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Research paper

Systematic analysis of maize class III peroxidase gene family reveals a conserved subfamily involved in abiotic stress response

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ABSTRACT

Class III peroxidases (PRXs) are plant-specific enzymes that play key roles in the responses to biotic and abiotic stress during plant growth and development. In this study, we identified 119 nonredundant PRX genes (designated *ZmPRXs*). These PRX genes were divided into 18 groups based on their phylogenetic relationships. We performed systematic bioinformatics analysis of the PRX genes, including analysis of gene structures, conserved motifs, phylogenetic relationships and gene expression profiles. The *ZmPRXs* are unevenly distributed on the 10 maize chromosomes. In addition, these genes have undergone 16 segmental duplication and 12 tandem duplication events, indicating that both segmental and tandem duplication were the main contributors to the expansion of the maize PRX family. Ka/Ks analysis suggested that most duplicated *ZmPRXs* experienced purifying selection, with limited functional divergence during the duplication events, and comparative analysis among maize, sorghum and rice revealed that there were independent duplication events besides the whole-genome duplication of the maize genome. Furthermore, microarray analysis indicated that most highly expressed genes might play significant roles in root. We examined the expression of five candidate *ZmPRXs* under H_2O_2, SA, NaCl and PEG stress conditions using quantitative real-time PCR (qRT-PCR), revealing differential expression patterns. This study provides useful information for further functional analysis of the PRX gene family in maize.

1. Introduction

Peroxidases are a large group of widely distributed enzymes that play important roles in the production and scavenging of reactive oxygen species (ROS) by catalyzing oxidoreduction between hydrogen peroxide (H_2O_2) and various organic and inorganic compounds (Hiraga et al., 2001; Passardi et al., 2004). Based on their protein structures, peroxidases are divided into two groups, including heme peroxidases and non-heme peroxidases (Hiraga et al., 2001). Heme peroxidases are further divided into three classes based on their sequences and catalytic properties, with the exception of animal peroxidases. Class I peroxidases, which are intracellular and can be found in most living organisms except animals, play key roles in protection against excess H_2O_2. Class II peroxidases are extracellular fungal enzymes that are mainly involved in lignin degradation (Welinder and Gajhede, 1993). Class III peroxidases (PRXs; EC 1.11.1.7) include all secretory plant-specific peroxidases (Welinder, 1992a, 1992b; Cosio and Dunand, 2009), which comprise large multigene families in many plants, such as *Arabidopsis thaliana*, *Oryza sativa* and *Populus trichocarpa*, with 73, 138 and 93 PRXs, respectively (Tognolli et al., 2002; Passardi et al., 2004; Ren et al., 2014).

PRXs are characterized by the presence of highly conserved amino acids. PRXs are hemoproteins consisting of a single peptide chain and protoporphyrin IX. These proteins weigh approximately 35 KD and contain approximately 33 amino acid residues. Most plant PRXs combine with carbohydrates to form glycosylated proteins. This glycosylation plays significant roles in preventing protease degradation and maintaining enzyme stability (Zheng and Van Huystee, 1991). In addition, two histidine residues interact with the heme group and eight cysteine residues, forming disulfide bridges; the distal histidine is necessary for catalytic activity (Passardi et al., 2004).

Class III secreted peroxidases carry out various functions in a broad range of physiological processes during plant growth and development, including lignin and suberin formation, crosslinking of cell wall components, wound healing, H_2O_2 removal, the oxidation of toxic reductants and defense against pathogens or insect attack (Gabaldón et al., 2005; Passardi et al., 2005; Bindschedler et al., 2006; Cosio and Dunand, 2009; Daudi et al., 2012). In addition, plant peroxidases can oxidize the growth hormone auxin, as well as other substrates, producing H_2O_2

Abbreviations: PRXs, class III peroxidases; ROS, reactive oxygen species; H_2O_2, hydrogen peroxide; Mya, million years ago; CDS, coding sequences; HMM, Hidden Markov Model; NJ, Neighbor-Joining; *Os*, *Oryza sativa*; *Zm*, *Zea mays*; *Sb*, *Sorghum bicolor*.

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Table 1
The 119 PRX genes identified in maize and their sequence characteristics.

