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Amyloid Proteins in Plant-Associated Microbial Communities

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Abstract
Amyloids have proven to be a widespread phenomenon rather than an exception. Many proteins presenting the hallmarks of this characteristic beta sheet-rich folding have been described to date. Particularly common are functional amyloids that play an important role in the promotion of survival and pathogenicity in prokaryotes. Here, we describe important developments in amyloid protein research that relate to microbe-microbe and microbe-host interactions in the plant microbiome. Starting with biofilms, which are a broad strategy for bacterial persistence that is extremely important for plant colonization. Microbes rely on amyloid-based mechanisms to adhere and create a protective coating that shelters them from external stresses and promotes cooperation. Another strategy generally carried out by amyloids is the formation of hydrophobic surface layers. Known as hydrophobins, these proteins coat the aerial hyphae and spores of plant pathogenic fungi, as well as certain bacterial biofilms. They contribute to plant virulence through promoting dissemination and infectivity. Furthermore, antimicrobial activity is an interesting outcome of the amyloid structure that has potential application in medicine and agriculture. There are many known antimicrobial amyloids released by animals and plants; however, those produced by bacteria or fungi remain still largely unknown. Finally, we discuss amyloid proteins with a more indirect mode of action in their host interactions. These include virulence-promoting harpins, signaling transduction that functions through amyloid templating, and root nodule bacteria proteins that promote plant-microbe symbiosis. In summary, amyloids are an interesting paradigm for their many functional mechanisms linked to bacterial survival in plant-associated microbial communities.

Introduction

Plants are an important system for the study of microbe-microbe and microbe-host interactions together with their mechanisms. Plants constitute approximately 80% of Earth's total biomass, which makes them the world's largest living surface area [Bar-On et al., 2018]. Furthermore, all plants are ubiquitously colonized by microbes, including bacteria, fungi, and oomycetes, to a variable extent [Beattie and Lindow, 1999; Kandel et al., 2017]. Plant-colonizing microbes thrive on primary and secondary plant-derived metabolites, which include nutrients and protective compounds. In addition, plants

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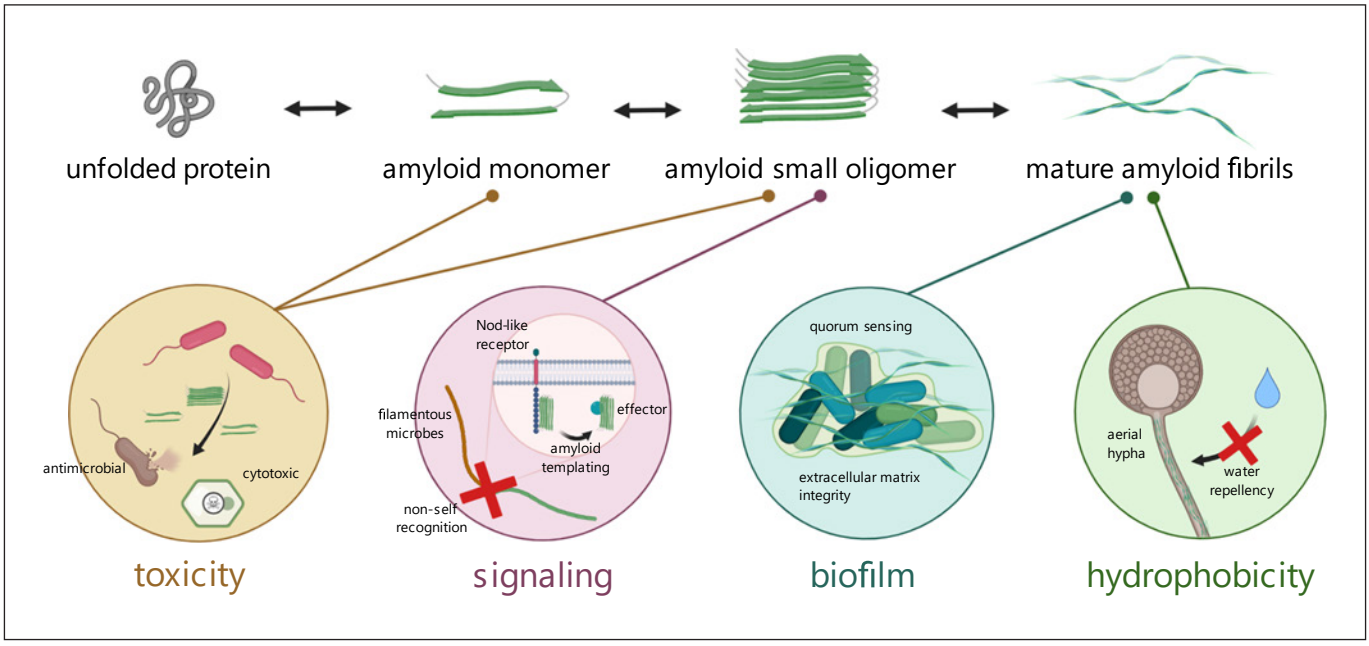

