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# 1-CYSTEINE PEROXIREDOXIN: A LESS STUDIED MEMBER OF PEROXIREDOXIN IN PLANTS

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## ABSTRACT

1-Cysteine Peroxiredoxin (1Cys Prx) is a thiol dependent antioxidative enzyme of molecular weight 20-30 kDa. It contains one catalytic cysteine residue and is found in cytosol. Prx plays an important role in growth, development and dessication tolerance in dormant seeds. It detoxifies $H_2O_2$ and various other organic peroxides. It protects lipids, enzymes and DNA against reactive oxygen species. This review highlights our current understanding of 1Cys Prx with focus on its expression in seeds and transgenic plants.

**KEYWORDS: Ascorbate Peroxidase, Cysteine, Peroxiredoxin, Glutathione Peroxidase, Hydrogen peroxide, NADPH thioredoxin reductase**

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# INTRODUCTION

Reactive oxygen species (ROS) produced in a cell due to various reasons like incomplete reduction of $O_2$ to water during respiration, beta- oxidation of fatty acids under stressed conditions exposure to radiation, light, metals & floods. When present in high concentration. They pose an oxidative threat to cells for the scavenging of ROS a number of enzymes are present in the cell which include catalase, glutathione peroxidase, and haem-containing peroxidase & peroxiredoxin. Studies have shown that enhanced levels of ROS lead to redox modifications, such as dithiol-/disulfide transitions, S-nitrosylation, glutathionylation, and subsequently to oxidative damage. A number of ROS are produced in the cell, like superoxide ion ($O_2^-$), hydroxyl ion ($OH^-$) and hydrogen peroxide ($H_2O_2$). Out of these, $H_2O_2$ is least reactive. $H_2O_2$ is reduced in the presence of $Fe^{2+}$ in the Fenton reaction and yields hydroxyl radical ($OH^\cdot$). Due to its ability to diffuse over significant distances within and between cells, $H_2O_2$ serves a signalling function in cellular communication [1, 2]. Thus $H_2O_2$ plays two opposite roles simultaneously, first as a damaging ROS compounds and second as a messenger in cell signalling. For the effective functioning of this molecule its concentration must be balanced in the cell. During normal conditions $H_2O_2$ concentrations are kept very low. However, level of $H_2O_2$ increases in response to various abiotic and biotic stresses and takes part in the reactive oxygen regulatory network [3].To combat these ROS cells express a number of antioxidative enzymes which decompose $H_2O_2$, namely catalase (CAT), ascorbate peroxidase (APX) glutathione peroxidase (GPX), peroxiredoxin (Prx), and type- III peroxidases [4]. Glutathione peroxidase and Prx also decompose alkyl hydroperoxides in addition to $H_2O_2$. This review surveys the current literature and presents a comprehensive coverage of current knowledge of 1-Cys Prx with molecular size of 20-30kDa. They are thiol-dependent enzymes containing one (1-cysteine [-Cys]) or two (2-Cys) conserved Cys residues that protect lipids, enzymes, and DNA against ROS. Prx undergoes redox dependent conformational changes and interacts in a conformation-dependent manner with various proteins. These enzymes are truly ubiquitous having been identified in yeast [5], plant [6] and animal cells [7] including both protozoan and helminth parasites, and most of eubacteria and archaea. The Prxs are primarily located in the cytosol. These (Prx) antioxidants were first identified in yeast thiol-specific antioxidant[5]. Prxs can reduce $H_2O_2$, alkyl hydroperoxides, and hydroxyl radicals [8]. *In vitro* they have been shown to have antioxidant activity through protection of biomolecules against radical attack. Based on the sequence, structural similarities and positions of conserved cysteinyl residues the whole Prx family is divided in six groups, named A, B, C, D, E, and F [9, 10]. Prx from the groups A to D are common and conserved in higher plants. As per the nomenclature, the A-type Prx corresponds to the (typical) 2-Cys Peroxiredoxin (2-CysPrx), the B-type Prx to the (typical) 1-Cys Peroxiredoxin (1-CysPrx), the C-type Prx to peroxiredoxin Q (PrxQ), and the D-type Prx to type II Peroxiredoxins (PrxII). PrxQ and PrxII are also termed atypical 2-Cys Prx [11].

