

Plant Chitinases and Their Roles in Resistance to Fungal Diseases¹

ZAMIR K. PUNJA AND YE-YAN ZHANG²

Abstract: Chitinases are enzymes that hydrolyze the N-acetylglucosamine polymer chitin, and they occur in diverse plant tissues over a broad range of crop and noncrop species. The enzymes may be expressed constitutively at low levels but are dramatically enhanced by numerous abiotic agents (ethylene, salicylic acid, salt solutions, ozone, UV light) and by biotic factors (fungi, bacteria, viruses, viroids, fungal cell wall components, and oligosaccharides). Different classes of plant chitinases are distinguishable by molecular, biochemical, and physicochemical criteria. Thus, plant chitinases may differ in substrate-binding characteristics, localization within the cell, and specific activities. Because chitin is a structural component of the cell wall of many phytopathogenic fungi, extensive research has been conducted to determine whether plant chitinases have a role in defense against fungal diseases. Plant chitinases have different degrees of antifungal activity to several fungi *in vitro*. *In vivo*, although rapid accumulation and high levels of chitinases (together with numerous other pathogenesis-related proteins) occur in resistant tissues expressing a hypersensitive reaction, high levels also can occur in susceptible tissues. Expression of cloned chitinase genes in transgenic plants has provided further evidence for their role in plant defense. The level of protection observed in these plants is variable and may be influenced by the specific activity of the enzyme, its localization and concentration within the cell, the characteristics of the fungal pathogen, and the nature of the host-pathogen interaction. The expression of chitinase in combination with one or several different antifungal proteins should have a greater effect on reducing disease development, given the complexities of fungal-plant cell interactions and resistance responses in plants. The effects of plant chitinases on nematode development *in vitro* and *in vivo* are worthy of investigation.

Key words: antifungal protein, biotechnology, chitinase, disease resistance, enzyme, fungus, genetic engineering, hydrolase, nematode.

Chitin, a β -1,4-linked polymer of N-acetylglucosamine, is a structural component in a diverse array of organisms, including fungi, insects, various crustaceans, and nematode eggs (32,47,53,149,157). In nature, chitin forms a complex with various other substances, such as polysaccharides and proteins (149). Chitin can also be found in agricultural and noncultivated soils. It has not, however, been reported as a constituent of higher plant cell walls. The enzyme chitinase (poly [1,4-(N-acetyl- β -D-glucosaminide) glycanhydrolase, EC 3.2.1.14] hydrolyzes the chitin polymer to release N-acetyl glucosamine oligomers, following either endo or exo cleavages of the β -1,4 bond. Other enzymes such as chitosanases act on the related substrate chi-

tosan (a polymer of β -1,4-D-glucosamine) (55,137).

Various techniques for assaying for chitinases have been described (15,47,138, 197). Higher plants produce endochitinases, either constitutively or following induction, and the possible functions of these enzymes within the plant have generated much interest and speculation. Chitinases are also secreted by a number of different microorganisms, including actinomycetes, soil bacteria, and various fungi (30,67,101,136), and in many cases appear to be involved in the biological control of fungal pathogens (30,67,101,136,166). One of the roles attributed to chitinases in higher plants is a defense mechanism against attack by pathogens, especially fungi, because the expression of chitinases is significantly enhanced following infection. Furthermore, chitinases have antifungal activity and cause hyphal tips to lyse *in vitro* (113,165,166). Some chitinases also have lysozymal activity and can hydrolyze the peptidoglycans in bacterial cell walls (10,35,74,106,110,150,183), whereas others have exohydrolytic activity (110,112,

Received for publication 20 May 1993.

¹ Symposium paper presented at the 31st Annual Meeting of the Society of Nematologists, 2-6 August 1992, Vancouver, British Columbia, Canada. This research was supported by the Natural Sciences and Engineering Research Council of Canada.

² Associate Professor and Research Associate, Department of Biological Sciences, Centre for Pest Management, Simon Fraser University, Burnaby, British Columbia, V5A 1S6, Canada.

154). The expression of chitinases could therefore be speculated to have a defensive role during both the early and the late stages of the infection process, depending on the levels of constitutive enzyme and the rapidity of induction.

Much of the evidence for the suggested roles of chitinases in plant defense has been based on dramatic and rapid enhancement of enzyme levels in hypersensitive reactions, during induced host resistance (i.e., in association with several other pathogenesis-related [PR] proteins), and in tissues following infection by a pathogen. These observations, however, are not conclusive for the roles of these enzymes in resistance, because a cause-and-effect relationship cannot be discerned. The availability of techniques in molecular biology now permits the isolation of specific genes and their reintroduction into plants, providing a powerful tool to elucidate the roles of specific enzymes in plants. The objectives of this paper are to review the occurrence of chitinases in plants and factors enhancing chitinase expression, to summarize the evidence for the possible roles of chitinases in plants, and to review the application of genetic engineering to study the role of chitinases in plant defense against pathogens. This area of research has gained much attention, which is apparent from the vast recent published literature (for reviews, see also 34,47); therefore, only relevant articles published during 1987–93 are reviewed here.

OCURRENCE AND INDUCTION OF PLANT CHITINASES

Chitinases have been reported from over 41 monocotyledonous and dicotyledonous plant species and occur in widely different tissues, including embryos (23,106), seeds (66,72,83,94,95,106,130,179,200), cotyledons (33,106,202), leaves and stems (16,69,71,82,114,115,147,183,186), roots (106,120,129,162,180), flowers (98,102,129,183), leaf abscission zones (52), tissue-cultured calli (167,196), cell suspension cultures (10,44,50,61,62,

80,83,85–88,111,135,162,191,192,196), and protoplasts (56,152). Among cultivated crop species, chitinases occur in azuki bean (69,70), barley (71,72,82,83,94,95,178), bean (4,25,37,61,73,105,108,109,114,115,179,193), cabbage (29), cacao (170), carrot (39,85–88,201), celery (84), chickpea (191,192), corn (63,66,128,130,188), cucumber (16,68,106,122,123,201,202), garlic (186), leek (171), melon (153–155), oat (45,46), onion (40,196), pea (40,79,112,113,185), peanut (5,62), potato (51,81,89,142,164), pumpkin (44), rapeseed (58,71,144,145), rice (65,111,135,169,204), rye (200), soybean (174), sugarbeet (48,124,156), sunflower (77), tobacco (12,22,23,28,43,50,56,64,78,93,96,116,120,139,141,163,167,168,183,184,190,194,199), tomato (20,76), turnip (35), wheat (23,147), and yam (1,2). In addition, there are reports of chitinases in noncrop species, including *Arabidopsis* (159,187), bentgrass (80), chestnut (33), Job's Tears (3), petunia (98), poplar (38,140), rubber (74,110), spruce (162), stinging nettle (97), tall fescue (148), thornapple (23), and Virginia creeper (10).

Many plant chitinases are expressed constitutively, generally at a low level. Some evidence exists for the developmental regulation of chitinase expression in specific tissues and at specific stages during plant development (95,98,102,106,112,120,129,142,159,160,167,183,199,203). The biological significance of these chitinases have yet to be elucidated, and they may have as yet undetermined functions in plant development. In carrot, for example, chitinase was shown to enhance somatic embryo development (39).

In general, chitinases are induced by numerous unrelated factors: infection by viruses (4,12,16,19,64,93,96,122,123,128,139,141,183,190,194), viroids (20), pathogenic fungi (5,28,37,46,61,76,81,82,105,112,116,123,124,139,144,145,153,154,156,164,169,180,194,185), mycorrhizal fungi (40,162,171), endophytic fungi (148), and bacteria (22,35,73,116,123,193); application of ethylene (13,14,

19,20,25,28,52,69,70,78,112,114,115,120, 135,146,152,186), chitosan (79,84,111, 202), salicylic acid (69,111,142,194,186, 196), acetylsalicylic acid (77), salt solutions (68,146), heavy metals (4,71,128), fungal cell wall components and oligosaccharides (22,61,62,79,86–88,152,155,203), and pectic polysaccharides (22); exposure to UV light (19,62) and ozone (43,163); insect (27) or nematode (18,148) feeding; and mechanical wounding (61,69,140,186,202, 203). There are reports of a reduction in chitinase expression by various plant hormones (167), heat shock (21,186), and mycorrhizal development in roots (92). Chitinase induction in plants is therefore generally nonspecific and enhanced by both biotic and abiotic stresses, and is only one component of the plant response to various pathogens and stresses (12,17,99).

Following induction, chitinases may accumulate locally at the sites of challenge or systemically in other tissues (16,68,123, 139,140,155,184,194). In addition, chitinases may be extracellular or vacuolar (16, 100,118). In some plants, several closely related isoforms of chitinase can be induced (62,82,112,186). Thus, chitinases are encoded by members of a small gene family (28,38,61,62,64,81,93,95, 96,128,135,140,144,186,204).

CHARACTERISTICS OF PLANT CHITINASES

Many chitinases, like many other pathogenesis-related (PR) proteins (17,99,117) are acid extractable, have low molecular weights, are resistant to proteases, and are secreted extracellularly (12,99). Plant chitinases generally range in molecular weight from 25 to 36 kD and may be either acidic or basic. Based on amino acid sequences, chitinases can be grouped into at least four classes, many of which can occur in the same plant species. Class I includes the majority of chitinases described to date, e.g., in *Arabidopsis* (159), bean (25,109,151), barley (178), chickpea (192), pea (185), poplar (38,140), potato (51,89), rice (65,135,204), sugarbeet (124), and tobacco (100,168, 175). Class I chitinases have an N-terminal

cysteine-rich lectin or "hevein" (chitin-binding) domain and a highly conserved catalytic domain (70–88% homology). Class I chitinases are generally basic and vacuolar. A C-terminal extension of seven amino acids is involved in targeting of the protein to the vacuole (6,118,126,133), and a model for intracellular transport has been recently described (175,176).

