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REVIEW

Tree chitinases – stress- and developmental-driven gene regulation

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Summary

In recent years, a considerable number of studies have harnessed the power of genomics to decipher the role of pathogenesis-related (PR) proteins in plant defence against various biotic and abiotic stresses. Chitinases are PR antifungal proteins expressed constitutively at low levels in plants and induced during biotic pressures and are demonstrated to be involved in the plant defence responses. Remarkable induction of chitinase enzymes by various abiotic agents (salicylic acid, jasmonic acid, ethylene and ozone) and biotic components (pathogens, insect pest, fungal cell wall components and oligosaccharides) is well demonstrated in plants. Several reviews on plant chitinase expression during host–pathogen interaction are available for annual species, whilst reports of their expression in tree species are limited to a few woody perennials: *Populus, Pinus, Picea, Eucalyptus, Castanea* and *Pseudotsuga*. The aim of this paper is to review the induction of chitinase during various stresses and developmental processes in forest tree species.

1 Introduction

Understanding of host-plant resistance mechanisms at the molecular level against biotic and abiotic pressures is well documented in short-lived crop species. In tree species with long generation times, large physical size, architectural complexity, large genome size (especially in gymnosperms) and lack of suitable experimental material with known genetic backgrounds, in-depth studies on molecular mechanisms involved in stress tolerance are limited to a few species. However, advanced genomics work is ongoing on selected angiosperm trees like poplar and *Eucalyptus* (Paiva et al. 2011; Zhong et al. 2011), while genomic research on gymnosperm trees will improve greatly in the next few years when the complete genomes of both Norway spruce (Neale and Kremer 2011) and Loblolly pine become available. However, the extent of similarity in molecular responses of seedling when compared with the mature trees is still unclear (Haukioja 2006). Presumably, the basal defence mechanisms in trees are comparable with their annual counterparts with possible differences in spatial and temporal patterns of gene regulation in tree species (Veluthakkal and Dasgupta 2010).

Pathogenesis-related (PR) proteins are host proteins induced in response to attack by pathogens or by a related event (van Loon et al. 1994). They are induced locally in response to pathogen attack as well as systemically in both compatible and incompatible host–pathogen interactions. The recognized PR proteins have been extensively reviewed (Broekaert et al. 2000) and currently comprise 17 families of induced proteins (van Loon et al. 2006). These families include one each of 1,3-glucanases (Simmons 1994; Saikia et al. 2005), proteinase inhibitors (Mosolov et al. 2001), one specific peroxidase (Lagrimini et al.1987; Ghosh 2006), the PR-1 family with unknown biochemical properties (Niderman et al.1995), the thaumatin-like PR-5 family (van Loon 1982), the birch allergen Betv1-related PR-10 family (McGee et al. 2001), defensins (Terras et al.1992), lipid-transfer proteins (LTPs) (García-Olmedo et al.1995), thionins (Bohlmann and Apel 1991) and other proteins including 2S storage albumins (Terras et al.1993) and ribosome-inactivating proteins (RIPs) (Nielsen and Boston 2001).

Chitinases (EC 3.2.1.14) are glycosyl hydrolases that catalyse hydrolytic cleavage of the β-1, 4- linked N-acetyl glucosamine (GlcNAc) units of chitin. They are well-characterized antifungal proteins involved in the plant defence response against pathogens and insect pests (Bol et al. 1990; Stout et al. 1994). Chitinases are grouped into two families (families 18 and 19) of glycosyl hydrolases: exo-chitinases, which act only on the non-reducing end of the chitin chain; endo-chitinases, which hydrolyze internal β-1,4-glycoside bonds. Within these two families, the chitinases are further divided into seven classes (classes I to VII) based on structure, substrate specificity, mechanisms of catalysis, sensitivity to inhibitors and subcellular localization (Brunner et al. 1998). Class I, II, IV, VI and VII chitinases make up family 19, whereas class III and V chitinases constitute family 18 (Neuhaus 1999). They are classified under PR protein families PR3, PR4, PR8 and PR11 (van Loon and van Strien 1999; Neuhaus 1999). Many plant endochitinases, especially those with a high isoelectric point, exhibit an additional lysozyme or lysozyme like-activity hydrolysing the peptidoglycan of bacterial cell walls, thus acting as bifunctional enzymes with antifungal and antibacterial activity (Collinge et al. 1993; Brunner et al. 1998; Schultze et al. 1998; Subroto et al. 1999).