### *Structure and Mode of Action of 1 Cys Peroxiredoxin*

1 Cys Peroxiredoxin in plants is one of the very less studied member of Peroxiredoxins. The crystal structure of this enzyme reveals that it exists in a head to tail dimeric structure as shown in (Fig1). This 25 kDa protein contains a single conserved catalytic cysteine (47th position) towards the $NH_2$ terminal and is thus known as 1-Cys Prx [12].The peroxidase reaction is composed of two steps which are centered on this redox-active cysteine also known as the peroxidatic cysteine. It has been found that site directed mutagenesis of this Cysteine to Serine removes the peroxidase activity of the enzyme [13, 14, 15]. A number of recent reviews have addressed the structural and catalytic properties of Prx isoforms in general[16] and in plants specifically [17, 18, 19]. The crystal structure of 1-Cys Prx shows the peroxidatic cysteine as a sulphenic acid (–SOH). This sulphenic acid is highly stable in 1-Cys Prx. Close to this peroxidatic cysteine residue His 39 and the Arg 132 is present. This histidine is conserved for only this class

of Prxs enzymes. The presence of these amino acids stabilizes the Cys 47 thiolate anion. 1-Cys Prx act by reducing peroxide substrates to the corresponding alcohol and water. The reaction mechanism comprises of three steps:

1. Oxidation,
2. Derivatization and
3. Regeneration of ground state

In the first catalytic cycle, the peroxidatic thiol group is oxidized to the sulphenic acid and the reduced product, i.e. $H_2O$ in case of $H_2O_2$, alcohol in case of alkyl hydroperoxides and nitrite in case of alkoxynitrites is released. The sulphur atom is covered by sulfenate oxygen to prevent it's over oxidation to inactive sulfenic acid ($SO_2H$) and sulfenic acids ($SO_3H$). There are reports of over oxidation of Prxs [16] as shown in (Fig 2). It is possible due to local unfolding of the active site which exposes the Cys to accomplish this. The structures have shown that C terminal arm gets unfolded, positioning the resolving Cys for disulphide bond formation. This disulphide bond is exposed at one end, thereby allowing the resolving cysteine to be attacked by thiol containing reductants. Pulido *et al* [20]. have shown that the NADPH thioredoxin reductase (NTR)-mediates the regeneration of 1-Cys Prx in the nuclei of wheat seed cells exposed to various oxidative stresses. Crystal structures of the disulfide-bonded enzymes have shown that the C-terminal arm is unfolded beyond the resolving cysteine, indicating a high degree of mobility for this locally unfolded segment. The overall reaction can be summed as:

$ROOH + R'(SH)_2 \dashrightarrow ROH + R'S_2 + H_2O$

1 Cys Prx is a non heme containing enzyme; so it relies on an external electron donor to compensate for the lack of the prosthetic group. The oxidized Prx lose their enzymatic activity and must first be regenerated prior to the next catalytic cycle. For many Prx, it has been established that Thioredoxin serve as electron donor for the regeneration of the active form [21]. It has been shown that the yeast mitochondrial 1-Cys Prx is reactivated by glutathionylation of the catalytic cysteine residue and reduced by thioredoxin reductase coupled with glutathione. Prx 1 plays an important role in protection against mitochondrial oxidative stress [22].