Class II chitinases, e.g., in tobacco (141), petunia (100), and barley (95), are similar in sequence to Class I (60–64% homology) but lack the cysteine-rich domain. Class II chitinases are generally acidic and targeted to the apoplast. Class III chitinases have a different amino acid sequence in the catalytic domain from Classes I and II and lack a cysteine-rich domain. Class III chitinases include the acidic extracellular chitinases from *Arabidopsis* (159), adzuki bean (69,70), chickpea (192), cucumber (122), sugarbeet (48,134), and tobacco (93), and the basic chitinases of *Parthenocissus* (10), rubber (74,110), and tobacco (93).

Other described chitinases do not belong to the above three classes and may represent new classes. Acidic extracellular chitinases with a cysteine-rich domain occur in bean (109), poplar (38), and yam (1,2) and may be a subclass of Class I. A basic chitinase from rapeseed (140) and sugarbeet (124) was found to have little homology with any of the other classes and could constitute class IV (124,144,145). Because of the homology in amino acid sequences within the above classes, many (but not all) of the chitinases show serological relatedness, and several have strikingly similar biochemical and physicochemical characteristics (20,23,96). The chitinases from monocots appear to have diverged from those in dicotyledonous plants (63,66). For several plant chitinases, complementary DNA clones and genomic clones have been isolated, and the amino acid sequences have been deduced, as in *Arabidopsis* (159), adzuki bean (69), barley (95), bean (61,108,109), corn (66), cucumber (122), garlic (186), peanut (62), potato (51), rapeseed (58,144), rice (65,135,204), sugarbeet (124), and tobacco (28,50,64,93,

100,141,167,168). The promoter regions of the chitinase genes in bean and *Arabidopsis* have been characterized (25,160).

Chitinases show inhibitory activity to fungal spore germination and mycelial growth in disc plate diffusion or microtiter plate assays with partially purified or purified proteins. This finding has led to the long standing hypothesis that they must have a defense role against pathogen invasion in plants. The most frequently used test organisms have been species of *Trichoderma* (23,33,66,95,113,150,179,184), *Fusarium* (66,95,113,165,179), and *Alternaria* (66). However, because the proportions of polysaccharides such as chitins and glucans, and other components such as lipids and proteins, can vary considerably in fungal cell walls (157), their susceptibility to lysis by chitinase alone would be expected to differ, as has been observed for several fungi (23,66). In Oomycete fungi, chitin is almost absent and is replaced by cellulose (157), making plant pathogens in this group a less likely target for chitinases.

The different isoforms of plant chitinases may also differ in substrate-binding characteristics and specific activities (66, 70,96,106,192), important factors that can be overlooked when measuring total tissue chitinase activity in antifungal activity tests. Different chitinases from a given host species can also differ in specific and antifungal activity (66,96,106,165,192). For example, acidic (class II or III) chitinase from tobacco or chickpea (119,165,192) displayed less antifungal activity when tested in vitro than basic (class I) chitinase (119, 165,192). Therefore, all chitinases do not have equal antifungal activity, a fact that could impact the outcome of genetic engineering with chitinase-encoding genes.

ROLES OF CHITINASES IN DISEASE RESISTANCE

Because chitinases are induced by agents that simultaneously enhance other defense reactions and pathogenesis-related proteins in the same plant tissues (12,17,99), elucidation of the specific roles of these en-

zymes in resistance is difficult. Important considerations are the rapidity of chitinase induction, the concentrations in tissues, and localization in cells relative to growth of the incoming pathogen. Numerous studies have compared chitinase induction in tissues that are resistant (incompatible) or susceptible (compatible) to a fungal pathogen with regard to rate of induction and final concentrations in tissues. The results from these studies are not clear. In some plant species, resistant tissues accumulated chitinases more rapidly and in some instances to higher final concentrations than susceptible tissues (9,37,61,68, 76,144,145,185,191,199). Because in many of these cases, the resistant response initially was a hypersensitive reaction, with very rapid localized cell death (12,57,61, 164,190,193), the injury and stress response of the cells could have rapidly induced chitinase production in adjoining cells or tissues.

In other plant species, however, there was no difference between chitinase accumulation in susceptible and resistant tissues, or paradoxically the susceptible tissues accumulated higher levels of the enzymes (5,82,164,192). The latter response can be explained by greater fungal biomass accumulation in the diseased tissues than in healthy tissues, and greater stress on the diseased plant, two factors that can induce greater levels of chitinases. Thus, in the latter host-pathogen interactions, chitinases may have either no role or a secondary role in retarding pathogen development following infection. Chitinases may also indirectly trigger defense reactions within the plant, because fungal cell wall fragments released by enzymatic digestion can act as elicitors of the biosynthetic pathways that lead to the accumulation of phenolic compounds and lignins in the cell (13,49,87,147).

The rapidity of chitinase induction in plant tissues varies considerably depending on the specific host-pathogen interaction. The use of cell suspension cultures has greatly facilitated experimental approaches to study the effects of elicitors on

transcription and subsequent protein accumulation. These cultures permit synchronous induction and provide high quantities of mRNA. However, the results from suspension cultures should be extrapolated carefully to intact differentiated tissues. In bean, chitinase mRNA was detectable within 5–20 minutes after elicitation, with a maximum at 2 hours (61); in other species, mRNA or protein levels were maximal between 4 and 16 hours after elicitation (43,62,68,69,73,155,163). These findings point to transcriptional activation of gene expression, which in some plant species resulted in a differential pattern of gene expression depending on the type of stimulus. For example, specific mRNAs or isoforms of the chitinases were induced only by certain pathogens or specific stimuli (28,35,62,108,139,144). Although the signal transduction pathway is unknown, potential receptors for chitinase gene induction could be general and modulated by ethylene response (14,69) or salicylic acid (107,194) or be elicited by specific cues (90,91).

In a majority of the plant species examined, chitinase activity was enhanced after 1 to 28 days following induction by abiotic and biotic factors (16,20,46,81,82,93,96,105,116,123,139,142,145,153,154,156,184,185,190). This time frame indicates that the gradual accumulation of chitinases in diseased tissues may be involved only in slowing down pathogen growth and perhaps reducing growth and sporulation at later stages of disease development; in these cases, chitinases are not specifically involved in the early events of host–pathogen interactions. The delayed accumulation of chitinases in potato did not account for the race–cultivar specificity of *Phytophthora infestans* following the hypersensitive reaction (164).

The tissues in which chitinases accumulate can also influence their potential role in the defense response. Extracellular chitinases would intuitively be expected to have an initial role in limiting pathogen growth upon entry of hyphae into the host, with vacuolar chitinases having a sec-

ondary or delayed effect following cell lysis (115). In bean and tobacco leaves treated with ethylene, chitinase accumulated within specific cell types (78,114). The pathogen behavior and host–pathogen interaction at the cellular level may also influence the effectiveness of chitinases. Fungal pathogens may be obligate biotrophs or necrotrophs and can grow intercellularly or through cells. Obligate biotrophs or intercellular pathogens may never encounter the vacuolar forms of chitinase, whereas necrotrophs or intracellular hyphae would encounter both extracellular and intracellular forms of chitinase. As already discussed, various isoforms may differ in localization and in antifungal activity. Direct injection of chitinase into epidermal cells was shown to inhibit development of intracellular fungal haustoria (182). The accessibility of chitin in the fungal cell walls to chitinase action is another important consideration, given that chitin and β -1,3-glucans are generally found in the innermost layers of the cell wall and thus may be protected, except at the hyphal tips (8,13,195). Removal of fungal cell wall proteins and soluble carbohydrates by heat treatment increased binding of chitinase to the wall (171). Further cytochemical and immunocytochemical studies (6,7,9,30,114,115,171,198) are needed to elucidate the chitinase–fungal cell wall interactions at the cellular level in planta.

GENETIC ENGINEERING OF PLANTS WITH CHITINASE GENES

The currently available techniques in transformation of many plant species have permitted experiments to answer the following intriguing question: would the overexpression of a cloned chitinase gene, behind a constitutive or inducible promoter, lead to enhanced resistance or tolerance against fungal infection in the transgenic tissues? Another approach that could be utilized to elucidate the roles of constitutive chitinases in plants is through antisense or sense transformation (60, 132). There are several recent examples

of the successful introduction of heterologous chitinase genes into plants. The first such success was the introduction of an exochitinase gene from *Serratia marcescens* into tobacco (41,42,75,103,104,125,181). Subsequently, genes or promoter sequences of plant origin encoding endochitinases have been introduced into various plant species. In transgenic tobacco, the promoter regions of a bean and rice chitinase gene were shown to be regulated by ethylene (25) and fungal elicitors (203), respectively. In transgenic *Arabidopsis* and tomato, the promoter region of an *Arabidopsis* chitinase gene was regulated developmentally in various tissues and by pathogen infection (160). In both transgenic hosts, expression of a reporter gene under control of the chitinase gene promoter was enhanced around necrotic lesions caused by fungal infection (160). Similar results were also obtained with a bean chitinase promoter in transgenic tobacco following infection by various pathogens (151). These studies show that chitinase gene promoter activity can be induced by pathogen attack, ethylene, and elicitors (25,151,160).