Plant chitinases are likely to have arisen from one common ancestor by divergent evolution (Monzingo et al. 1996). All classes of chitinases have evolutionary relationships, wherein class I and II probably evolved from a more recent common ancestor (Shinshi et al. 1990; Araki and Torikata 1995) and form a monophyletic group with class IV (Hamel et al. 1997). Further, it is assumed that class IV chitinases have evolved from a class I chitinase gene by four deletions in the coding sequence (Araki and Torikata 1995). The derivation of the class IV lineage from class I or class II was assumed to have evolved before the separation of monocots and dicots (Hamel et al. 1997; Wiweger et al. 2003).

Chitinases and their pseudogenes are encoded by multigene families (Davis et al. 1991), and the recently sequenced *Populus trichocarpa* genome revealed that the chitinase gene families in poplar is larger with 25 members when compared with 12 in

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Arabidopsis and 15 in rice (Duplessis et al. 2009). Earlier studies have revealed that the non-synonymous substitution rates in plant class I chitinase often exceeded the synonymous rates of substitution (Bishop et al. 2000). This work revealed the evolutionary plasticity of this group of defence-related genes in trees because of the large diversity of gene families evolving from ancient and recent segmental duplications, suggesting the ecological advantage of perennials in pathogen response over short-lived herbaceous species.

In many crop plants including species like rice (Lin et al. 1995; Datta et al. 2000), wheat (Bliffeld et al. 1999) and oilseed rape (Grison et al. 1996), research on transgenics expressing chitinase genes has led to enhanced disease resistance against fungal pathogens. In trees, reports on genetic transformation using chitinase genes are limited to a few reports in hybrid poplar (*Populus simonii* × P. nigra) and *P. tomentosa*, where enhanced disease resistance was observed in the transgenic lines (Jia et al. 2010; Zhiying et al. 2010). Parsons et al. (2004) reported the transformation of silver birch (*Betula pendula*) with a sugar beet class IV endochitinase and demonstrated increased resistance of few transgenic lines against the rust disease caused by *Melampsoridium betulinum* under field conditions. Recently, in *Pinus monticola*, a class IV chitinase (*PmCh4B*) was used as a marker for selection of genotypes with resistance against the pine blister rust pathogen *Cronartium ribicola*. Association analysis of *PmCh4B* revealed that allelic variants and multiple single nucleotide polymorphisms were significantly associated with quantitative levels of *P. monticola* resistance against *C. ribicola* (Liu et al. 2011).

Chitinases are also reported to play a role in organ growth and development, nodulation (Staehelin et al. 1995), ectomycorrhizal formation (Salzer et al. 1997) and embryo development (Wiweger et al. 2003). The focus of this review paper is to assimilate the reports on induction of chitinases during various stresses and developmental processes in perennial tree species.

2 Induction of chitinase during biotic interactions

Stress is an external factor that exerts a negative influence on plants (Levitt 1980). On perceiving stress, plants switch on several signal transduction pathways, resulting in physiological and molecular changes in them. These signal transductions are mediated through isolated, linear pathways (Kariola 2006). The systemic induction of chitinases during fungal pathogen infection in plants is well documented. In trees, chitinases and their homologues are reported to be induced during pathogen infection in *Picea abies, P. sitchensis Pinus sylvestris, Pinus monticola, Pseudotsuga menziesii, Castanea sativa, Casuarina equisetifolia* and *Ulmus* sp. The different classes of chitinases induced in these species was briefly reviewed earlier (Veluthakkal and Dasgupta 2010). Wargo (1975) reported that the chitinase from oak caused *in vitro* hydrolysis of cell walls of *Armillaria mellea*, signifying an important role for chitinase in resistant mechanisms of oak trees. In Norway spruce, a decrease in transcript levels of class I chitinase was reported when inoculated with *Heterobasidion annosum*, while the expression of class II and IV chitinases increased (Hietala et al. 2004). High constitutive levels of chitinases in Norway spruce suggested a significant role in releasing fungal cell wall elicitors at the onset of infection and also in inducing the early systemic defence response (Fossdal et al. 2007). Rinaldi et al. (2007) reported the up-regulation of three distinct groups of chitinase-like genes, including basic (PR-8) and acidic (PR-3) chitinases in rust-infected (*Melampsora larici-populina*) leaves of *P. trichocarpa* × Populus deltoides. Islam et al. (2010) identified three class II and six class IV chitinase genes from Douglas-fir (*Pseudotsuga menziesii)* seedlings infected by *Phellinus sulphurascens*. Quantitative reverse-transcriptase–polymerase chain reaction analyses showed significant differential expression patterns of expression locally in root tissues and systemically in needle tissues after fungal invasion. Table 1 gives a list of all the reported classes of chitinases induced in tree species during host–pathogen interaction.