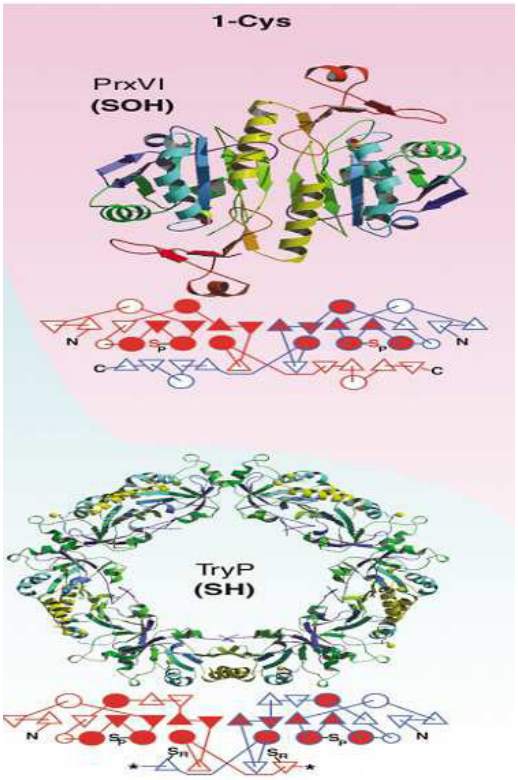


**Figure 1**
***Structure of 1 Cys Prx as generated by using MOLSCRIPT and TOPS.***

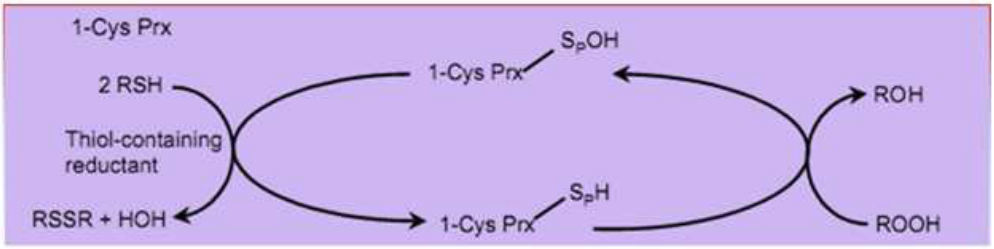


**Figure 2**
***Catalytic mechanism of 1- Cys Prx in peroxide detoxification.***

***1 Cys Peroxiredoxin in Seeds /Plants***

ROS are the molecules which intervene in cellular signalling and growth processes occurring at early embryogenesis and gene expression during seed development [23].Studies have shown that reactive oxygen species are involved in various aspects of programmed cell death [24], seed physiology and desiccation [25], seed germination and dormancy [26], ageing, cellular damage. In seeds, 1 Cys Prx plays an important role in combating the oxidative stress and help in the survival of seeds of the plants. Detoxification done by 1 Cys Prx in vital acquisition of dessication tolerance of developing seeds, their germination and storability.1-Cys Prx genes are expressed solely in seeds, and only in the parts of the seeds surviving desiccation, i.e. the embryo and the aleurone layer. 1-Cys Prx found in seeds have been characterized in several species, examined at both the transcript and protein level in relation to dormancy, and described in relation to function and localization. 1-Cys Prx have been identified in a number of plants at gene level like pBS128 in brome grass. Per1 in barley (also called B15C) and FePer1 in buckwheat (*Fagopyrum esculentum*) [27] are expressed in developing seeds. The studies have shown that the PER1 the first antioxidant belonging to the 1-Cys subgroup protein of barley is present in high concentrations in the nucleus at the onset of desiccation. Barley seed Peroxiredoxin is encoded by a single Per 1 gene. The studies have shown that levels of 1-Cys transcript can be up regulated by ABA and osmotic stresses and can be suppressed by gibberellic acid. The dormancy-related Prx antioxidant, PER1, is localized in the nucleus of barley embryo and aleurone cells and the protein level is maintained in imbibed dormant seeds. In contrast to most seed-expressed antioxidants Per1 disappears in germinating embryos, and in the mature aleurone, the transcript is down-regulated by the germinating embryo or by gibberellic acid (GA) [28]. Dominguez *et al.* studied the nuclear NADPH thioredoxin reductase NTR/1-Cys Prx system and found that NADPH is able to detoxify $H_2O_2$ under oxidative stress conditions in cereal seeds [29]. It controls the stress conditions in nucleus which is important for redox regulation of gene expression in germinating seed cells. The studies have shown NADPH thioredoxin reductase (NTR) supports the antioxidant activity of 1-Cys Prx as shown in (Fig 3).This Redox system is also localized in the nucleus of wheat seed cells and probably plays an important role in antioxidant protection in aleurone and scutellun cells suffering from oxidative stress during seed development and germination. The pattern of localization of NADPH thioredoxin reductase NTR in developing and germinating wheat seeds were studied using an immunocytochemical analysis. The presence of NTR in transfer cells, vascular tissue, developing embryo and root meristematic cells, agrees with the localization of Trx h, and it supports the important function of the NTR/Trx system in cell proliferation and communication. Interestingly, NTR is found to be co-localized with Trx and 1 Cys Prx in the nuclei of seed cells suffering oxidative stress [20]. A full length cDNA encoding 1 Cys Prx was cloned from wheat and the recombinant protein was expressed in *Escherichia coli*, to test whether the NTR/Trx systems serves as an electron donor. From the purified components, it was found that activity of 1 Cys Prx is NTR dependent. Mutants of the 1-Cys Prx show that the peroxidatic residue of the wheat enzyme is Cys46, which is over oxidized *in vitro* under oxidant conditions. The