Name	Sequenced ID	Size (aa)	MW (Da)	PI	Chr.
ZmPRX1	GRMZM2G040638_T01	335	35,724.81	5.39	1
ZmPRX2	GRMZM2G047456_T04	356	37,055.89	4.54	1
ZmPRX3	GRMZM2G047656_T01	332	34,948.53	6.94	1
ZmPRX4	GRMZM2G047968_T01	223	23,795.06	9.01	1
ZmPRX5	GRMZM2G068699_T01	326	34,832.4	9.64	1
ZmPRX6	GRMZM2G085198_T02	319	32,928.37	6.51	1
ZmPRX7	GRMZM2G088765_T01	337	35,978.20	4.45	1
ZmPRX8	GRMZM2G116846_T02	371	39,773.97	8.86	1
ZmPRX9	GRMZM2G116902_T01	334	34,928.34	5.58	1
ZmPRX10	GRMZM2G127945_T01	361	38,630.41	6.12	1
ZmPRX11	GRMZM2G130904_T01	328	35,435.02	5.14	1
ZmPRX12	GRMZM2G131525_T01	1063	11,5331.73	5.95	1
ZmPRX13	GRMZM2G136534_T01	337	36,320.38	5.79	1
ZmPRX14	GRMZM2G320269_T01	355	38,510.92	9.23	1
ZmPRX15	GRMZM2G341934_T01	329	33,465.78	5.04	1
ZmPRX16	AC210003.2_FGT004	332	35,436.75	9.36	2
ZmPRX17	AC211164.5_FGT004	335	35,663.54	6.14	2
ZmPRX18	GRMZM2G029144_T01	373	40,401.69	6.34	2
ZmPRX19	GRMZM2G044049_T01	368	39,582.33	9.08	2
ZmPRX20	GRMZM2G048775_T01	336	34,947.8	8.61	2
ZmPRX21	GRMZM2G067096_T02	384	40,480.37	4.78	2
ZmPRX22	GRMZM2G108077_T01	329	34,020.62	6.09	2
ZmPRX23	GRMZM2G108123_T01	344	36,603.94	8.08	2
ZmPRX24	GRMZM2G108153_T01	337	35,476.22	5.35	2
ZmPRX25	GRMZM2G108219_T01	364	38,700.75	5.66	2
ZmPRX26	GRMZM2G133475_T01	320	33,474.55	8.39	2
ZmPRX27	GRMZM2G136042_T01	329	34,766.75	8.74	2
ZmPRX28	GRMZM2G156227_T01	351	38,365.52	8.62	2
ZmPRX29	GRMZM2G408963_T01	334	35,851.92	9.59	2
ZmPRX30	GRMZM2G443885_T01	339	35,807.04	4.78	2
ZmPRX31	AC230013.2_FGT002	372	40,033.14	9.76	3
ZmPRX32	GRMZM2G000107_T01	322	34,869.23	9.57	3
ZmPRX33	GRMZM2G029479_T01	333	36,519.62	9.64	3
ZmPRX34	GRMZM2G101221_T01	337	35,013.68	4.78	3
ZmPRX35	GRMZM2G103342_T01	362	37,988.26	8.62	3
ZmPRX36	GRMZM2G104394_T01	367	38,356.59	6.81	3
ZmPRX37	GRMZM2G107228_T01	368	38,300.2	5.19	3
ZmPRX38	GRMZM2G144648_T01	346	36,491.42	8.81	3
ZmPRX39	GRMZM2G321839_T02	342	37,420.5	4.84	3
ZmPRX40	GRMZM2G361475_T01	237	25,133.86	9.52	3
ZmPRX41	AC205154.3_FGT005	342	36,904.4	5.46	4
ZmPRX42	AC197758.3_FGT004	333	34,729.15	6.87	4
ZmPRX43	GRMZM2G061230_T02	345	36,262.03	5.63	4
ZmPRX44	GRMZM2G117706_T01	324	34,009.77	6.5	4
ZmPRX45	GRMZM2G419953_T01	342	35,601.8	7.04	4
ZmPRX46	GRMZM2G439422_T01	357	38,627.16	5.92	4
ZmPRX47	GRMZM2G006791_T04	547	59,640.5	5.43	5
ZmPRX48	GRMZM2G028219_T01	286	31,868.89	8.56	5
ZmPRX49	GRMZM2G035506_T01	322	33,796.08	6.49	5
ZmPRX50	GRMZM2G061776_T01	320	34,061.24	4.69	5
ZmPRX51	GRMZM2G080183_T01	331	35,763.72	9.19	5
ZmPRX52	GRMZM2G085967_T03	361	38,911.76	8.5	5
ZmPRX53	GRMZM2G129543_T01	317	34,368.15	6.88	5
ZmPRX54	GRMZM2G133434_T01	317	33,997.47	5.72	5
ZmPRX55	GRMZM2G134947_T01	331	35,508.8	4.37	5
ZmPRX56	GRMZM2G142011_T02	322	33,942.66	5.27	5
ZmPRX57	GRMZM2G150893_T02	342	36,201.86	5.11	5
ZmPRX58	GRMZM2G160327_T01	330	34,476.36	8.45	5
ZmPRX59	GRMZM2G176085_T01	328	34,803.33	5.84	5
ZmPRX60	GRMZM2G405459_T02	357	37,110.35	8.47	5
ZmPRX61	GRMZM2G405581_T02	322	32,765.77	4.89	5
ZmPRX62	GRMZM2G442008_T01	362	39,250.05	5.78	5
ZmPRX63	GRMZM2G702176_T01	482	52,653.14	5.37	5
ZmPRX64	GRMZM2G012263_T01	421	46,858.12	5.4	6
ZmPRX65	GRMZM2G081928_T01	341	35,278.43	4.5	6
ZmPRX66	GRMZM2G089895_T01	340	37,107.49	6	6
ZmPRX67	GRMZM2G093346_T01	154	17,022.27	5.32	6
ZmPRX68	GRMZM2G095404_T02	366	40,285.76	5.04	6
ZmPRX69	GRMZM2G104109_T01	338	36,670.87	7.09	6
ZmPRX70	GRMZM2G135108_T01	360	38,672.02	6.52	6
ZmPRX71	GRMZM2G171078_T02	338	35,191.61	10.71	6
ZmPRX72	GRMZM2G313184_T01	323	34,847.89	5.25	6
ZmPRX73	GRMZM2G410175_T01	323	35,053.8	6.18	6
ZmPRX74	GRMZM2G010640_T01	364	39,226.14	8.34	7
ZmPRX75	GRMZM2G025441_T01	321	33,411.97	9.08	7