Fig. 1. Different functions of amyloid proteins related to plant microbial communities at different stages of amyloid structural conformations.

provide a niche that defends microbes against biotic and abiotic factors, in both the phyllosphere (above ground) and rhizosphere (below ground) parts of the plant [Mercado-Blanco, 2014]. As a consequence, complex interactions between prokaryotes and eukaryotes have evolved, where fungi and oomycetes are major determinants of the diversity and abundance of plant-associated bacteria [Agler et al., 2016]. This results in competition between microbes for access to the specific plant niches [Anderson et al., 2010; Chaudhry et al., 2021].

On one side of the spectrum, some microbes develop symbiotic relationships that benefit all parties by sharing common goods, which can be defined as secreted metabolites that benefit not just the producer but the whole community [Saikkonen et al., 2004]. On the other side, they can develop antagonistic relationships either toward other microbes or the host. In the first case, either a specific microbe or a number of them are inhibited through physical or chemical mechanisms. As a consequence, the competitors, either directly or indirectly, are denied access to the plant's resources. In the second, a pathogenic relationship develops, which benefits the microbe to the detriment of the host. Thus, pathogenic interactions primarily benefit the pathogen and depending on symptoms to the host can be fatal to the native community. The key to colonization of both beneficial and pathogenic microbes is therefore a robust interaction with the host that can resist perturbations. Crucial mechanisms include biofilm formation and the release of antimicrobial and cytotoxic peptides to enforce niche colonization.

One intriguing class of proteins that is increasingly linked with pathogenicity and microbial survival in plant-associated communities are amyloids. Amyloids are proteins diverse in nature that have a set of common structural properties, the most salient of which is the capacity to polymerize as long unbranched fibrils with convergent characteristics (Fig. 1) [Makin et al., 2005]. These fibrils show a consistent cross beta structure, which consists of two parallel or antiparallel beta-sheets held together on their perpendicular axis through intermolecular hydrogen bonds [Nelson et al., 2005]. Single protofibrils may associate laterally with other protofibrils and lead to mature amyloid fibrils, which are about 6–10 nm thick and up to several micrometers long [Khurana et al., 2003]. Amyloid fibrils result in the same X-ray refraction pattern and are detectable via binding of Congo Red and Thioflavin T dyes [Eanes and Glenner, 1968; Kuznetsova et al., 2012; Wu et al., 2012; Girych et al., 2016]. Other more general characteristics of amyloids include their resistance toward proteases and ionic detergents, and a nucleation-mediated growth, which is mostly homogeneous but can be heterogeneous at lower levels [Soto and Castaño, 1996; Šarić et al., 2014; Törnquist et al., 2018]. This latter feature makes it interesting for potential cross-in-