Genes expressing chitinases under control of the cauliflower mosaic virus 35S promoter have been introduced into several plant species. Results from inoculation studies of these transgenic plants with various filamentous fungal pathogens have differed. In tobacco transformed with the exochitinase gene from *Serratia* (41) or the vacuolar chitinase from bean (26), the disease severity and rate of development of *Rhizoctonia solani* (a necrotrophic pathogen) were reduced (26,41). Different levels of chitinase activity occurred in leaves, stems, and roots of transgenic plants (26, 60,131). Rapeseed plants transformed with a bean chitinase gene also had reduced disease development due to *R. solani* (26). In contrast, transgenic tobacco plants with enhanced constitutive levels of vacuolar chitinase were not more tolerant to infection by *Cercospora nicotianae* than the untransformed plants (131). Perhaps the intracellular localization of the chitinase in

these transgenic plants precluded early involvement in defense against this pathogen, which initially grows intercellularly. Recent reports of the reaction of transformed tobacco (134) and tomato (63) plants containing acidic chitinase genes from sugarbeet and corn, respectively, to inoculation with various fungi indicated that there was no increase in resistance to infection. The greater antifungal activity of basic chitinases compared to acidic chitinases discussed previously could in part explain this lack of resistance. Manipulation of the carboxy-terminal region involved in vacuolar targeting can result in secretion of these basic chitinases into the extracellular space (118,165). These plants would be worthy of further study to determine if inhibition of pathogen growth was subsequently enhanced. The events that take place at the cellular level in these transgenic plants following inoculation should also be studied using ultrastructural and immunocytochemical techniques.

Considerable evidence exists for the coordinated regulation and expression of other pathogenesis-related proteins in tissues that also express chitinases (12,14,54, 99,189,194). In particular, accumulation of β -1,3-glucanases closely parallels accumulation of chitinases in diseased tissues or abiotically stressed tissues (9,13,14,112, 189). Furthermore, β -1,3-glucanases and chitinases act synergistically to inhibit fungal growth in vitro (36,113,165). Other potential synergisms occur with lectins (24). Therefore, the engineering of chitinase-encoding genes into plants in conjunction with other genes encoding antifungal proteins should provide enhanced protection against fungal pathogens (31,36,59,91). Indeed, when a basic chitinase and a glucanase were simultaneously introduced into tomato, the level of protection was significantly higher than in plants expressing either one alone (119). This approach could lead to control of a broad range of fungal pathogens. Yet another strategy would be to introduce specific inhibitors of chitin synthesis into plants, such as polyox-

ins, to reduce development of pathogens that contain chitin (32,147,173).

CURRENT RESEARCH IN OUR LABORATORY

We are currently characterizing chitinase isozyme banding patterns in both cucumber and carrot following induction by biotic and abiotic factors. We have observed the appearance of new chitinase isoforms in cucumber cotyledons following wounding, pathogen inoculation, and application of salicylic acid; these isoforms differ from the constitutively produced isoforms (201,202). The induction of these isoforms in other plant tissues, in different cultivars, by different pathogens, and in tissue-cultured cells of cucumber and carrot are being studied (201,202). In additional research, we are introducing chitinase-encoding genes into both crops via *Agrobacterium*-mediated transformation (143,161) and evaluating the response of these transgenic plants to inoculation with various leaf- and root-infecting fungi. The results from this work should provide additional insights into the roles of chitinases in plant defense in these two important horticultural crops.

APPLICATION OF CHITINASES TO NEMATODE CONTROL

In some cases, the addition of chitinaeous amendments, e.g., crab shell, to soil has reduced the severity of diseases caused by plant-parasitic nematodes (53,172,177). This reduction was partly attributed to the enhancement of populations of soil microorganisms with chitinolytic activity (e.g., various fungi, bacteria, and actinomycetes), which could have reduced nematode activity and survival (53,172,177).

Chitin is a major structural component of nematode egg shells. This chitin layer can vary in thickness and is located between the outer vitelline layer and the inner lipid layer and may occur in association with proteins (11). As such, the chitin may not be readily exposed to the effects of chitinases, similar to the case with fungal pathogens. Furthermore, eggs that are

laid within a gelatinous matrix may be protected against enzymatic activity. Studies are needed to determine the effects of partially or totally purified chitinases of plant and microbial origin on nematode egg shell integrity and larval emergence and growth. In a recent study, chitinases increased hatch rates of *Meloidogyne* eggs (121); however, premature hatching led to mortality of juveniles and, in some cases, the eggs died. If chitinases do indeed have this type of activity against nematodes, then screening of currently available transgenic plants expressing chitinases for increased resistance to nematode development may be worthy of further investigation. Intuitively, endoparasitic pathogens (e.g., *Meloidogyne*, *Pratylenchus*) would be excellent candidates for evaluation because their eggs are laid on or in the host tissues, allowing maximum exposure to the chitinases. However, as with fungal pathogens, the same concerns of cellular localization, in vivo activity, and isoform of chitinase would have to be addressed in experiments with nematodes. As the results with fungal pathogens seem to indicate, chitinases alone may not significantly affect nematode development within the transgenic tissues. Therefore, the introduction of genes that encode proteins with proven nematocidal properties should also be considered in genetic engineering of plants for resistance to nematodes.

CONCLUSION

The widespread occurrence of chitinases in plants and their induction by a broad range of biotic and abiotic factors suggests that these enzymes must serve some general function related to plant stress or defense, or have as yet undetermined roles in development or senescence. Because different isoforms of the enzyme are known in plants, however, these isoforms may have different specific activities and roles and may be elicited by different agents through as yet undetermined signal transduction pathways. The introduction of genes encoding chitinases into trans-

genic plants will provide opportunities to specifically elucidate roles of these enzymes in defense. However, the outcome may be affected by the specific activity, concentration, and targeting of the enzyme within the cell, and the characteristics of the fungal–host cell interaction. The effects of plant chitinases on nematode development *in vitro* and *in vivo* are worthy of investigation.

LITERATURE CITED

- Araki, T., J. Funatsu, M. Kuramoto, and T. Torikata. 1992. Amino acid sequence of the N-terminal domain of yam (*Dioscorea japonica*) aerial tuber acidic chitinase. Evidence for the presence of a wheat germ agglutinin domain in matured acidic chitinase from unstressed tuber. *Plant Molecular Biology* 19:351–354.
- Araki, T., J. Funatsu, M. Kuramoto, H. Konno, and T. Torikata. 1992. The complete amino acid sequence of yam (*Dioscorea japonica*) chitinase. A newly identified acidic Class I chitinase. *Journal of Biological Chemistry* 267:19944–19947.
- Ary, M. B., M. Richardson, and P. R. Shewry. 1989. Purification and characterization of an insect α -amylase inhibitor/endochitinase from seeds of Job's Tears (*Coix lachryma-jobi*). *Biochemica et Biophysica Acta* 993:260–266.
- Awade, A., M. de Tapia, L. Didierjean, and G. Burkard. 1989. Biological function of bean pathogenesis-related (PR3 and PR4) proteins. *Plant Science* 63:121–130.
- Bama, M. S., and R. Balasubramanian. 1991. Chitinases and glucanases in *Arachis hypogaea* L. in detached leaves infected with *Puccinia arachidis* Speg. *Journal of Plant Diseases and Protection* 98:305–316.
- Bednarek, S. Y., and N. V. Raikhel. 1991. The barley lectin carboxyl-terminal propeptide is a vacuolar protein determinant in plants. *Plant Cell* 3:1195–1206.
- Benhamou, N., and A. Asselin. 1989. Attempted localization of a substrate for chitinases in plant cells reveals abundant N-acetyl-D-glucosamine residues in secondary walls. *Biology of the Cell* 67:341–350.
- Benhamou, N., K. Broglie, R. Broglie, and I. Chet. 1993. Antifungal effect of bean endochitinase on *Rhizoctonia solani*: Ultrastructural changes and cytochemical aspects of chitin breakdown. *Canadian Journal of Microbiology* 39:318–328.
- Benhamou, N., M. H. A. J. Joosten, and P. J. G. M. de Wit. 1990. Subcellular localization of chitinase and of its potential substrate in tomato root tissues infected by *Fusarium oxysporum* f. sp. *radicis-lycopersici*. *Plant Physiology* 92:1108–1120.
- Bernasconi, P., R. Locher, P. E. Pilet, J. Jolles, and P. Jolles. 1987. Purification and N-terminal amino-acid sequence of a basic lysozyme from *Parthenocissus quinquefolia* cultured *in vitro*. *Biochemica et Biophysica Acta* 915:254–260.
- Bird, A. F., and J. Bird. 1991. The structure of nematodes, 2nd ed. San Diego: Academic Press.
- Bol, J. F., H. J. M. Linthorst, and B. J. C. Cornelissen. 1990. Plant pathogenesis-related proteins induced by virus infection. *Annual Review of Phytopathology* 28:114–138.
- Boller, T. 1987. Hydrolytic enzymes in plant disease resistance. Pp. 385–413 in T. Kosuge and E. Nester, eds. *Plant–microbe interactions, molecular and genetic perspectives*, vol. 2. New York: McMillan Press.
- Boller, T. 1988. Ethylene and the regulation of antifungal hydrolases in plants. Pp. 145–174 in B. J. Mifflin, ed. *Oxford surveys in plant molecular and cell biology*, vol. 5. Oxford: Oxford University Press.
- Boller, T. 1992. Biochemical analysis of chitinases and β -1,3-glucanases. Pp. 23–30 in S. J. Gurr, M. J. McPherson and D. J. Bowles, eds. *Molecular plant pathology*, vol. 2—A practical approach. Oxford: Oxford University Press.
- Boller, T., and J. P. Métraux. 1988. Extracellular localization of chitinase in cucumber. *Physiological and Molecular Plant Pathology* 33:11–16.
- Bowles, D. J. 1990. Defense-related proteins in higher plants. *Annual Review of Biochemistry* 59:873–907.
- Bowles, D. J., S. J. Gurr, C. Scollan, H. J. Atkinson, and K. E. Hammond-Kosack. 1991. Local and systemic changes in plant gene expression following root infection by cyst nematodes. Pp. 225–236 in C. J. Smith, ed. *Biochemistry and molecular biology of plant–pathogen interactions*. Oxford: Clarendon Press.
- Brederode, F. T., H. J. M. Linthorst, and J. B. Bol. 1991. Differential induction of acquired resistance and PR gene expression in tobacco by virus infection, ethephon treatment, UV light and wounding. *Plant Molecular Biology* 17:1117–1125.
- Breijo, F. J. G., R. Garro, and V. Conejero. 1990. C7(P32) and C6(P34) PR proteins induced in tomato leaves by citrus exocortis viroid infection are chitinases. *Physiological and Molecular Plant Pathology* 36:249–260.
- Brodli, M. R., and T.-H. D. Ho. 1991. Heat shock causes selective destabilization of secretory mRNAs in barley aleurone cells. *Plant Physiology* 96:1048–1052.
- Broekaert, W. F., and W. J. Peumans. 1988. Pectic polysaccharides elicit chitinase accumulation in tobacco. *Physiologia Plantarum* 74:740–744.
- Broekaert, W. F., J. van Parijs, A. K. Allen, and W. J. Peumans. 1988. Comparison of some molecular, enzymatic and antifungal properties of chitinases from thorn-apple, tobacco and wheat. *Physiological and Molecular Plant Pathology* 33:319–331.
- Broekaert, W. F., J. van Parijs, F. Leyns, H. Joos, and W. J. Peumans. 1989. A chitin-binding lectin from stinging nettle rhizomes with antifungal properties. *Science* 245:1100–1102.
- Broglie, K. E., P. Biddle, R. Cressman, and R. Broglie. 1989. Functional analysis of DNA sequences responsible for ethylene regulation of a bean chitinase gene in transgenic tobacco. *Plant Cell* 1:599–607.

