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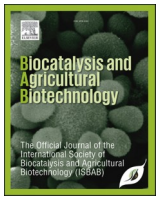

Tannin degradation by phytopathogen's tannase: A Plant's defense perspective

Kanti Prakash Sharma

Department of Biosciences, Mody University of Science and Technology, Lakshmangarh, Sikar, Rajasthan, 332311, India

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ABSTRACT

Tannins are plant secondary metabolites and characterized as plant defensive molecules. They impose a barrier against phytopathogens invasion in plants and thus oppose diseases occurrence in them. Tannase is an enzyme known for its ability to degrade plant tannins. Important plant pathogens also possess tannase coding sequence in their genome. Researches on tannase are till date focused on its applications in animal nutrition, in bioremediation and in food industries etc. The information about tannase role with respect to pathogen's virulence is very scanty or almost nil in scientific literature. The presence of tannase in pathogen's genome is an adaptive feature which may be a part of its strategy to overcome the negative effects of plants tannins. The present review summarizes important aspects of tannase and its possible role in disease causing ability of pathogens in plants.

1. Introduction

Tannins are universally present in plants and represent the fourth most abundant group of secondary metabolites after cellulose, hemicellulose and lignins (Chowdhury et al., 2004). These are naturally occurring water soluble polyphenols and found in many parts of plants such as leaves, bark and wood etc. (Haslam, 1989). Besides above, these compounds also widely occur in common foodstuffs such as tea, strawberries, blackberries, grapes, mangoes, cashew nuts, hazelnuts and walnuts etc. (Clifford and Scalbert, 2000). They are unique among their contemporaries as they precipitate proteins, minerals, starch, cellulose etc. from solutions (Aguilar et al., 2001).

Broadly tannins are classified into two major groups; hydrolysable and condensed tannins. Hydrolyzable tannins are esters of gallic acid (gallotannins) and ellagic acid (ellagitannins) with a sugar core (usually glucose) and are readily hydrolysed by the action of either enzymes or acids into their respective monomeric units. Condensed tannins are lacking in sugar core and are composed of flavonoids (flavan 3-ol or flavan 3, 4-diol) units. These are also commonly known as proanthocyanidins. Some researchers classify tannins into four groups named as gallotannins, ellagitannins, complex tannins, and condensed tannins (Khanbabaee and Ree, 2001). In gallotannins, galloyl units are bound to diverse polyols, catechins or tri-terpenoid units. In ellagitanins at least two galloyl units are C–C coupled to each other, and do not contain glycosidically linked catechin units. The ellagitannins are not hydrolysable, but they are nevertheless for historical reasons classified as hydrolyzable tannins (Zhang et al., 2001). In complex tannins, a catechin or epicatechin unit is bound glycosidically to a gallotannin or an ellagitannin unit to yield catechin or epicatechin and gallic acid or ellagic acid upon hydrolysis. The fourth categories of tannins are the condensed tannins. These are oligomeric and polymeric proanthocyanidins formed by linkage of C-4 of one catechin with C-6 or C-8 of other catechin, and are more difficult to be hydrolysed (Hagerman, 1988).

Tannins serve dual functions in plants. They protect plants against insects, pathogens and animal herbivory (Peters and Constabel, 2002; Barbehenn et al., 2005; Kumar et al., 2013). They also attract insects towards flowers and thus are helpful in cross pollination (Winkel-Shirley, 2002; Bovy et al., 2007). On the other hand tannins slow down the process of soil humus formation by inhibiting the activity of various enzymes of the soil microorganisms. This is because of their ability to precipitate pectinase, amylase, lipase, protease, β-galactosidase and cellulase and other macromolecules by virtue of their functional groups (Mueller-Harvey et al., 1987; Scalbert, 1991; Chung et al., 1998). They also reduce food digestibility in animals by precipitating digestive enzymes and thus are classified with anti-nutritive compounds (Makkar et al., 1988). These are also responsible to reduce quality of fruit juices, beer and wine during their low temperature storage owing to precipitation of proteins and carbohydrates present in them (Rout and Banerjee, 2006).

E-mail address: kantipsharma@gmail.com.

