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Peroxidases are enzymes which reduce hydrogen peroxide to water (H_2O_2 + 4e + $2H^+ \rightarrow 2H_2O$) by taking electrons to a wide variety of donor molecules [13]. Every living organism contains such enzymes, whose primary function has been most likely to scavenge the hydrogen peroxide generated as by-product of many reactions using oxygen. During the course of evolution, the redox properties of peroxidases became used to catalyze other reactions. They were then involved in various mechanisms either in plants or in animals. These mechanisms fall into a few categories: the defence against pathogens [31], the cross-linking of macromolecules [15], the oxidation and chemical modification of various molecules [17], including hormones [18], and the production of reduced species of oxygen [3].

Two kinds of peroxidases exist, those containing a heme group and those which do not. Plant and bacterial peroxidases have been classified into three classes, according to the structural characteristics of the apoprotein [51]. All contain ferriprotoporphyrin IX as prosthetic group. In addition to these hemoproteins, plants contain glutathion peroxidases [10] and algae have vanadate peroxidases [22].

The numerous peroxidases of an organism can be considered as forming a system covering all the compartments of a cell. The main function of this system is to scavenge hydrogen peroxide formed as toxic by-product by several metabolic pathways. It ensures also the achievement of a great deal of oxidation reactions essential for the cells. It is generally considered that the first function is mediated mainly by ascorbate peroxidase (EC 1.11.1.11), glutathione peroxidase (EC 1.11.1.9) and catalases (EC 1.11.1.6), a particular peroxidase using hydrogen peroxide both as substrate to be reduced and as hydrogen donor. The second function is achieved in plants by secreted plant peroxidases, also called class III peroxidases (EC 1.11.1.7).

Considering the great number of isoforms of these secreted plant peroxidases, it appeared necessary to classify them into various categories according to different criteria: isoelectric point, substrate specificity, sequence homology, subcellular localization, or mode of interaction with cell wall.

Isoelectric point

Few plant enzymes were as much submitted to electrophoretic studies as peroxidases. The great number of bands visualized after electrophoresis, the ease of staining procedures and the multiple changes observed in relation to plant development stages, environmental conditions, or chemical treatments explain this situation [17]. The main techniques used were starch gel electrophoresis [5], non-denaturating gel electrophoresis [28], and isoelectric focusing [37]. When using this latter technique, it appears often strikingly that isoperoxidase bands are distributed into two main groups, the acidic (or anionic) and the basic (or cationic) isoforms, albeit neutral isoforms also exist. It was at one time hypothesized that basic and acidic peroxidases fulfil distinct functions [16,17]. Acidic isoforms were supposed to be associated to lignin formation [19] and basic ones to auxin catabolism [12,30]. This generalization based on particular cases has not been supported by sound experimental evidences.

Numerous peroxidase sequences are now available on databases. It is possible that in the future a relationship between particular sequence features and the function of peroxidases will be found.

Substrate specificity

In the presence of H_2O_2, peroxidases are able *in vitro* to catalyze the oxidation of loads of molecules, most of them being phenols, aromatic amines, or alkaloids [17]. The problem is to know which of these reactions they are really catalyzing *in vivo* and what is the function of each isoform. This question is related to the catalytic specificity of each isoperoxidase. A test has been realized with thirteen recombinant *Arabidopsis* peroxidases. It turned out that they were almost all able to oxidize three of the hydrogen donors (substrates) commonly used for peroxidase assays (Table 1, [50]). This observation supports the widely held idea that plant peroxidases have little or no substrate specificity. However, as shown by the data presented in Table 1 and by many other examples, each isoperoxidase exhibits a particular catalytic profile. This means that a given isoperoxidase has a maximum catalytic efficiency towards one substrate and another isoperoxidase towards another substrate, both being able to oxidize both substrates. In addition, the optimum pH may vary from one peroxidase to the other (Table 1). In some cases, a substrate can be oxidized by only a few peroxidases. The best known example is extensin, a cell wall structural protein, which is cross-linked by only some peroxidases called extensin peroxidases [45]. Indolylacetic acid is also oxidized by particular peroxidases [18,30]. They do not need the supply of exogenous H_2O_2 for this reaction. Finally, some isoperoxidases are able, in the presence of a reducing molecule (NADH, cysteine) to produce H_2O_2 [3] or hydroxyl radicals [46].

A particular isoperoxidase will be active *in vivo* only if it is in contact with a substrate and, in most cases, H_2O_2. This substrate must be in a sufficient concentration and the surrounding pH must be appropriate to make possible the reaction. These conditions will be met only if the enzyme and its substrate occur at the same time, at the same place.