26. Broglie, K., I. Chet, M. Holliday, R. Cressman, P. Biddle, S. Knowlton, C. J. Mauvais, and R. Broglie. 1991. Transgenic plants with enhanced resistance to the fungal pathogen *Rhizoctonia solani*. *Science* 254: 1194–1197.
27. Bronner, R., E. Westphal, and F. Dreger. 1991. Pathogenesis-related proteins in *Solanum dulcamara* L. resistant to the gall mite *Aceria caldophthirus* (Nalepa) (syn *Eriophyes cladophthirus* Nal.). *Physiological and Molecular Plant Pathology* 38:93–104.
28. Buuren, M. van, J.-M. Neuhaus, H. Shinshi, J. Ryals, and F. Meins, Jr. 1992. The structure and regulation of homeologous tobacco endochitinase genes of *Nicotiana sylvestris* and *N. tomentosiformis* origin. *Molecular and General Genetics* 232:460–469.
29. Chang, C. T., H. F. Lo, C. T. Wu, and H. Y. Sung. 1992. Purification and properties of chitinase from cabbage. *Biochemistry International* 28:707–715.
30. Chérif, M., and N. Benhamou. 1990. Cytochemical aspects of chitin breakdown during the parasitic action of a *Trichoderma* sp. on *Fusarium oxysporum* f.sp. *radicis-lycopersici*. *Phytopathology* 80: 1406–1414.
31. Chrispeels, M. J., and N. V. Raikhel. 1991. Lectins, lectin genes, and their role in plant defense. *Plant Cell* 3:1–9.
32. Cohen, E. 1993. Chitin synthesis and degradation as targets for pesticide action. *Archives of Insect Biochemistry and Physiology* 22:245–261.
33. Collada, C., R. Casado, A. Fraile, and C. Aragoncillo. 1992. Basic endochitinases are major proteins in *Castanea sativa* cotyledons. *Plant Physiology* 100:778–783.
34. Collinge, D. B., K. M. Kragh, J. D. Mikkelsen, K. K. Nielsen, U. Rasmussen, and K. Vad. 1993. Plant chitinases. *Plant Journal* 3:31–40.
35. Conrads-Strauch, J., J. M. Dow, D. E. Milligan, R. Parra, and M. J. Daniels. 1990. Induction of hydrolytic enzymes in *Brassica campestris* in response to pathovars of *Xanthomonas campestris*. *Plant Physiology* 93:238–243.
36. Cornelissen, B. J. C., and L. S. Melchers. 1993. Strategies for control of fungal diseases with transgenic plants. *Plant Physiology* 101:709–712.
37. Daugrois, J. H., C. Lafitte, J. P. Barthe, and A. Touze. 1990. Induction of β -1,3-glucanase and chitinase activity in compatible and incompatible interactions between *Colletotrichum lindemuthianum* and bean cultivars. *Journal of Phytopathology* 130:225–234.
38. Davis, J. M., H. R. G. Clarke, H. D. Bradshaw, Jr., and M. P. Gordon. 1991. *Populus* chitinase genes: Structure, organization, and similarity of translated sequences to herbaceous plant chitinases. *Plant Molecular Biology* 17:631–639.
39. De Jong, A. J., J. Cordewener, F. L. Schiavo, M. Terzi, J. Vandekerckhove, A. van Kammen, and S. C. de Vries. 1992. A carrot somatic embryo mutant is rescued by chitinase. *Plant Cell* 4:425–433.
40. Dumas-Gaudot, E., J. Grenier, V. Furlan, and A. Asselin. 1992. Chitinase, chitosanase, and β -1,3-glucanase activities in *Allium* and *Pisum* roots colonized by *Glomus* species. *Plant Science* 84:17–24.
41. Dunsmuir, P., W. Howie, E. Newbigin, L. Joe, E. Penzes, and T. Suslow. 1992. Resistance to *Rhizoctonia solani* in transgenic tobacco. Pp. 567–571 in E. W. Nester and D. P. S. Verma, eds. *Advances in molecular genetics of plant-microbe interactions*, vol. 2. Dordrecht: Kluwer Academic Publishers.
42. Dunsmuir, P., and Suslow, T. 1989. Structure and regulation of organ- and tissue-specific genes: Chitinase genes in plants. Pp. 215–227 in I. K. Vasil, ed. *Cell culture and somatic cell genetics of plants*, vol. 6. New York: Academic Press.
43. Ernst, D., M. Schraudner, C. Langebartels, and H. Sandermann, Jr. 1992. Ozone-induced changes of mRNA levels of β -1,3-glucanase, chitinase and 'pathogenesis-related' protein 1b in tobacco plants. *Plant Molecular Biology* 20:673–682.
44. Esaka, M., K. Enoki, B. Kouchi, and T. Sasaki. 1990. Purification and characterization of abundant secreted protein in suspension-cultured pumpkin cells. *Plant Physiology* 93:1037–1041.
45. Fink, W., M. Liefland, and K. Mendgen. 1988. Chitinases and β -1,3-glucanases in the apoplastic compartment of oat leaves (*Avena sativa* L.). *Plant Physiology* 88:270–275.
46. Fink, W., M. Liefland, and K. Mendgen. 1990. Comparison of various stress responses in oat in compatible and nonhost resistant interactions with rust fungi. *Physiological and Molecular Plant Pathology* 37:309–321.
47. Flach, J., P.-E. Pilet, and P. Jollès. 1992. What's new in chitinase research? *Experientia* 48:701–716.
48. Fleming, T. M., D. A. McCarthy, R. F. White, J. F. Antoniw, and J. D. Mikkelsen. 1991. Induction and characterization of some of the pathogenesis-related proteins in sugar beet. *Physiological and Molecular Plant Pathology* 39:147–160.
49. Fritig, B., J. Rouster, S. Kauffman, A. Stinzi, P. Geoffroy, M. Kopp, and M. Legrand. 1989. Virus-induced glycanhydrolases and effects of oligosaccharide signals on plant-virus interactions. Pp. 161–168 in B. J. J. Lugtenburg, ed. *Signal molecules in plants and plant-microbe interactions*. Berlin: Springer-Verlag.
50. Fukuda, Y., M. Ohme, and H. Shinshi. 1991. Gene structure and expression of a tobacco endochitinase gene in suspension-cultured tobacco cells. *Plant Molecular Biology* 16:1–10.
51. Gaynor, J. J., and K. M. Unkenholz. 1989. Sequence analysis of a genomic clone encoding endochitinase from *Solanum tuberosum*. *Nucleic Acids Research* 17:5855–5856.
52. Gomez Lim, M. A., P. Kelly, R. Sexton, and A. J. Trewavas. 1987. Identification of chitinase mRNA in abscission zones from bean (*Phaseolus vulgaris* Red Kidney) during ethylene-induced abscission. *Plant, Cell and Environment* 10:741–746.
53. Gooday, G. W. 1990. The ecology of chitin degradation. *Advances in Microbial Ecology* 11:387–430.
54. Graham, T. L., and M. Y. Graham. 1991. Cellular coordination of molecular responses in plant defense. *Molecular Plant-Microbe Interactions* 4:415–422.
55. Grenier, J., and A. Asselin. 1990. Some pathogenesis-related proteins are chitosanases with lytic ac-

tivity against fungal spores. *Molecular Plant-Microbe Interactions* 3:401-407.