extracts from developing and germinating seeds were analysed and it was found that there is over oxidation of 1- Cys Prx *in vivo*. Based on these results, it was proposed that NADPH is the source of the reducing power to regenerate 1-Cys Prx in the nuclei of wheat seeds cells suffering oxidative stress, in a process that is catalyzed by NTR [30].1-Cys Prx gene has also been identified in a medicinal Mushroom Antrodia *camphorata* [31]. It was found to contain 23 amino acid residues with calculated molecular mass of 25,081 Da. The protein obtained shared 44-58% identity with 1- Cys Prx from *Homosapiens*, *Bos Taurus* and *Saccharomyces cerevisia*. The purified recombinant enzyme was thermo stable with a half life of inactivation 15.5 min at 60degree C. It was stable in the pH range 7.8-10.2.Ikegami in (2009)[32] showed that 1 Cys Prx (DkPrx) is present in abundance in fruits of persimmon (Diospyros kaki Thunb.) which accumulate large amounts of proanthocyanidins (PAs) in early stages of development. The DkPrx reported is the first member of 1Cys Prx reported from fruits of any plant species. However, whether this enzyme play role in biosynthesis/ accumulation of PAs or it is the accumulation of PAs that induce its gene expression is not clear yet. Peroxiredoxins are one of the key players of the thiosulfide redox regulatory network of plant cells. The role of theses peroxiredoxins was studied in Lotus japonicas [33] and it was found that 1 Cys Prx gene shows high expression in the seed embryos and low expression in vegetative tissues. The expression was induced by nitric oxide and cytokinin.

