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Chromosomal Localization of Plant Peroxidase Genes

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More than 70 genes coding for peroxidases have been assigned to linkage maps in 21 species of plants. Peroxidases have been most precisely mapped in barley and wheat using a combination of electrophoretic and molecular techniques. On the basis of temporal, developmental, and tissue specific peroxidase expression, the peroxidase genes comprise at least 9 gene families. These families may represent functional groups of genes under similar genetic control.

Peroxidases (EC 1.11.1.7) are ubiquitous in the plants. They have become a standard isozyme marker due to their ease of detection. In addition, the enzyme is extremely stable. A list of the peroxidase genes that have been mapped to chromosomes or adjacent markers is given in Table I and II. The grasses: barley, wheat, rice, maize and rye have been listed separately because of their agronomic importance (Table II). There appears to be no consistent rules for naming plant peroxidase genes. For example genes coding for peroxidases have been designated *prx*, *Ep*, *per*, *pox*, *P*, *Iso*, *Px*, etc. Because many more peroxidase genes will be identified in the near future, there is a need for a standard set of rules to be followed when naming these loci.

Traditionally, peroxidases have been detected using starch gel or polyacrylamide gel electrophoresis as well as isoelectric focusing. Western blot techniques are utilized when antibodies are available. However, isozyme techniques have inherent limitations. They will only detect genes that are expressed and they are impaired if the gene product undergoes secondary modifications such as glycosylation or C–terminal processing.

Cloning of peroxidase genes have made it possible to use RFLP's (restriction fragment length polymorphisms) to create genetic maps which include these loci. This approach has been successful in barley, wheat and rye. For example, the cloning of four barley peroxidases uncovered at least three new peroxidase loci by means of RFLP analysis. One new locus is the gene coding for barley seed peroxidase BP1 which has been mapped to chromosome 1 (21). This gene may be identical to the basic seed peroxidase mapped to chromosome 1 using native polyacrylamide gels (28). A second gene locus identified using this method codes for the BP 2 gene family on chromosome three (8,32). Using the nucleotide sequence from this gene in studies involving wheat and rye RFLP maps, a rearrangement between wheat chromosomes 3 and 7 was observed as well as a rearrangement between rye chromo–

Table 1

Plant species	Chromosome	Locus	Organ/tissue	Reference
Petunia hybrida	I	*prx*B		van den Berg and Wijsman (1982)
	II	*prx*E		Hendriks *et al.* (1985)
	III	*prx*D	L, St	Hartings and Wijsman (1985)
		*prx*A		van den Berg *et al.* (1982)
	IV	*prx*C	AO	van den Berg *et al.* (1982)
	VII	*prx*F		
Cicer arietinum	L	*Prx*3	L	Gaur & Slinkard (1990a)
	L	*Prx*2,3'	L	Gaur & Slinkard (1990b)
Glycine max	L	*Ep*	S	Griffin et al. (1989)
Prunus persica	P	*Per*1	L	Durham *et al.* (1987)
Setaria Italica	L	*Pox*1	L?	de Cherisey *et al.* (1985)
Helianthus annus	L	*Prx*3		Kahler & Lay (1985)
Nicotiana alata	L	PI,PII		Ph. Labroche *et al.* (1983)
Liniodendron tulipifera	P	?		Houston & Hood (1982)
Linum usitatissimum	P	*Iso*1, *Iso*2		Cullis (1979)
Mulberry Morus	P		L	Hirano & Nagamuma (1979)
Lycopersicon esculentum	10	*Prx*4		Tanksley & Rick (1980)
	3	*Prx*7		
	3	*Prx*6		
	1	*Prx*1		
	2	*Prx*2		
	1	*Prx*3		
Populus	LG	*Per*–L1, *Per*–L2		Rajora *et al.* (1991)
Pisum sativum	6	*Prx*3	L	Timmerman *et al.* (1993)
Petunia hybrida	III	*Prx*A	L	van den Berg & Weijsman (1982)

Table 2

Plant species	Chromosome	Locus	Organ/tissue	Reference
Avena sativa	6	*Px6*	Lf	Morikawa (1988)
Oat 2n=48	18	*Px0*	Lf	Morikawa (1988)
Avena fatura		APX4		Clegg & Allard (1973)
Avena barbata	LG	APX5		Hutchinson *et al.* (1983)
2n=4x=28	LG	APX5		Marshall & Allard (1969)
Hordeum vulgare	1	*Prx1*, *Prx2*		Gale & Kleinhofs (pers. commun.)
	2	*Prx7*, pBH6-301		Giese *et al.* (1993), Brown & Munday (1982), Benito *et al.* (1988)
	3	*Prx5*		Johanson *et al.* (1992)
	3	*Prx6*		Theilade & Rasmussen (1992)
	5			Ainsworth *et al.* (1984)
	2	*PerH*^{ch}2		Fernández & Jouve (1990)
Hordeum chilense	2R	*L2Per-2*,	L	Benito *et al.* (1991) (review)
Secale cereale		*L2Per-3a*,	L	
		L2Per-3b,	L	
		L2Per-4	L	
	4RL	*EPer-1*	E	
	6RL	*SPer-1*	S	
	of 'Imperial' or 2R of 'King II'	*SPer-2*	S	
	7RS	*EPer-2-*	E	
		EPer-6	E	
	LG	*SPer5*	Sc	
		SPer6	Sc	
	1BS, 1DS	*Per-1*	L	Liu *et al.* (1990)
Triticum aestivum	2AS, 2BS, 2DS	*Per-2*	Root/Coleopt.	Liu *et al.* (1990)
	3AL, 3BL, 3DL	*Per3*	Embryo	Liu *et al.* (1990)
	7AS, 7AL, 4AL	*Per4*	E	Liu *et al.* (1990)
	2DS	*PerDS*	Root	Liu *et al.* (1990)
	2L	*Px1*, *Px2*		Hoisington *et al.* (1988)
Zea mays	7L	*Px3*, *Px4*, *Px5*, *Px6*, *Px7*, *Px8*, *Px9*		

Abbreviations:
AO = all organs; E = endosperm; L = leaves; Lf = flag leaf; LG = linkage group; P = polymorphism; S = seed; Sc = scutellum; St = stem.

somes (8). In addition to these two seed peroxidases, two cDNA's induced by the barley powdery mildew fungus have been mapped. They are located on chromosome 2 in barley and are separated by approx. 110 cM(15). This value should be considered only an estimate since only 74 offspring were analyzed and it has been demonstrated that the background genotype of the parents may influence the genetic map distance.

In addition to mapping studies, peroxidase genes can be utilized as markers to initiate chromosome walking. For example, in barley, *Prx7* is tightly linked to the *MlLa* locus which confers resistance to the powdery mildew fungus (15). As of yet the structure and function of this resistance gene is unknown. A clone tightly linked to this locus could prove useful in a mapbased cloning strategy involving barley chromosomal fragments in yeast artificial chromosomes.

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