Table 1. Catalytic activities of *Arabidopsis* peroxidases expressed in the baculovirus/insect cell system. The peroxidases were assayed with OPD, ABTS and guaiacol as hydrogen donors. The optimal pH for each substrate is given in brackets. The preferred substrate for each peroxidase is underlined, and the highest value obtained for each substrate is italicized. The activity ($\Delta A.min^{-1}$) is given per ml of spent medium of the insect cell culture; t = traces of activity (from [50]).

Recombinant peroxidases	Activity (µmol/min.ml)		
	OPD	ABTS	Guaiacol
P2	*36.7* (4)	23.3 (4)	*20.3* (6)
P4	1.77 (5)	0.97 (5)	t
P6	0.51 (6)	0.16 (6)	1.55 (7)
P7	12.0 (4)	*32.3* (6)	10.8 (6)
P8	0.28 (4)	0.19 (4)	t
P9	0.65 (4)	1.23 (6)	0.59 (6)
P10	0.95 (5)	0.83 (5)	0.95 (6)
P14	10.6 (4)	10.6 (5)	2.03 (6)
P15	3.74 (4)	t	5.62 (6)
P17	10.0 (4)	8.33 (5)	2.50 (5)
P20	7.34 (5)	20.0 (6)	14.8 (6)
P21	6.14 (5)	0.67 (6)	3.97 (6)
P22	t	0.10 (4)	t

OPD: 1,2-phenylenediamine; ABTS: 2,2'-azino-di-3-ethyl-benzothiazoline-6-sulphonic acid; t: trace of activity.

Subcellular localization

Peroxidases are mainly found in the apoplast and the vacuoles. They are secreted enzymes, produced by genes that encode also a signal peptide which mediates the entry of the nascent peroxidase peptide into the endoplasmic reticulum [52]. There are some recent reports on the presence of peroxidases other than ascorbate peroxidases in chloroplasts and mitochondria, but they need to be confirmed by molecular studies. The transport towards the exterior of the cell is the default pathway for proteins synthesized in the endoplasmic reticulum. A specific sorting signal is necessary to target them to the vacuole. It has been demonstrated that this signal is a propeptide at the C-terminus of the protein [52], but it appeared in the case of a peroxidase from zucchini for example that, despite the existence of such a propeptide, the enzyme was found in cell walls [6]. Although no general rule exists, it seems that isoperoxidases with an acidic isoelectric point are rather found in cell walls and basic isoperoxidases are found either in vacuoles or in cell walls [29,39]. It has been shown in at least one case that a same isoperoxidase was present simultaneously in the two compartments [39].

If at least some of the functions of peroxidases in cell wall are more or less clearly identified, it is not the case for the roles played by peroxidases in vacuoles. One of these roles seems to be the scavenging of cytoplasmic H_2O_2 [48].

Interaction with cell walls

Plant peroxidases fulfil many important functions in cell walls: cross-linking of matrix polymers, lignin and suberin deposition, formation of H_2O_2 and $^{\bullet}OH$, destruction of auxin. In general, the isoperoxidases responsible for each of these reactions have not been expressively identified. However, it can be assumed that to achieve properly these various tasks, isoperoxidases must be positioned at the appropriate position within the polymer network forming the cell wall. This spatial control supposes an interaction with a structural element of the cell wall. In this respect, apoplastic peroxidases have often been classified into three categories according to the kind of interactions they have with cell walls: i) *soluble* isoperoxidases which move freely within the apoplast and can be collected from plant tissues by vacuum infiltration with a low-salt solution followed by centrifugation [8,43], ii) *ionically-bound* isoperoxidases which are released from plant tissues or isolated cell walls by a solution containing enough salts [20], iii) *covalently-bound* isoperoxidases which are tightly bound to cell walls and are released only after digestion with cellulase and pectinase [27]. Electrophoretic separations have shown that these three fractions contain completely or partially different isoperoxidases. This classification of apoplastic peroxidases constitutes in fact a rough approach of their mode of interaction with the constituents of the cell walls. Since they move freely, it can be assumed that soluble peroxidases are more or less evenly distributed throughout cell walls. As a consequence, they must be present at any point of the cell walls or intercellular spaces. This means that the determining factor for the control of their activity *in muro* is the occurrence of the appropriate substrates. In contrast, the so-called covalently-bound peroxidases are immobilized in the network of the cell wall polymers, even if they are probably not really linked to them by covalent bonds. These isoperoxidases are supposed to be active only at their site of immobilization. In that case, their substrates must be brought to them either by diffusion or by an active mechanism. There is no explanation concerning the association of these peroxidases to cell walls. The ionically-bound peroxidases are attached to the extracellular matrix through electrostatic interactions. The matrix polymers susceptible of providing negative or positive charges for such interactions are pectins or structural proteins such as extensin. As the salt concentrations necessary to fully release these isoperoxidases are rather high, it can be hypothesized that the interactions are rather strong, suggesting some specificity. This specifity has been demonstrated in the case of peroxidases from zucchini (*Cucurbita pepo*) which binds strongly to the calcium-induced conformation of pectin [38]. One of these peroxidases, an anionic isoform (APRX), contains a motif of four clustered arginines which form a Ca^{2+}-pectate binding site [7]. This property could provide a spatial control mechanism which could be crucial for the function of certain enzymes like APRX.