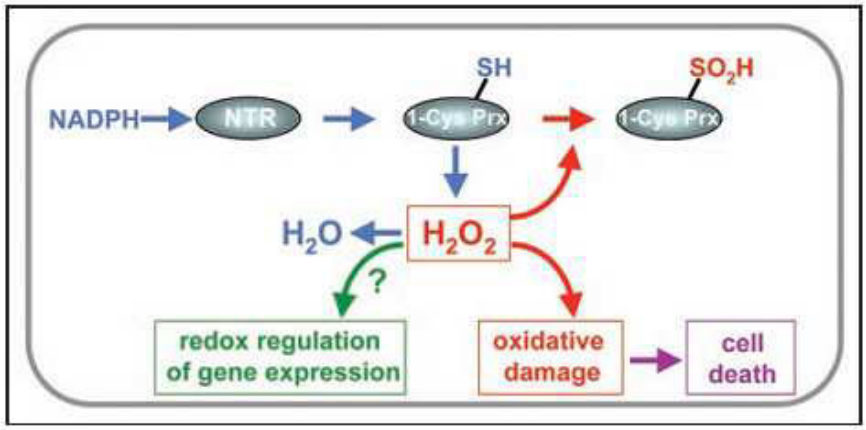


**Figure 3**
***NTR and 1 Cys Prx forms nuclear localized redox system under oxidative stress.***

***Chaperone Activity of 1 Cys Peroxiredoxin***

Over oxidation of the conserved cys residue, on $H_2O_2$ treatment increased its chaperone activity two folds. However, its peroxidase activity decreased considerably without enzyme. Kim et al. (2011)[34] have shown that during seed germination 1-Cys Prx not only relieve mild oxidative stress but also act as molecular chaperons and it is the overoxidation that controls the switch in function of 1-Cys Prx from Peroxidase to molecular chaperones.

***1 Cys Peroxiredoxins in Transgenic Plants***

Proteomic analysis of rice callus was done and 10 ABA induced proteins were identified as the product of the embryo specific promoter candidates.1 Cys Prx, was cloned and analyzed. Beta glucuronidase (GUS) expression driven by 1 Cys Prx promoters increases by ABA treatment and rapidly induced by wounding in callus and at the leaf of the transgenic plants. Ectopic expression of the GUS construct in *Arabidopsis* suggested that the 1-Cys Prx promoter also has strong activity in seeds of dicot plants [35, 36]. The transcript level of rice 1Cys-Prx (R1C-Prx) rapidly decreased after imbibition of rice seeds, but the protein was detected for 15 days after imbibitions. Transgenic tobacco plants constitutively expressing the R1C-Prx gene were considered to study the function of 1 Cys Prx. These plants showed a germination frequency similar to control

plants, however, they exhibited higher resistance against oxidative stress, suggesting that antioxidant activity may be the primary function of 1 Cys Prx [37].1-Cys Prx has been shown to be higher in seedlings of soybean (*Glycine max* (L.) Merr.) Suffering from flooding stress than in normally growing seedlings. In a study, soybean genome was found to contain two genes corresponding to 1-Cys Prx and is designated as GmPer1a, GmPer1b. GmPer1a encodes a polypeptide containing the putative catalytic site, and the GmPer1b contains a stop codon inside the deduced polypeptide-coding region, indicating that GmPer1b might be a pseudogene. Two gene forms of GmPer1 protein existed in both submerged and normally grown seedlings, and both forms were higher in the submerged seedlings [38]. From *Xerophyta viscose* a monocotyledonous dessication tolerant plant, a stress inducible gene named XvPer1 has been isolated. The length of the cDNA sequence was found to be 849bp, containing one major reading frame of 660 bp. It was found to exhibit 70% similarity with other 1 Cys Prx proteins. The amino acid sequence constituting the active site of the enzyme, PVCTTE, has been found to be highly conserved in XvPer1. Western blot analysis and immunoflorescence analysis revealed that XvPer1 is localized in the nucleus of dehydrated *Xerophyta viscosa* leaf cells. These results suggest that XvPer1 is a stress-inducible gene, which may function to protect nucleic acids within the nucleus against oxidative injury [12].

## CONCLUSION

1 Cys Prx is a ubiquitous enzyme playing diverse roles ranging from the antioxidant defense of the cell[39] to growth, development and dessication tolerance in dormant seeds. They are known to catalyze a diverse range of peroxides by using a thiol based catalytic mechanism. It efficiently works at low peroxide concentrations. This enzyme is also involved in redox dependent signalling by altering $H_2O_2$ concentration, processing alkyl hydroperoxides and decomposing peroxynitrite. They perform redox interactions with other proteins and undergo redox dependent conformational changes. The literature within the 1 Cys prx field is currently focussed on their more recently identified roles as molecular chaperones under oxidative stress conditions.

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