In addition to their role during biotic interactions, Class I chitinases have also been identified as major panallergens in fruits associated with the latex-fruit syndrome (latex allergy and allergy to plant-derived foods) such as avocado and banana. In Japanese cedar (*Cryptomeria japonica*), three allergens, *Cry j 1, Cry j 2* and *CJP-6,* were characterized from pollen, of which *CJP-4* cDNA encoded 281 amino acids with significant sequence homology to class IV chitinases and which revealed endochitinase activity (Fujimura et al. 2005). Similarly, in chestnut, the presence of two major allergens, lipid-transfer proteins and class I chitinases, were reported in the context of the latex-fruit syndrome (Monge et al. 2006).

Table 1. Expression of different classes of chitinase in tree species during biotic interactions.

Classes of chitinase	Tree species	Biotic agent	References
Class I chitinase	*Casuarina equisetifolia*	*Trichosporium vesiculosum*	Veluthakkal and Dasgupta 2010
	Ulmus americana	*Ophiostoma ulmi*	Sticklen, et al.1998
	Picea abies	*Heterobasidion annosum*	Hietala et al. 2004
Class II chitinase	*Pseudotsuga menziesii*	*Phellinus sulphurascens*	Islam et al. 2010
	P. abies	*H. annosum*	Hietala et al. 2004
	Pinus sylvestris	*Trichoderma aureoviride*	Adomas et al. 2007
Class III chitinase	*Casuarina glauca*	*Frankia*	Fortunato et al. 2007
	Quercus robur	*Piloderma croceum*	Frettinger et al. 2006
Class IV chitinase	*Pinus monticola*	*Cronartium ribicola*	Liu et al. 2005
	P. abies	*Ceratobasidium bicorne*	Johnk et al. 2005; Hietala et al. 2004
		H. annosum	
	P. menziesii	*Phellinus sulphurascens*	Islam et al. 2010
	Picea sitchensis	*H. annosum*	Deflorio et al. 2011
Chitinase-like genes	*Populus trichocarpa* × *Populus deltoides*	*Melampsora larici-populina*	Rinaldi et al. 2007

Although mainly studied for their antifungal properties, chitinases are also interesting as a protective agent against insects, particularly Hemipterans (Gatehouse and Gatehouse 1998). Induction of an endochitinase was reported in poplar leaves in response to herbivory by forest tent caterpillars, *Malacosoma disstria* (Ralph et al. 2006). Similarly, a poplar chitinase, *WIN6*, was induced during infestation by gypsy moth larvae, *Lymantria dispar* (Parsons et al. 1989; Constabel et al. 2000; Lawrence and Novak 2006).

Co-ordinated expression of PR genes is mediated partially by the accumulation of small diffusible signalling molecules, salicylic acid (SA) and jasmonic acid (JA) (Enyedi et al. 1992; Yang et al. 1997; Schenk et al. 2000). Chitinases are also induced by compounds including ethylene, chitin, chitosan, SA and JA (Dixon et al. 1994; Graham and Sticklen 1994). Methyl jasmonate (MeJA) treatment enhanced resistance of Norway spruce seedlings to *Pythium ultimum* through the activation of the salicylic acid pathway and subsequent induction of chitinase. MeJA induced the accumulation of free salicylic acid in all parts of the seedlings, whereas bound SA increased only in hypocotyls and cotyledons (Kozlowski et al. 1999). Similarly, in *Ficus carica*, the expression of chitinase was induced by JA (Kim et al. 2003). In Western white pine (*Pinus monticola*), the application of MeJA and protein phosphatase 1 and 2A inhibitor (okadaic acid) increased the accumulation of a class IV chitinase *PmCh4A* (Liu et al. 2005). This finding suggests that a subset of genes is coregulated by both SA and JA and comprises a uniquely evolved sector of plant signalling during defence reactions (Salzman et al. 2005). In the *Eucalyptus* hybrid *E. grandis* × *E. urophylla,* a chitinase gene was induced on treatment with the acetyl salicylic acid analogue acibenzolar-S-methyl (Boava et al. 2010). Other compounds, including chitosan, induced secreted chitinase activity in loblolly pine cell cultures (Popp et al. 1997), indicating the likely role in pine–fungi interactions (Wu et al. 1997). The pine chitinase *Pschi4* was induced by chitosan both in cell culture conditions and in transgenic tobacco, suggesting similar signalling pathways for chitin-induced transcription in gymnosperms and angiosperms (Wu et al. 1997).