Expression pattern

The studies concerning the expression of the genes encoding an isoperoxidase are still scarce. Table 2 shows a non exhaustive list of works published on this subject. It seems that the expression pattern is quite different from one peroxidase to the other. Some genes are constitutively expressed in particular tissues, others are turned in only

in response to an external stimulus. Among those belonging to the first category, we can distinguish peroxidase genes expressed in specific tissues such as epidermis or differentiating xylem elements from those active in a great number of different tissues [6]. Generally, root is the organ which contains the higher peroxidase activity and in which the greatest number of peroxidase genes are expressed. It can be expected that the expression pattern of a particular gene is related to the biochemical function of the peroxidase it encodes. Thus, it is supposed that the products of the peroxidase genes active in differentiating xylem are involved in lignin formation [9] or those found in root endoderm in suberization [40].

Table 2. Expression of peroxidase genes measured by *in situ* hybridization or promoter activity with a reporter gene.

Peroxidase	Plant	Expression	References
ATP1a, ATP2a	*Arabidopsis*	seeds, roots, leaves, stems, flowers	[25]
ATP A2	*Arabidopsis*	root	[36]
BP1	barley	endosperm	[42]
pCS1	cucumber	pathogen-induced	[41]
	cucumber	ethylene-induced	[34
FLXPRE2	flax	stem	[35]
prxC1	horseradish	stem	[24]
prxC2, prxC3	horseradish	root	
prxC2	horseradish	wound-induced	[23]
	Mercurialis	male flowers	[2]
	potato	pathogen-induced	[44]
	tobacco	trichomes, epidermis, flower	[26]
	tobacco	aluminium stress	[14]
tpoxN1	tobacco	root (constitutive)	[21]
		aerial parts (wounding)	
tap1	tomato	epidermis, stem, flowers, wounding	[33]
TPX1	tomato	roots (epidermis)	[4]
TPX1	tomato	lignifying or suberizing cells	[40]
"		cell-cycle-dependent (cell suspension)	[32]
pox1, pox2, pox4	wheat	root	[1]
	wheat	pathogen-induced	[47]
APRX	zucchini	root, vascular tissues, epidermis	[6]
ZmAP1	*Zea mays*	root (epidermis, pericycle), coleoptile	[49]

Conclusion

Each part of a plant and each compartment of a plant cell contains one or several peroxidases. As already indicated, these peroxidases belong to four categories. Only the class III secreted plant peroxidases have been briefly reviewed here. Ascorbate peroxidases, and in a lesser extent glutathion peroxidases and catalases, exist also under several different molecular forms. This means that a plant has probably over hundred genes encoding enzymes using or scavenging H_2O_2. Apparently, only the

secreted plant peroxidases are using H_2O_2 to catalyze a large spectrum of reactions. The function of the other peroxidase is just to keep at a low level H_2O_2 concentration. In a given domain of the cell this concentration will be lowered proportionally to the density of peroxidases present. In this way, peroxidases have an influence on the general redox level of cell compartments.

In the apoplast, many different isoperoxidases coexist. They are all able to reduce H_2O_2, provided there is an adequate substrate in their vicinity. Each of these different isoperoxidases has its preferred substrates. This means that two or more different reactions can be catalyzed in the same time at the same point of a cell wall. These reactions can eventually be coupled, the product of one isoperoxidase being the substrate of another one. In addition, some isoperoxidases are able to produce H_2O_2, which could be used by other ones. If there is really a cooperation between certain apoplastic isoperoxidases, a mechanism of anchoring would be useful to maintain them in close contact. The existence of multienzyme complexes including isoperoxidases and maybe other enzymes providing H_2O_2 for example may be hypothesized. In this respect, the observation that some isoperoxidases (and other enzymes, unpublished data) can bind to Ca^{2+}-pectate could be very important. The function of the pectic structure could be to organize the various components of multienzymatic complexes designed to fulfil a precise function, such as lignin deposition. In the future, it will be necessary to understand how are spatially distributed and organized the various enzymes operating within the complex cell wall network. This will allow to better understand the multiple reactions occurring in this compartment. It is also likely that the interactions of specific proteins with particular binding sites in the apoplast are crucial for some physiological or developmental processes [11].

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