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2. Tannase in last decade

Tannase is now known to be a ubiquitous enzyme in the microbial world. The enzyme showed widespread occurrence in various fungi, bacteria and yeasts (Field and Lettinga, 1992). It catalyzes the hydrolysis of the ester bond formed between the glucose and gallic acid moiety, and the depside linkage formed between two galloyl residues of hydrolyzable tannins (Mingshu et al., 2006). Tannase was discovered by Scheele in 1786 (Adachi et al., 1968). Initially it was characterized in plants by Madhavakrishna et al. (1960). Later on many studies were done on the source, assay, application, immobilization, purification and characterization of tannase from various sources. In the last two decades there has been a strong focus on the production of tannase by microbial strains (Kumar et al., 1999; Mondal and Pati, 2000; Ayed and Hamadi, 2002). A number of investigations on microbial tannase illustrate that tannase of fungi, bacteria and yeast responds differently on tannins present in the environment. Yeast's tannase is very much selective with reference to its substrates. It prefers to act on tannic acid only (Deschamps et al., 1983). In ***Arxula adeninivorans*** it is composed of 1764 nucleotides coding for 587 amino acids. The active site contains glycine and serine residues (Boer et al., 2009). Fungal tannase is quite versatile and can efficiently degrade various types of tannins but shows a lower affinity for naturally occurring tannins. However bacterial tannase is very much responsive for natural tannins (Bhat et al., 1998).

The most abundant group of bacteria able to degrade tannins are found in the gastrointestinal tract of ruminants. It is because of their adaptation to the forage tannins consumed by them in their diet (Rusniok et al., 2010). These were subsequently isolated by various researchers from time to time. A few of them are ***Streptococcus caprinus*** from goat faeces (Brooker et al., 1995); ***Streptococcus bovis*** **biotype I** from the faeces of Koalas (Osawa et al., 2000) and ***Lactobacilli*** and ***S. lugdunensis*** from human intestine (Noguchi et al., 2007). In view of increasing evidences of tannase presence in gastrointestinal tract microflora, Noguchi et al. (2009) suggested the use of tannase as a biomarker to identify ***Staphylococcus lugdunensis*** in human intestine. Ruiz et al. (2010) used tannase along with other enzyme to characterize oenological starter culture responsible for alcoholic fermentation. ***Lactobacillus's*** tannase is very well characterized among bacterial tannase and attempts were also made to explore reaction mechanism. Tannase gene is present on the chromosomal DNA (Reveron et al., 2017) of ***Lactobacillus***. The enzyme displays α/β structure, featured by a large cap domain inserted into the classical serine hydrolase fold. Ser 163, His 451, and Asp 419 are forming catalytic traid. During the binding of gallic acid, carboxyl group of the molecule forges hydrogen-bonding interactions with the catalytic triad of the enzyme while the three hydroxyl groups make contacts with Asp 421, Lys 343, and Glu 357 to form another hydrogen-bonding network (Ren et al., 2013). Popularity of ***Lactobacillus***'s tannase enforced Ueda et al. (2014) to compare tannase in three closely related species as ***Lactobacillus plantarum, L. paraplantarum,*** and ***L. pentosus*** and they found a difference in their substrate specificities. A tannic acid tolerant bacteria belonging to ***Klebsiella*** genus was isolated by Pepi et al. (2013). The bacteria can tolerate tannic acid concentration up to 20 g/l and thus suggested a promising one for bioremediation process of waste rich in tannic acid and other polyohenols. Hyper producer tannase of ***Streptococcus gallolyticus*** UCN34 was cloned and characterized by Jiménez et al. (2014). The tannase enzyme from above study was found superior in many aspects as compared to ***Lactobacillus plantarum***. First time tannase production in gas lift bioreactor was reported by Aguilar-Zarate et al. (2014) at 1 L scale. At industrial scale solid and submerged fermentation are known for enzyme production. The enzyme produced by solid state fermentation is different in its property from the enzyme produced in submerged fermentation as the type of process affects the structure of the enzyme produced. Kumar et al. (2016) suggested the use of agro-residues as a potential substrate for tannase production with an aim to decrease the production costs so that the enzyme could be used proficiently for commercial purposes. It was observed that the enzyme produced by solid state fermentation is of superior quality (Renovato et al., 2011; Beena et al., 2011a; Mahmoud et al., 2018).

