	34.8	40.5	31.7	33.9
OsILOX9									100.0	89.8	29.7	40.5	38.7
OsILOX10										100.0	34.9	45.4	44.7
OsILOX11											100.0	32.4	29.7
OsILOX12												100.0	85.3
OsILOX13													100.0

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Acknowledgements

Authors thank granting agencies from the research capability enhancement program through graduate student scholarship and Salt-tolerant Rice Research Group, Department of Biology Faculty of Science, Khon Kaen University. Special thanks go to Dr. Maysaya Thitisaksakul for her kindness on sequence analysis.