56. Grosset, J., Y. Meyer, Y. Chartier, S. Kauffmann, M. Legrand, and B. Fritig. 1990. Tobacco mesophyll protoplasts synthesize 1,3- β -glucanase, chitinases, and "osmotins" during in vitro culture. *Plant Physiology* 92:520-527.

57. Hahlbrock, K., N. Arabatzis, M. Becker-Andre, H.-J. Joos, E. Kombrink, M. Schroder, G. Strittmatter, and J. Taylor. 1989. Local and systemic gene activation in fungus-infected potato leaves. Pp. 241-249 in B. J. J. Lugtenberg, ed. *Signal molecules in plants and plant-microbe interactions*. Berlin: Springer-Verlag.

58. Hamel, F., and G. Bellemare. 1993. Nucleotide sequence of a *Brassica napus* endochitinase gene. *Plant Physiology* 101:1403.

59. Harms, C. T. 1992. Engineering genetic disease resistance into crops: Biotechnological approaches to crop protection. *Crop Protection* 11:291-306.

60. Hart, C. M., B. Fischer, J.-M. Neuhaus, and F. Meins, Jr. 1992. Regulated inactivation of homologous gene expression in transgenic *Nicotiana sylvestris* plants containing a defense-related tobacco chitinase gene. *Molecular and General Genetics* 235:178-188.

61. Hedrick, S. A., J. N. Bell, T. Boller, and C. J. Lamb. 1988. Chitinase cDNA cloning and mRNA induction by fungal elicitor, wounding, and infection. *Plant Physiology* 86:182-186.

62. Herget, T., J. Schell, and P. H. Schreier. 1990. Elicitor-specific induction of one member of the chitinase gene family in *Arachis hypogaea*. *Molecular and General Genetics* 224:469-476.

63. Hironaka, C. M., A. E. Otal, and D. M. Shah. 1993. The characterization of four maize genes encoding chitinase and the expression of an acidic isoform in transgenic tomato plants. Abstract No. 46, *Molecular genetics of plant-microbe interactions conference*, Rutgers, N.J.

64. Hooft van Huijsduijzen, R. A. M., S. Kauffmann, F. Th. Brederode, B. J. C. Cornelissen, M. Legrand, B. Fritig, and J. F. Bol. 1987. Homology between chitinases that are induced by TMV infection of tobacco. *Plant Molecular Biology* 9:411-420.

65. Huang, J.-K., L. Wen, M. Swegle, H.-C. Tran, T. H. Thin, H. M. Naylor, S. Muthukrishnan, and G. R. Reeck. 1991. Nucleotide sequence of a rice genomic clone that encodes a class I chitinase. *Plant Molecular Biology* 16:479-480.

66. Huynh, Q. K., C. M. Hironaka, E. B. Levine, C. E. Smith, J. R. Borgmeyer, and D. M. Shah. 1992. Antifungal proteins from plants. Purification, molecular cloning, and antifungal properties of chitinases from maize seed. *Journal of Biological Chemistry* 267:6635-6640.

67. Inbar, J., and I. Chet. 1991. Evidence that chitinase produced by *Aeromonas caviae* is involved in the biological control of soil-borne plant pathogens by this bacterium. *Soil Biology and Biochemistry* 23:973-978.

68. Irving, H. R., and J. A. Kuc. 1990. Local and systemic induction of peroxidase, chitinase and resis-

tance in cucumber plants by K_2HPO_4 . *Physiological and Molecular Plant Pathology* 37:355-366.

69. Ishige, F., H. Mori, K. Yamazaki, and H. Imaseki. 1993. Cloning of a complementary DNA that encodes an acidic chitinase which is induced by ethylene and expression of the corresponding gene. *Plant and Cell Physiology* 34:103-111.

70. Ishige, F., K. Yamazaki, H. Mori, and H. Imaseki. 1991. The effects of ethylene on the coordinated synthesis of multiple proteins: Accumulation of an acidic chitinase and a basic glycoprotein induced by ethylene in leaves of Azuki bean, *Vigna angularis*. *Plant Cell Physiology* 32:681-690.

71. Jacobsen, S., M. Z. Hauschild, and U. Rasmussen. 1992. Induction by chromium ions of chitinases and polyamines in barley (*Hordeum vulgare* L.) and rape (*Brassica napus* L. spp. *oleifera*). *Plant Science* 84:119-128.

72. Jacobsen, S., J. D. Mikkelsen, and J. Hejgaard. 1990. Characterization of two antifungal endochitinases from barley grain. *Physiologia Plantarum* 79:554-562.

73. Jakobek, J. L., and P. B. Lindgren. 1993. Generalized induction of defense responses in bean is not correlated with the induction of the hypersensitive reaction. *Plant Cell* 5:49-56.

74. Jekel, P. A., J. B. H. Hartmann, and J. J. Beintema. 1991. The primary structure of hevamine, an enzyme with lysozyme/chitinase activity from *Hevea brasiliensis* latex. *European Journal of Biochemistry* 200:123-130.

75. Jones, J. D. G., C. Dean, D. Gidoni, D. Gilbert, D. Bond-Nutter, R. Lee, J. Bedbrook, and P. Dunsmuir. 1988. Expression of bacterial chitinase protein in tobacco leaves using two photosynthetic gene promoters. *Molecular and General Genetics* 212:536-542.

76. Joosten, M. H. A. J., and P. J. G. M. de Wit. 1989. Identification of several pathogenesis-related proteins in tomato leaves inoculated with *Cladosporium fulvum* (syn. *Fulvia fulva*) as 1,3- β -glucanases and chitinases. *Plant Physiology* 89:945-951.

77. Jung, L.-L., B. Fritig, and G. Hahne. 1993. Sunflower (*Helianthus annuus* L.) pathogenesis-related proteins. Induction by aspirin (acetylsalicylic acid) and characterization. *Plant Physiology* 101:873-880.

78. Keefe, D., U. Hinz, and F. Meins, Jr. 1990. The effect of ethylene on the cell-type-specific and intracellular localization of β -1,3-glucanase and chitinase in tobacco leaves. *Planta* 182:43-51.

79. Kendra, D. F., D. Christian, and L. A. Hadwiger. 1989. Chitin oligomers from *Fusarium solani*/pea interactions, chitinase/ β -glucanase digestion of sporelings and from fungal cell wall chitin actively inhibit fungal growth and enhance disease resistance. *Physiological and Molecular Plant Pathology* 35:215-230.

80. Koga, D., Y. Nomura, H. Tabata, A. Ide, and Y. Nakamura. 1992. Induction of fine bent-grass callus and appearance of chitinase during the subculture. *Bioscience Biotechnology and Biochemistry* 56:1331-1332.