3. Tannase in chemical industry

Enzymes have to function in the presence of organic solvents for many industrial biotransformations. Immobilization is technique by which the negative effect of organic solvent on enzyme can be minimized. The effect of organic solvent on tannase of ***Aspergillus awamori*** MTCC 9299 showed that acetic acid, isoamylalcohol, chloroform, isopropyl alcohol and ethanol inhibits the enzyme activity while butanol and benzene supports the enzyme function (Chhokar et al., 2010). Belur et al. (2010) produced tannase from ***Serratia fecaria*** DTC and advocated the use of isolate to carry out biotransformation's in alkaline pH above 8. Curiel et al. (2010) and Mateo et al. (2013) suggested the use of covalent immobilization of tannase of ***Lactobacillus plantarum*** on glyoxyl agarose. Sodium alginate entrapped tannase of ***Aspergillus niger*** were found better in comparison to soluble enzyme preparation to reduce the tannin content of ***Phyllanthus emblica*** juice (Srivastava and Kar, 2010). The entrapment by sodium alginate also improved stability of ***Paecilomyces variotii*** tannase to work in acidic conditions (Schons et al. (2011). Flores-Maltos et al. (2011) envisaged the application of immobilization for bioremediation purpose. ***Bacillus sphaericus*** was reported as highest tannase producer strain by Raghuwanshi et al. (2011) to synthyesize gallic acid. Beena et al., 2011b reported synthesis of propyl gallate using acidophilic tannase of ***Aspergillus awamori***. Bioimprinting technique was also suggested to increase propyl gallate synthesis in non-aqueous medium (Nie et al., 2012). Taskin (2013) first time used immobilized cells of ***Rhodotorula glutinis*** **MP-10** for co-production of tannase and pectinase. Wu et al. (2016) immobilized tannase on carboxyl-functionalized Fe_3O_4 nanoparticles (CMNPs) and improved its catalytic efficiency. The studies also suggested the use of nanotechnology in conjugation with enzyme technology for industrial applications of tannase (Choi et al., 2018; Li et al., 2018; Ong and Annuar, 2018). Hasan et al. (2018) compared the property of free and immobilized tannase of marine fungus ***Aspergillus nomius*** and optimized culture conditions for its production. In another study tannase from a marine fungus ***Aspergillus nomius*** GWA5 was purified, characterized and explored for its industrial applications by Farag et al. (2018).

4. Tannase in food and nutrition

Tannase treatment was suggested to improve quality of tea extract by increasing polyphenols content of it (Chandini et al., 2011; Hayashi et al., 2012). Castor bean and Sorghum residues were detoxified by the use of tannase and phytase of ***Paecilomyces varioti*** (Madeira et al., 2011; Schons et al., 2012). Hong et al. (2012) suggested the application of tannase treated green tea extract in reducing the damage caused UV-B on mice skin. Tannase and pectinase both were applied to improve anti-oxidant and nutritional value of grape seed extract and grape pomace by releasing polyphenols and monosaccharides from them (Chamorro et al., 2012). Green tea biotransformation with tannase showed potential against cancer treatment (Macedo et al., 2012). Tannic acid biotransformation by tannase of ***Azotobacter*** was first time reported by Gauri et al. (2013). Sharma et al. (2014) used tannase of ***Aspergillus niger*** to increase the bioavailability of Vit C and minerals in guava juice by removing tannin present in it.

Raghuwansi et al. (2014) emphasized on the importance of tannase to improve the nutritional content of cattle feed. Tannase along with other enzymes helps in the extraction of proanthocyanidins from grape seeds and skins which are found very effective in lowering cardiovascular risk (Fernandez et al., 2015). Similar study was also done by Ahrén et al., 2015 in which tannase of ***Lactobacillus plantarum*** was used to ferment blueberries to increase their anti-hypertensive effects. Considering the medicinal importance of flavanones, Madeira and Macedo