3 Induction of chitinase during symbiosis

Trees with well-developed ectomycorrhizal associations are assumed to be generally more resistant to environmental stresses like drought and infection by root pathogens (Smith and Read 1997; Finlay et al. 2008). Molecular and biochemical analyses have shown that mycorrhizal association triggers the induction of several defence-related proteins in host plants including the up-regulation of chitinases (Spanu and Bonfante-Fasolo 1988; Albrecht et al. 1994; Vierheilig et al. 1994; Pozo et al. 1996; Xie et al. 1999). However, the expression of these genes is low and transient during symbiotic association when compared with expression during host–pathogen interactions. The possible role of chitinases in the regulation of symbiosis and during plant defence against root pathogens has been reviewed by Lambais and Mehdy (1998), and Guadot et al. (1996). Vasse et al. (1993) reported that chitinases might play a role in autoregulation mechanisms in plants to control infection and nodulation. They are also reported to inactivate *Nod* factors, the key signal molecules secreted by rhizobia during nodule development, by cleaving the chito-oligosaccharide backbone of the *Nod* factors. Staehelin et al. (1994, 1995) reported that the initial step during nodulation is controlled through the degradation of lipochito-oligosaccharide nodulation signals by chitinases that are secreted from root tissues of host plants. Salzer et al. (1997) suggested that the response of host plants to the elicitor signal is attenuated to allow symbiotic interactions.

Expression of two different chitinases was studied in the lateral and principal roots of *Quercus robur* during interactions with the ectomycorrhizal fungus *Piloderma croceum*, revealing an up-regulation of a chitinase (*QrchitIII-1*) in lateral roots and no significant differential expression in principal roots, indicating that the enhanced expression of *QrchitIII-1* in lateral roots may have a role in symbiosis (Frettinger et al. 2006). Similarly, *cgchi3,* the gene encoding a class III chitinase, was cloned and characterized from actinorhizal nodules of *Casuarina glauca*, which was specifically activated in root nodules (Fortunato et al. 2007). In spruce cell cultures, elevated chitinase activity was induced by the ectomycorrhizal symbiont *Amanita muscaria* (Sauter and Hager 1989). Interestingly, in *Eucalyptus*, the extent of chitinase isoform induction was correlated with the aggressive or non-aggressive nature of ectomycorrhizal strains. Further, no difference in chitinase activity was observed on induction following root colonization by pathogenic or ectomycorrhizal fungi, and the systemic expression of chitinase was observed even during symbiotic interaction (Albrecht et al. 1994).

4 Induction of chitinase during abiotic stress

Water-deficit conditions, low temperature (chilling and freezing), heat, salinity and oxygen deficiency are some of the major stress factors that affect plant growth. To surmount such situations, therefore, plants acclimatize by undergoing various biochemical and physiological changes including induction of certain defence-related genes. Abiotic stresses like ozone treatment, wounding and osmotic stress up-regulate chitinase expression (Schraudner et al. 1992; Hamel and Bellemare 1995; Arie et al. 2000). Nagy et al. (2004) demonstrated that drought stress in Norway spruce seedlings induced defences similar to those of pathogen infection including expression of chitinases. Two chitinases (*PhCT 1* and *PtCTL*) were up-regulated in *Pinus halepensis* and *Pinus taeda* in response to drought stress (Sathyan 2004). In *Cryptomeria japonica* sapwood, ESTs encoding class I chitinase were abundant during drying (Yoshida et al. 2007). Investigation of the local and systemic-induced defence responses in the Norway spruce – *Rhizoctonia* sp. pathosystem revealed a significant impact of drought on induction of defence-related genes and both stresses synergistically induced earlier transcriptional changes when compared with individual stresses. In shoots, an increase in chitinase transcripts (*CHI4c, CHI2*) was induced systemically in shoots and locally in root tissues during both stresses (Fossdal et al. 2007). The mechanism of action of chitinase during drought stress remains unclear. Nevertheless, the induction of chitinase in plants during water stress was explained, in part, as a second defence mechanism to

protect the plant from pathogen attack (Chen et al. 1994), a condition in which plants become more susceptible to diseases (Colhoun 1979).