81. Kombrink, E., M. Schröder, and K. Hahlbrock.

1988. Several "pathogenesis-related" proteins in potato are 1,3- β -glucanases and chitinases. *Proceedings of the National Academy of Science USA* 85:782-786.
82. Kragh, K. M., S. Jacobsen, and J. D. Mikkelsen. 1990. Induction, purification and characterization of barley leaf chitinase. *Plant Science* 71:55-68.
83. Kragh, K. M., S. Jacobsen, J. D. Mikkelsen, and K. A. Nielsen. 1991. Purification and characterization of three chitinases and one β -1,3-glucanase accumulating in the medium of cell suspension cultures of barley (*Hordeum vulgare* L.). *Plant Science* 76:65-77.
84. Krebs, S. L., and R. Grumet. 1991. Characterization and biological significance of *Fusarium*-induced celery hydrolases. *Phytopathology* 81:1196 (Abstr.).
85. Kurosaki, F., N. Tashiro, and A. Nishi. 1987. Induction, purification and possible function of chitinase in cultured carrot cells. *Physiological and Molecular Plant Pathology* 31:201-210.
86. Kurosaki, F., N. Tashiro, and A. Nishi. 1987. Secretion of chitinase from cultured cells treated with fungal mycelium walls. *Physiological and Molecular Plant Pathology* 31:211-216.
87. Kurosaki, F., N. Tashiro, and A. Nishi. 1988. Role of chitinase and chitin oligosaccharides in lignification response of cultured carrot cells treated with mycelial walls. *Plant Cell Physiology* 29:527-531.
88. Kurosaki, F., N. Tashiro, and A. Nishi. 1990. Chitinase induction in carrot cell cultures treated with various fungal components. *Biochemistry International* 20:99-106.
89. Laflamme, D., and R. Roxby. 1989. Isolation and nucleotide sequence of cDNA clones encoding potato chitinase genes. *Plant Molecular Biology* 13:149-150.
90. Lamb, C. J., M. A. Lawton, M. Dron, and R. A. Dixon. 1989. Signals and transduction mechanisms for activation of plant defenses against microbial attack. *Cell* 56:215-224.
91. Lamb, C. J., J. A. Ryals, E. R. Ward, and R. A. Dixon. 1992. Emerging strategies for enhancing crop resistance to microbial pathogens. *Biotechnology* 10:1436-1445.
92. Lambais, M. R., and M. C. Mehdy. 1993. Suppression of endochitinase, β -1,3-endoglucanase, and chalcone isomerase expression in bean vesicular-arbuscular mycorrhizal roots under different soil phosphate conditions. *Molecular Plant-Microbe Interactions* 6:75-83.
93. Lawton, K., E. Ward, G. Payne, M. Moyer, and J. Ryals. 1992. Acidic and basic class III chitinase mRNA accumulation in response to TMV infection of tobacco. *Plant Molecular Biology* 19:735-743.
94. Leah, R., Mikkelsen, J. D., J. Mundy, and I. Svendsen. 1987. Identification of a 28,000 dalton endochitinase in barley endosperm. *Carlsberg Research Communications* 52:31-37.
95. Leah, R., H. Tommerup, I. Svendsen, and J. Mundy. 1991. Biochemical and molecular characterization of three barley seed proteins with antifungal activity. *Journal of Biological Chemistry* 266:1564-1573.
96. Legrand, M., S. Kauffmann, P. Geoffroy, and B. Fritig. 1987. Biological function of pathogenesis-related proteins: Four tobacco pathogenesis-related proteins are chitinases. *Proceedings of the National Academy of Sciences USA* 84:6750-6754.
97. Lerner, D. R., and N. V. Raikhel. 1992. The gene for stinging nettle lectin (*Urtica dioica* agglutinin) encodes both a lectin and a chitinase. *Journal of Biological Chemistry* 267:11085-11091.
98. Leung, D. W. M. 1992. Involvement of plant chitinase in sexual reproduction of higher plants. *Phytochemistry* 31:1899-1900.
99. Linthorst, H. J. M. 1991. Pathogenesis-related proteins of plants. *CRC Critical Reviews in Plant Sciences* 10:123-150.
100. Linthorst, H. J. M., L. C. van Loon, C. M. A. van Rossum, A. Mayer, J. F. Bol, J. S. C. van Roekel, E. J. S. Meulenhoff, and B. J. C. Cornelissen. 1990. Analysis of acidic and basic chitinases from tobacco and petunia and their constitutive expression in transgenic tobacco. *Molecular Plant-Microbe Interactions* 3:252-258.
101. Lorito, M., G. E. Harman, C. K. Hayes, R. M. Broadway, A. Tronsmo, S. L. Woo, and A. DiPietro. 1993. Chitinolytic enzymes produced by *Trichoderma harzianum*. Antifungal activity of purified endochitinase and chitobiosidase. *Phytopathology* 83:302-307.
102. Lotan, T., N. Ori, and R. Fluhr. 1990. Pathogenesis-related proteins are developmentally regulated in tobacco flowers. *Plant Cell* 1:881-887.
103. Lund, P., and P. Dunsmuir. 1992. A plant signal sequence enhances the secretion of bacterial ChiA in transgenic tobacco. *Plant Molecular Biology* 18:47-53.
104. Lund, P., R. Y. Lee, and P. Dunsmuir. 1989. Bacterial chitinase is modified and secreted in transgenic tobacco. *Plant Physiology* 91:130-135.
105. Mahe, A., J. Grisvard, and M. Dron. 1992. Fungal- and plant-specific gene markers to follow the bean anthracnose infection process and normalize a bean chitinase mRNA induction. *Molecular Plant-Microbe Interactions* 5:242-248.
106. Majeau, N., J. Trudel, and A. Asselin. 1990. Diversity of cucumber chitinase isoforms and characterizations of one seed basic chitinase with lysozyme activity. *Plant Science* 68:9-16.
107. Malamy, J., J. P. Carr, D. F. Klessig, and I. Raskin. 1990. Salicylic acid: A likely endogenous signal in the resistance response of tobacco to viral infection. *Science* 250:1102-1104.
108. Margis-Pinheiro, M., C. Martin, L. Didierjean, and G. Burkard. 1993. Differential expression of bean chitinase genes by virus infection, chemical treatment and UV irradiation. *Plant Molecular Biology* 22:659-668.
109. Margis-Pinheiro, M., M. H. Metz-Boutigue, A. Awade, M. de Tapia, M. le Ret, and G. Burkard. 1991. Isolation of a complementary DNA encoding the bean PR4 chitinase: An acidic enzyme with an amino-terminus cysteine-rich domain. *Plant Molecular Biology* 17:243-253.
110. Martin, M. N. 1991. The latex of *Hevea brasiliensis* contains high levels of both chitinases and chitinase/lysozymes. *Plant Physiology* 95:469-476.
111. Masuta, C., M. van den Bulcke, G. Bauw, M.

- van Montagu, and A. B. Caplan. 1991. Differential effects of elicitors on the viability of rice suspension cells. *Plant Physiology* 97:619-629.
112. Mauch, F., L. A. Hadwiger, and T. Boller. 1988. Antifungal hydrolases in pea tissue. I. Purification and characterization of two chitinases and two β -1,3-glucanases differentially regulated during development and in response to fungal infection. *Plant Physiology* 87:325-333.
113. Mauch, F., B. Mauch-Mani, and T. Boller. 1988. Antifungal hydrolases in pea tissue. II. Inhibition of fungal growth by combinations of chitinase and β -1,3-glucanase. *Plant Physiology* 88:936-942.
114. Mauch, F., J. B. Meehl, and L. A. Staehelin. 1992. Ethylene-induced chitinase and β -1,3-glucanase accumulate specifically in the lower epidermis and along vascular strands of bean leaves. *Planta* 186:367-375.
115. Mauch, F., and L. A. Staehelin. 1989. Functional implications of the subcellular localization of ethylene-induced chitinase and β -1,3-glucanase in bean leaves. *Plant Cell* 1:447-457.
116. Meins, F., Jr., and P. Ahl. 1989. Induction of chitinase and β -1,3-glucanase in tobacco plants infected with *Pseudomonas tabaci* and *Phytophthora parasitica* var. *nicotianae*. *Plant Science* 61:155-161.
117. Meins, F., Jr., J. M. Neuhaus, C. Sperisen, and J. Ryals. 1992. The primary structure of plant pathogenesis-related glucanohydrolases and their genes. Pp. 245-282 in T. Boller and F. Meins, Jr., eds. *Genes involved in plant defense*. Vienna: Springer-Verlag.
118. Melchers, L. S., M. B. Sela-Buurlage, S. A. Vloemans, C. P. Woloshuk, J. S. C. van Roekel, J. Pen, P. J. M. van den Elzen, and B. J. C. Cornelissen. 1993. Extracellular targeting of the vacuolar tobacco proteins AP24, chitinase and β -1,3-glucanase in transgenic plants. *Plant Molecular Biology* 21:583-593.
119. Melchers, L. S., H. Tigelaar, M. B. Sela-Buurlage, A. S. Ponstein, J. S. C. van Roekel, S. A. Bres-Vloemans, B. J. C. Cornelissen, J. Logemann, and E. Jongedijk. 1993. Synergistic activity of chitinases and β -1,3-glucanases enhances *Fusarium* resistance in transgenic tomato plants. Abstract No. 83, Molecular genetics of plant-microbe interactions conference, Rutgers, NJ.
120. Memelink, J., H. J. M. Linthorst, R. A. Schilperoort, and J. H. C. Hoge. 1990. Tobacco genes encoding acidic and basic isoforms of pathogenesis-related proteins display different expression patterns. *Plant Molecular Biology* 14:119-126.
121. Mercer, C. F., D. R. Greenwood, and J. L. Grant. 1992. Effect of plant and microbial chitinases on the eggs and juveniles of *Meloidogyne hapla* Chitwood (Nematoda: Tylenchida). *Nemotologica* 38:227-236.
122. Métraux, J. P., W. Burkhart, M. Moyer, S. Dincher, W. Middlestead, S. Williams, G. Payne, M. Carnes, and J. Ryals. 1989. Isolation of a complementary DNA encoding a chitinase with structural homology to a bifunctional lysozyme/chitinase. *Proceedings of the National Academy of Sciences USA* 86:896-900.
123. Métraux, J. P., L. Streit, and Th. Staub. 1988. A pathogenesis-related protein in cucumber is a chitinase. *Physiological and Molecular Plant Pathology* 33:1-9.
124. Mikkelsen, J. D., L. Berglund, K. K. Nielsen, H. Christiansen, and K. Bojsen. 1992. Structure of endochitinase genes from sugar beets. Pp. 344-353 in C. J. Brine, P. A. Sandford, and J. P. Zikakis, eds. *Advances in chitin and chitosan*. London: Elsevier Science Publishers.
125. Nagel, R., R. G. Birch, and J. M. Manners. 1990. Detection of bacterial chitinase activity in transformed plant tumour cells using a specific exochitinase substrate. *Plant Cell Reports* 8:729-732.
126. Nakamura, K., and K. Matsuoka. 1993. Protein targeting to the vacuole in plant cells. *Plant Physiology* 101:1-5.
127. Nasser, W., M. de Tapia, and G. Burkard. 1990. Maize pathogenesis-related proteins: Characterization and cellular distribution of 1,3- β -glucanases and chitinases induced by bromo mosaic virus infection or mercuric chloride treatment. *Physiological and Molecular Plant Pathology* 36:1-14.
128. Nasser, W., M. de Tapia, S. Kauffman, S. Montasser-Koushari, and G. Burkard. 1988. Identification and characterization of maize pathogenesis-related proteins. Four maize PR proteins are chitinases. *Plant Molecular Biology* 11:529-538.
129. Neale, A. D., J. A. Wahleithner, M. Lund, H. T. Bonnett, A. Kelly, D. R. Meeks-Wagner, W. J. Peacock, and E. S. Dennis. 1990. Chitinase, β -1,3-glucanase, osmotin, and extensin are expressed in tobacco explants during flower formation. *Plant Cell* 2:673-684.
130. Neucere, J. N., T. C. Cleveland, and C. Dischinger. 1991. Existence of chitinase activity in mature corn kernels (*Zea mays* L.). *Journal of Agricultural and Food Chemistry* 39:1326-1328.
131. Neuhaus, J.-M., P. Ahl-Goy, U. Hinz, S. Flores, and F. Meins, Jr. 1991. High-level expression of a tobacco chitinase gene in *Nicotiana sylvestris*. Susceptibility of transgenic plants to *Cercospora nicotianae* infection. *Plant Molecular Biology* 16:141-151.
132. Neuhaus, J.-M., S. Flores, D. Keefe, P. Ahl-Goy, and F. Meins, Jr. 1992. The function of vacuolar β -1,3-glucanase investigated by antisense transformation. Susceptibility of transgenic *Nicotiana sylvestris* plants to *Cercospora nicotianae* infection. *Plant Molecular Biology* 19:803-813.
133. Neuhaus, J.-M., L. Sticher, F. Meins, Jr., and T. Boller. 1991. A short C-terminal sequence is necessary and sufficient for the targeting of chitinases to the plant vacuole. *Proceedings of the National Academy of Sciences USA* 88:10362-10366.
134. Nielsen, K. K., K. Bojsen, K. M. Kragh, and J. D. Mikkelsen. 1993. An acidic class III chitinase in sugar beet: Induction by *Cercospora beticola*, characterization and expression in transgenic tobacco plants. Abstract No. 88, Molecular Genetics of Plant-Microbe Interactions Conference, Rutgers, N.J.
135. Nishizawa, Y., and T. Hibi. 1991. Rice chitinase gene: cDNA cloning and stress-induced expression. *Plant Science* 76:211-218.
136. Ordentlich, A., Y. Elad, and I. Chet. 1988.