(2015) attempted extraction and biotransformation of citrus fruit residues with the help of tannase enzyme to improve its antioxidant activities. De-Queirós et al. (2016) first time used tannase to increase soymilk isoflavones content and its antioxidant activity. In another study immobilized tannase was used to increase the anti-obesity and hypoglycemic effects of tea (Roberto et al., 2016). Kanpiengjai et al. (2016) isolated tannin tolerant yeast in a fermented beverages prepared from tea leaf in Thailand. Similar study was also carried out by Chaikaew et al. (2017) to determine the diversity of tannin tolerant lactic acid bacteria in order to know their health beneficial effects. Sharma et al. (2017) showed that importance of ***Klebsiella*'s tannase** to detoxify the toxin euptox A in goat. Tannase producing ***Lactobacillus*** strains were found beneficial to improve amino acid availability and antioxidant activities of kidney bean's sourdoughs (Saez et al., 2017). The direct suppressive effect of tannase on fat deposition in mice was observed when they were fed tannase treated ethanolic extract of ***Chrysanthemum indicum* Linné** (Lee et al., 2019). Tannase treatment of green tea extract was found good in increasing its therapeutic role in the treatment of atopic dermatitis (Hwang et al., 2019).

5. Tannin in plant defense

Tannins are classified under plant secondary metabolites which may be either constitutively stored as in inactive forms (phytoanticipins) or induced in response to the pathogen's attack as phytoalexins (War et al., 2102). The role of tannins in plant defense against various stresses has been studied in many plants (Barbehenn and Constabel, 2011). Miranda et al. (2007) and Mellway et al. (2009) found accumulation of proanthocyanindins during herbivory, wounding and fungal attack in plants. Wang et al. (2012) compared proteins synthesis in groundnut upon infection of pathogenic and non-pathogenic strains of ***Aspergillus flavus*** and revealed that gene involved in condensed tannin synthesis were up regulated when pathogenic strains of ***Aspergillus*** infects host plants. The absence of polyphenols production in grapes resulted into infection of ***Xylella fastidiosa*** (Wallis and Chen, 2012). Strawberry plants accumulate ellagitannins in response to attack of ***Colletotrichum fragariae***. The study of Mamani et al. (2012) revealed that plant tannins may be common plant defense responsive molecules capable of inducing pathogen resistance in different plant species. Tannins modulate plant microbe and herbivore interaction above and below ground differently. Tuominen (2013) quantified various water-soluble phenolic compounds and measured their biological activity *in* ***G. sylvaticum*.** The study revealed that the plant allocates a significant amount of tannins in those plant parts which are important to the fitness of the plant and susceptible to natural enemies. He also suggested that pistil and leaf tannins protect plants against insects and herbivores while root tannins provide protection against soil pathogens. In Zebra Chip disease of potato caused by ***Candidatus liberibacter solanacearum***, plant showed alteration in tannin metabolism. Wallis et al. (2015) found an increase in ellgitannins level with other defense related chemicals in infected plants. Hellenbrand et al. (2015) quantified proanthocyanidins in the reproductive organs of plant parts and suggested their role in plant defense system.

Zhao et al. (2016) noted highest fluctuations in plant phenolics in ***Robinia pseudoacacia*** seedlings due to climate changes and suggested their role in plant adaptation to acclimatize aginst abiotic stresses. Cui et al. (2016) observed an increase in tannins concentration in tomato plants upon infection by ***Tomato yellow leaf curl virus*** and in the presence of high ozone concentration. Herbivory by ungulates affects forest regeneration process. Rhodes et al. (2017) studied the long term impact of it on tree functions and survival and observed that ungulate herbivory depute condensed tannins as a defense molecules in aspen plants. Tannins content is reduced in red alder (***Alnus rubra***) upon colonization by ***Frankia* sp.** and the plant became more susceptible for herbivory (Ballhorn et al., 2017). Foliar application of ellagitannins of strawberry leaves prior to inoculation with a virulent pathogen was found to increase in resistance in strawberry plants against ***Colletotrichum acutatum*** and against ***Xanthomonas citri*** subsp. ***citri*** infection in lemon plants (Martos et al., 2018). Shafique et al. (2018) suggested the role of tannins in making the chillies resistant to wilting disease caused by ***Fusarium*** infection. In order to determine marker traits in snapmelon (***Cucumis melo*** var. ***momordica***) and to make it more resistant against melon fly (***Bactrocera cucurbitae*)** infection, Haldhar et al. (2018) observed a negative relationship between tannin content of the fruits and fruit infestation by the pest. The study also showed that as tannin content decreases, infection progresses. Tannin synthesis was found to be induced by mechanical defoliation in ***Quercus* sp.** by Gallardo et al., 2019. They also observed the infection of ***Phytophthora*** interferes with the regulatory process of tannin synthesis and makes the plant more susceptible for biotic stresses. Lazaro-Gonzalez et al. (2019) investigated the alteration of chemical defense molecules upon infection by parasites. They found the accumulation of phenols and tannin compounds in parasitized plant compared to less parasitized one and suggested their role in defense.