Most plants from temperate regions can acclimatize to cold and develop freeze tolerance (Guy 1990). The antifreeze property of chitinase is well documented, and the ice-binding activity has been experimentally demonstrated in several plant species (Yeh et al. 2000; Griffith and Yaish 2004; Kikuchi and Masuda 2009; Gao et al. 2011). In trees, the only report on antifreeze activity of chitinases was from Douglas fir. An extracellular protein from *Phellinus weirii* that infected Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) roots and needles showed endochitinase-like enzyme activity, and the accumulation of the protein in the winter months suggested a probable antifreeze activity (Zamani et al. 2003).

Wounding is a continual threat to the survival of all organisms, and the response to this damage has been extensively studied in plants. The type of wounding, whether strictly mechanical or combined with other components such as insect saliva, is critical for determining the plant response (Reymond et al. 2000; Arimura et al. 2002). Wounding can induce formation of jasmonates and ethylene, each of which is independently capable of inducing signal transduction pathways, leading to resistance against insect pests. Young leaves of poplar trees accumulated novel mRNAs, two of which, *win6* and *win8*, encoded proteins similar to chitinases from other plants (Parsons et al. 1989). Similarly, Win6 and the related protein, Win8, accumulated in wounded plants of *Populus trichocarpa* and *P. deltoides* × *P. trichocarpa*, indicating that mechanical wounding induced chitinases, imparting tolerance to opportunistic pathogens (Clarke et al. 1994, 1998). It was also demonstrated that the *win6* promoter had regulatory elements responsive to wound signals, which responded to wounding locally and remotely in transgenic tobacco (Clarke et al. 1994). Similarly, expression of the class IV chitinase *PmCh4A* was strongly induced in the needles of Western white pine in response to mechanical wounding (Liu et al. 2005). Wounding also enhanced transcript levels of class II and IV chitinases and decreased class I chitinase in Norway spruce (Hietala et al. 2004).

5 Induction of chitinase during development

Apart from playing a role in plant defence reactions, chitinases probably have functions related to plant growth such as cell division, differentiation and development (Collinge et al. 1993; Sahai and Manocha 1993). Developmental regulation, revealing a morphogenetic role of chitinases especially during cell wall disrupting events, such as flowering and reproduction, has been described earlier (Lotan et al. 1989; Leung 1992; Sahai and Manocha 1993). Chitinases are also induced during leaf senescence (Hanfrey et al. 1996), seed germination (Petruzzelli et al. 1999; Wu et al. 2001) and embryogenesis (Jong et al. 1992; van Hengel et al. 1998; Helleboid et al. 2000).

Extracellular signal molecules, including arabinogalactan proteins, lipochito oligosaccharides and chitinases, were reported to regulate somatic embryogenesis in Norway spruce. A transcript *Chia4-Pa1* with similarity to basic class IV chitinase was isolated from proliferating embryogenic cultures of Norway spruce. The encoded chitinase had a different intron-exon organization from that in angiosperm class IV chitinases (Wiweger et al. 2003). Similarly, a cDNA corresponding to a basic class IV chitinase (*PgChi-1)* was isolated from *Picea glauca* somatic embryos (Dong and Dunstan 1997). *PgChi-1* was also reported to be enhanced by wounding, drying and flooding stresses.

6 Conclusions

Disease resistance in long-lived woody perennials is commonly explained by polygenic models, where resistance is continuous and controlled by many genes, each with additive effects (von Weissenberg 1990). Chitinases, which are included predominantly under the PR3, are the most studied defence-related proteins in plants. The induction of chitinases during systemic disease resistance is well documented *in* Planta, and the genetic transformation studies using chitinases as transgenes have demonstrated increased resistance to pathogens in poplars and silver birch. Chitinases are also targets for incorporating insect resistance into trees, as insect growth and morphogenesis are dependent on chitin, the degradation of which affects insect development. Hence, chitinases have a potential role in the development of biopesticides or chemical defence proteins in plants against insect pests (Kramer and Muthukrishnan 1997). Further, these genes were also identified as candidates for marker-assisted selection for quantitative resistance against fungal pathogens in pine (Liu et al. 2011).

Apart from the importance of chitinases in tree defence, expression during symbiosis, abiotic stresses and developmental stages highlight the additional functions of these proteins in plants. Hence, identification and functional analysis of chitinases during biotic resistance will provide a repository of characterized defence-related genes for future genetic transformation studies or as candidates for marker-assisted selection during tree-breeding programmes.

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