The role of chitinase of *Serratia marcescens* in biocontrol of *Sclerotium rolfsii*. *Phytopathology* 78:84–88.

137. Ouakfaoui, S. E., and A. Asselin. 1992. Diversity of chitinase activity in cucumber. *Plant Science* 85:33–41.

138. Pan, S. Q., X. S. Ye, and J. Kuc. 1991. A technique for detection of chitinase, β -1,3-glucanase, and protein patterns after a single separation using polyacrylamide gel electrophoresis or isoelectrofocusing. *Phytopathology* 81:970–974.

139. Pan, S. Q., X. S. Ye, and J. Kuc. 1992. Induction of chitinases in tobacco plants systemically protected against blue mold by *Peronospora tabacina* or tobacco mosaic virus. *Phytopathology* 82:119–123.

140. Parsons, T. J., H. D. Bradshaw, Jr., and M. P. Gordon. 1989. Systemic accumulation of specific mRNAs in response to wounding in poplar trees. *Proceedings of the National Academy of Sciences USA* 86:7895–7899.

141. Payne, G., P. Ahl, M. Moyer, A. Harper, J. Beck, F. Meins, Jr., and J. Ryals. 1990. Isolation of complementary DNA clones encoding pathogenesis-related proteins P and Q, two acidic chitinases from tobacco. *Proceedings of the National Academy of Sciences USA* 87:98–102.

142. Pierpoint, W. S., P. J. Jackson, and R. M. Evans. 1990. The presence of a thaumatin-like protein, a chitinase and a glucanase among the pathogenesis-related proteins of potato (*Solanum tuberosum*). *Physiological and Molecular Plant Pathology* 36:325–338.

143. Rahaarjo, S. H. T., M. O. Hernandez, and Z. K. Punja. 1992. Introduction of chitinase genes into carrot and cucumber via *Agrobacterium*-mediated transformation: Methodology and applications. *Phytopathology* 82:1167 (Abstr.).

144. Rasmussen, U., K. Bojsen, and D. B. Collinge. 1992. Cloning and characterization of a pathogen-induced chitinase in *Brassica napus*. *Plant Molecular Biology* 20:277–287.

145. Rasmussen, U., H. Giese, and J. D. Mikkelsen. 1992. Induction and purification of chitinase in *Brassica napus* L. ssp. *oleifera* infected with *Phoma lingam*. *Planta* 187:328–334.

146. Raz, V., and R. Fluhr. 1992. Calcium requirement for ethylene-dependent responses. *Plant Cell* 4:1123–1130.

147. Ride, J. P., and M. S. Barber. 1990. Purification and characterization of multiple forms of endochitinase from wheat leaves. *Plant Science* 71:185–197.

148. Roberts, C. A., S. M. Marek, T. L., Niblack, and A. L. Karr. 1992. Parasitic *Meloidogyne* and mutualistic *Acremonium* increase chitinase in tall fescue. *Journal of Chemical Ecology* 18:1107–1116.

149. Roberts, G. A. F. 1992. Chitin chemistry. London: MacMillan Press.

150. Roberts, W. K., and C. P. Selitrennikoff. 1988. Plant and bacterial chitinases differ in antifungal activity. *Journal of General Microbiology* 134:169–176.

151. Roby, D., K. Broglie, R. Cressman, P. Biddle, I. Chet, and R. Broglie. 1990. Activation of a bean

chitinase promoter in transgenic tobacco plants by phytopathogenic fungi. *Plant Cell* 2:999–1007.

152. Roby, D., K. Broglie, J. Gaynor, and R. Broglie. 1991. Regulation of a chitinase gene promoter by ethylene and elicitors in bean protoplasts. *Plant Physiology* 97:433–439.

153. Roby, D., and M.-T. Esquerre-Tugaye. 1987. Induction of chitinases and of translatable mRNA for these enzymes in melon plants infected with *Colletotrichum lagenarium*. *Plant Science* 52:175–185.

154. Roby, D., and M.-T. Esquerre-Tugaye. 1987. Purification and some properties of chitinases from melon plants infected by *Collectotrichum lagenarium*. *Carbohydrate Research* 165:93–104.

155. Roby, D., A. Gabelle, and A. Toppan. 1987. Chitin oligosaccharides as elicitors of chitinase activity in melon plants. *Biochemical and Biophysical Research Communications* 143:885–892.

156. Rousseau-Limouzin, M., and B. Fritig. 1991. Induction of chitinases, 1,3- β -glucanases and other pathogenesis-related proteins in sugar beet leaves upon infection with *Cercospora beticola*. *Plant Physiology and Biochemistry* 29:105–117.

157. Ruiz-Herrera, J. 1992. Fungal cell wall: Structure, synthesis, and assembly. Boca Raton, FL: CRC Press.

158. Rozeboom, H. J., A. Budiani, J. J. Beintema, and B. W. Dijkstra. 1990. Crystallization of hevamine, an enzyme with lysozyme/chitinase activity from *Hevea brasiliensis* latex. *Journal of Molecular Biology* 212:441–443.

159. Samac, D. A., C. M. Hironaka, P. E. Yallaly, and D. M. Shah. 1990. Isolation and characterization of the genes encoding basic and acidic chitinase in *Arabidopsis thaliana*. *Plant Physiology* 93:907–914.

160. Samac, D. A., and D. M. Shah. 1991. Developmental and pathogen-induced activation of the *Arabidopsis* acidic chitinase promoter. *Plant Cell* 3:1063–1072.

161. Sarmiento, G. G., K. Alpert, F. A. Tang, and Z. K. Punja. 1992. Factors influencing *Agrobacterium tumefaciens* mediated transformation and expression of kanamycin resistance in pickling cucumber. *Plant Cell, Tissue and Organ Culture* 31:185–193.

162. Sauter, M., and A. Hager. 1989. The mycorrhizal fungus *Amanita muscaria* induces chitinase activity in roots and in suspension-cultured cells of its host *Picea abies*. *Planta* 179:61–66.

163. Schraudner, M., D. Ernst, C. Langebartels, and H. Sandermann, Jr. 1992. Biochemical plant responses to ozone. III. Activation of the defense-related proteins β -1,3-glucanase and chitinase in tobacco leaves. *Plant Physiology* 99:1321–1328.

164. Schröder, M., K. Hahlbrock, and E. Kombrink. 1992. Temporal and spatial patterns of 1,3- β -glucanase and chitinase induction in potato leaves infected by *Phytophthora infestans*. *Plant Journal* 2:161–172.

165. Sela-Buurlage, M. B., A. S. Ponstein, S. A. Bres-Vloemans, L. S. Melchers, P. J. M. van den Elzen, and B. J. C. Cornelissen. 1993. Only specific tobacco (*Nicotiana tabacum*) chitinases and β -1,3-glucanases exhibit antifungal activity. *Plant Physiology* 101:857–863.