6. Plant defense and pathogen's hydrolytic enzymes

Plant defense is an ability of a plant to resist disease onsets and progression. It is basically of two types: Constitutive and Induced. Constitutive (continuous) defense is provided by cell walls, waxy epidermal cuticles, and bark etc. The second type of defense is based upon detection of invading pathogens and to respond them by production of defense chemicals, pathogen-degrading enzymes, and deliberate cell suicide (Van Baarlen et al., 2007; Anderson et al., 2010). Plant cell wall and its components represent an important barrier against pathogens. To initiate the process of infection all pathogens have to break this barrier. Among various mechanisms suggested by researchers in pathogenic microorganisms to invade plant tissue, one is the use of enzymes to degrade plant cell wall and fruit wall barriers by cellulase, xylanase, and cellobiosidase, polygalacturonases, pectin esterases and pectate lyase etc. (Esquerre-Tugaye et al., 2000; Rajeshwari et al., 2005; Gudlur et al., 2009). Cellulase was found responsible for virulence in ***Magnaporthe oryzae*** causing rice blast disease (Van et al., 2012). Xia et al. (2016) identified the importance of endoglucanase for showing the complete virulence by ***Xanthomonas citri*** subsp. ***citri*** in citrus canker disease. The role of extracellular enzymes in root rot disease of soybean caused by ***Rhizoctonia bataticola*** was illustrated by Gawade et al. (2017).

Tannins are plant defensive molecules. Tannase is also reported in various species of genus ***Agrobacterium*** (Goodner et al., 2001), ***Xanthmonas*** (Da Silva et al., 2002), ***Pseudomonas*** (Selwal et al., 2010), ***Erwinia*** (Muslim, 2015) etc. which are among the top ten bacterial pathogens (Mansfield et al., 2012), but literature is not available about the role microbial tannase in dilution of tannin based plant defense. A study conducted of Bernays and Chapman (2000) reported use of tannase in invasion of plant tissue by insects. They found that some polyphagous insect species tolerates tannins by hydrolysing them rapidly with tannase enzyme. Ishikawa et al. (2014) observed that suppression of tannin synthesis in plants by pathogens is essential to cause disease. Mason et al. (2016) studied the interaction between aspen defense chemicals and ***Acinetobacter*** and found that bacteria utilize condensed tannins as a sole source of carbon for their growth irrespective of glucose and phenolic glycosides. The author also suggested that degradation of phenolic glycosides alleviates the cytotoxicity of these compounds. The study of Tahmourespour et al. (2016) revealed that microorganisms capable to grow in the presence of tannins degrade them with their tannase and utilize them as a sole source of carbon. ***Xanthomonas fragariae*** causes Bacterial Angular Leaf Spot Disease in strawberry. Kim et al. (2016) showed a decrease in the level of gallic acid and ellagitannins in infected leaves during the disease establishment as they might be utilized by the pathogen for its growth. The presence of tannase in an endophyte isolated from (***Ailanthus excelsa* (Roxb)** suggested its role to extract energy by degrading tannin present

in plants (Roy et al., 2018) and it may be one of the strategies among others applied by microorganisms to cause infection.

Till date research on tannase mediated tannin degradation is mainly focussed on to increase antioxidant activities of fruits juices, minimization of its negative effects on ecosystem with reference to soil and water pollution and in reducing forage toxicity in herbivores. Tannins are important defense molecules and their degradation helps in disease onset and progression. The generation of tannase deficient mutants and its effect on their virulence will pave a path to understand the mechanism of tannin dilution and disease occurrence in plants. Thus there is need to characterize tannase of phytopathogens and to design its inhibitors to understand tannase role in tannins degradation with reference to plant's defense response.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.bcab.2019.101342.

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