166. Shapira, R., A. Ordentlich, I. Chet, and A. B. Oppenheim. 1989. Control of plant diseases by chitinase expressed from cloned DNA in *Escherichia coli*. *Phytopathology* 79:1246-1249.
167. Shinshi, H., D. Mohnen, and F. Meins, Jr. 1987. Regulation of a plant pathogenesis-related enzyme: Inhibition of chitinase and chitinase mRNA accumulation in cultured tobacco tissues by auxin and cytokinin. *Proceedings of the National Academy of Sciences USA* 84:89-93.
168. Shinshi, H., J.-M. Neuhaus, J. Ryals, and F. Meins, Jr. 1990. Structure of a tobacco endochitinase gene: Evidence that different chitinase genes can arise by transposition of sequences encoding a cysteine-rich domain. *Plant Molecular Biology* 14:357-368.
169. Smith, J. A., and J.-P. Métraux. 1991. *Pseudomonas syringae* pv. *syringae* induces systemic resistance to *Pyricularia oryzae* in rice. *Physiological and Molecular Plant Pathology* 39:451-461.
170. Snyder, T., P. Fritz, and D. Furtek. 1992. Isolating genomic chitinase clones from *Theobroma cacao* using a PCR probe. *Plant Physiology* 99:86 (Abstr.).
171. Spanu, P., T. Boller, A. Ludwig, A. Wiemken, A. Faccio, and P. Bonfante-Fasolo. Chitinase in roots of mycorrhizal *Allium porrum*: Regulation and localization. *Planta* 177:447-455.
172. Spiegel, Y., I. Chet, and E. Cohn. 1987. Use of chitin for controlling plant-parasitic nematodes II. Mode of action. *Plant and Soil* 98:337-345.
173. Spindler, K.-D., M. Spindler-Barth, and M. Londershausen. 1990. Chitin metabolism: A target for drugs against parasite. *Parasitology Research* 76: 283-288.
174. Staehelin, C., J. Müller, R. B. Mellor, A. Wiemken, and Th. Boller. 1992. Chitinase and peroxidase in effective (fix⁺) and ineffective (fix⁻) soybean nodules. *Planta* 187:295-300.
175. Sticher, L., J. Hofsteenge, A. Milani, J.-M. Neuhaus, and F. Meins, Jr. 1992. Vacuolar chitinases of tobacco: A new class of hydroxyproline-containing proteins. *Science* 257:655-657.
176. Sticher, L., J. Hofsteenge, J.-M. Neuhaus, T. Boller, and F. Meins, Jr. 1993. Posttranslational processing of a new class of hydroxyproline-containing proteins. *Plant Physiology* 101:1239-1247.
177. Stirling, G. R. 1991. Biological control of plant parasitic nematodes: Progress, problems and prospects. Wallingford, UK: C.A.B. International.
178. Swegle, M., J.-K. Huang, G. Lee, and S. Muthukrishnan. 1989. Identification of an endochitinase cDNA clone from barley aleurone cells. *Plant Molecular Biology* 12:403-412.
179. Swegle, M., K. J. Kramer, and S. Muthukrishnan. 1992. Properties of barley seed chitinases and release of embryo-associated isoforms during early stages of imbibition. *Plant Physiology* 99:1009-1014.
180. Tahiri-Alaoui, A., E. Dumas, and S. Gianinazzi. 1990. Detection of Pr-b proteins in tobacco roots infected with *Chalara elegans*. *Plant Molecular Biology* 14:869-871.
181. Taylor, J. L., J. D. G. Jones, S. Sandler, G. M. Mueller, J. Bedbrook, and P. Dunsmuir. 1987. Optimizing the expression of chemeric genes in plant cells. *Molecular and General Genetics* 210:572-577.
182. Toyoda, H., Y. Matsuda, T. Yamaga, S. Ikeda, M. Morita, T. Tamai, and S. Ouchi. 1991. Suppression of the powdery mildew pathogen by chitinase microinjected into barley coleoptile epidermal cells. *Plant Cell Reports* 10:217-220.
183. Trudel, J., P. Audy, and A. Asselin. 1989. Electrophoretic forms of chitinase activity in Xanthin tobacco, healthy and infected with tobacco mosaic virus. *Molecular Plant-Microbe Interactions* 2:315-324.
184. Tuzun, S., M. N. Rao, U. Vogeli, C. L. Schardl, and J. Kuc. 1989. Induced systemic resistance to blue mold: Early induction and accumulation of β -1,3-glucanases, chitinases, and other pathogenesis-related (b-proteins) in immunized tobacco. *Phytopathology* 79:979-983.
185. Vad, K., J. D. Mikkelsen, and D. B. Collinge. 1991. Induction, purification and characterization of chitinase isolated from pea leaves inoculated with *Ascochyta pisi*. *Planta* 184:24-29.
186. Van Damme, E. J. M., P. Willems, S. Torrekens, F. Van Leuven, and W. J. Peumans. 1993. Garlic (*Allium sativum*) chitinases: Characterization and molecular cloning. *Physiologia Plantarum* 87:177-186.
187. Verburg, J. G., and Q. K. Huynh. 1991. Purification and characterization of an antifungal chitinase from *Arabidopsis thaliana*. *Plant Physiology* 95: 450-455.
188. Verburg, J. G., C. E. Smith, C. A. Lisek, and Q. K. Huynh. 1992. Identification of an essential tyrosine residue in the catalytic site of a chitinase isolated from *Zea mays* that is selectively modified during inactivation with 1-ethyl-3-(3-dimethylaminopropyl)-carbodiimide. *Journal of Biological Chemistry* 267: 3886-3893.
189. Vögeli, U., F. Meins, Jr., and T. Boller. 1988. Co-ordinated regulation of chitinase and β -1,3-glucanase in bean leaves. *Planta* 174:364-372.
190. Vogeli-Lange, R., A. Hansen-Gehri, T. Boller, and F. Meins, Jr. 1988. Induction of the defense-related glucanohydrolases, β -1,3-glucanase and chitinase, by tobacco mosaic virus infection of tobacco leaves. *Plant Science* 54:171-176.
191. Vogelsang, R., and W. Barz. 1990. Elicitation of β -1,3-glucanase and chitinase activities in cell suspension cultures of *Ascochyta rabiei* resistant and susceptible cultivars of chickpea (*Cicer arietinum*). *Zeitschrift für Naturforschung* 45:233-239.
192. Vogelsang, R., and W. Barz. 1993. Purification, characterization and differential hormonal regulation of a β -1,3-glucanase and two chitinases from chickpea (*Cicer arietinum* L.). *Planta* 189:60-69.
193. Voisey, C. R., and A. J. Slusarenko. 1989. Chitinase mRNA and enzyme activity in *Phaseolus vulgaris* (L.) increase more rapidly in response to avirulent than to virulent cells of *Pseudomonas syringae* pv. *phaseolicola*. *Physiological and Molecular Plant Pathology* 35:403-412.
194. Ward, E. R., S. J. Uknes, S. C. Williams, S. S. Dincher, D. L. Wiederhold, D. C. Alexander, P. Ahl-Goy, J.-P. Métraux, and J. A. Ryals. 1991. Coordinate

gene activity in response to agents that induce systemic acquired resistance. *Plant Cell* 3:1085-1094.

195. Wessels, J. G. H. 1990. Role of cell wall architecture in fungal tip growth regeneration. Pp. 1-29 in I. B. Heath, ed. *Tip growth in plant and fungal cells*. New York: Academic Press.

196. Williams, K. J., and D. W. M. Leung. 1993. Chitinase induction in onion tissue cultures. *Plant Cell, Tissue and Organ Culture* 32:193-198.

197. Wood, W. A., and S. T. Kellogg. 1988. *Methods in enzymology*, vol. 161. Biomass. Part B—Lignin, pectin, and chitin. San Diego: Academic Press.

198. Wubben, J. P., M. H. A. J. Joosten, J. A. L. van Dan, and P. J. G. M. De Wit. 1992. Subcellular localization of plant chitinases and 1,3- β -glucanases in *Cladosporium fulvum* (syn. *Fulvia fulva*)-infected tomato leaves. *Physiological and Molecular Plant Pathology* 41:23-32.

199. Wyatt, S. E., S. Q. Pan, and J. Kuc. 1991. β -1,3-glucanase, chitinase, and peroxidase activities in tobacco tissues resistant and susceptible to blue mould as related to flowering, age and sucker development. *Physiological and Molecular Plant Pathology* 39:433-440.

200. Yamagami, T., and G. Funatsu. 1993. Purification and some properties of three chitinases from the seeds of rye (*Secale cereale*). *Bioscience Biotechnology and Biochemistry* 57:643-647.

201. Zhang, Y.-Y., and Punja, Z. K. 1991. Induction and characterization of chitinases produced in cucumber and carrot tissues. *Canadian Journal of Plant Pathology* 13:288 (Abstr.).

202. Zhang, Y.-Y., and Punja, Z. K. 1992. Induction and characterization of chitinases among cucum-

ber (*Cucumis sativus* L.) cultivars. *Phytopathology* 82:1085 (Abstr.).

203. Zhu, Q., P. W. Doerner, and C. J. Lamb. 1993. Stress induction and developmental regulation of a rice chitinase promoter in transgenic tobacco. *Plant Journal* 3:203-212.

204. Zhu, Q., and C. J. Lamb. 1991. Isolation and characterization of a rice gene encoding a basic chitinase. *Molecular and General Genetics* 226:289-296.

NOTE ADDED IN PROOF

The following articles on chitinase-fungal interactions have been published while this article was in press.

Benhamou, N., K. Broglie, I. Chet, and R. Broglie. 1993. Cytology of infection of 35S-bean chitinase transgenic canola plants by *Rhizoctonia solani*: Cytochemical aspects of chitin breakdown in vivo. *Plant Journal* 4:295-305.

Broglie, R., K. Broglie, D. Roby, and I. Chet. 1993. Production of transgenic plants with enhanced resistance to microbial pathogens. Pp. 265-276 in S. Kung and R. Wu, eds. *Transgenic plants*, vol. 1. Engineering and utilization. New York: Academic Press.

Nielsen, K. K., J. D. Mikkelsen, K. M. Kragh, and K. Bojsen. 1993. An acidic class III chitinase in sugarcane: Induction by *Cercospora beticola*, characterization, and expression in transgenic tobacco plants. *Molecular Plant-Microbe Interactions* 6:495-506.

Sahai, M. S., and M. S. Manocha. 1993. Chitinases of fungi and plants: Their role in morphogenesis and host-parasite interactions. *FEMS Microbiology Reviews*, in press.