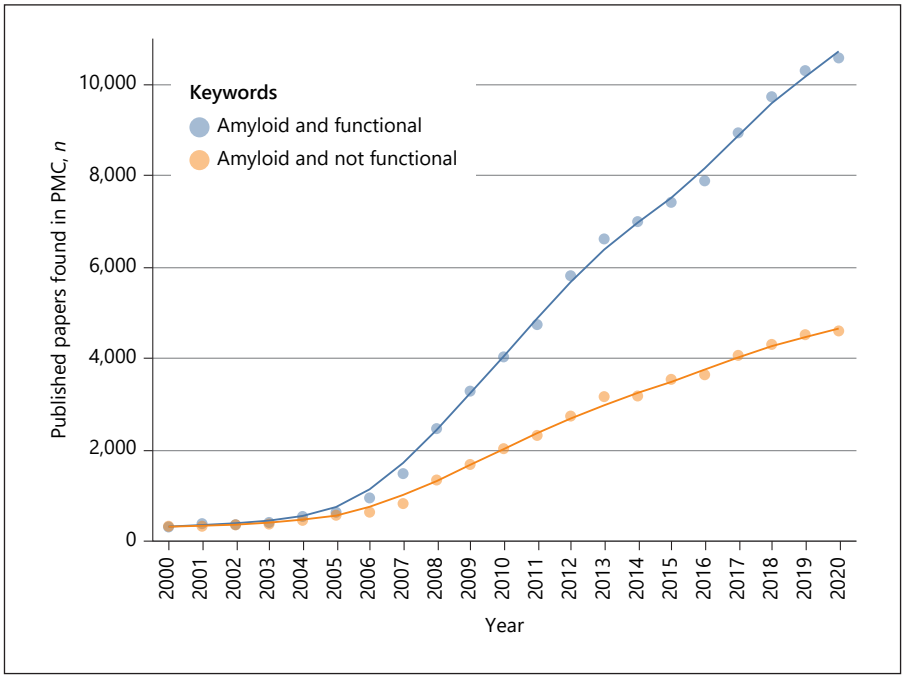

Fig. 2. Comparison of publications per year with the keyword "amyloid" and the presence/lack of the term "functional" as found in the PubMed Central (PMC) database as of December 30, 2020. Trend lines drawn over scatter plot with local regression based on the LOESS method.

teractions between amyloids of different species. Additionally, the study of antimicrobial properties of many of the known amyloids, including pathology-associated ones, has gained a lot of traction in recent years [Soscia et al., 2010; Kagan et al., 2011; Spitzer et al., 2016; Gosztyla et al., 2018; Martin et al., 2018]. Pore formation and general non-specific and irreversible interaction with phospholipid membranes have been proposed as mechanisms for antibiotic activity [Butterfield and Lashuel, 2010; Last and Miranker, 2013].

Initially, amyloids were investigated as the etiological agent of many neurodegenerative diseases [Muchowski, 2002]. However, over the last two decades, they have been increasingly studied in the context of their prevalence in many physiological processes in all three domains of life including bacteria, archaea, and eukarya [Levkovich et al., 2021]. Many amyloids that impact both virulence and survival in prokaryotes have been described [Antonets et al., 2020]. Thus, to distinguish pathogenic amyloids from the latter they are commonly referred to as functional amyloids in the literature [Badtke et al., 2009]. In Figure 2, the larger increase in recent years in publications containing the keyword "amyloid" related to functional as compared to those lacking the term "functional" is evident.

The characteristics of amyloids already mentioned, including resilience, heterogeneity, nucleation, and antimicrobial activity, underscore many of their physiological functions in plant-associated microbial communities. Here, we discuss in the context of plant colonization the history and recent developments of functional amyloids associated with bacterial survival strategies in host-associated and host-related communities. We classify these strategies into two main groups: structural modifications, which include biofilm and hydrophobic surface formation, and defense through antimicrobial activity. Lastly, miscellaneous plant niche-related functions are described, which include amyloids that regulate diverse aspects of their hosts survival and which do not fit within the other two categories. A visual summary of all of these functions is shown in Figure 1 and representative proteins mentioned in this mini-review are summarized in Table 1.

Structural Modifications of Microbial Amyloids

Biofilm Formation

Biofilms are complex microbial communities formed by the cooperation of single or multiple species that adhere to a surface and each other, secreting an extracellular matrix (ECM) [Dragoš and Kovács, 2017]. They represent one of the most widespread strategies for bacterial virulence and proliferation in the microbial world. Biofilms naturally exist in diverse niches of plants in both the

Table 1. Representative microbial, plant amyloids, and related proteins with a role in plant-associated microbial communities

Main function	Protein	Organism	Localization	Additional comments	References
Biofilm formation	CsgA CsgB	*Escherichia coli* *Salmonella enterica*	Extracellular	Virulence promotion Quorum sensing	[Barnhart and Chapman, 2006]
	TasA	*Bacillus* species	Extracellular	Antibacterial Membrane stabilization Quorum sensing	[Stöver and Driks, 1999; Romero et al., 2010]
	FapC	*Pseudomonas* species	Extracellular	Cell surface adhesion Quorum sensing	[Dueholm et al., 2013; Rouse et al., 2018a]
Hydrophobic layer formation	MPG1	*Magnaporthe oryzae*	Extracellular Cell wall	Surface detection Spore attachment	[Kershaw et al., 1998; Pham et al., 2016]
	BslA	*Bacillus subtilis*	Extracellular	Self-assembling protein that coats *Bacillus* biofilms	[Kovács et al., 2012; Hobley et al., 2013]
	Chaplins	*Streptomyces coelicolor*	Extracellular Cell wall	Surface attachment	[Elliot et al., 2003; Bokhove et al., 2013]
	Hum3 Rsp1	*Ustilago maydis*	Extracellular Cell wall	Shields fungus from the plant immune system	[Müller et al., 2008]
Antimicrobial activity	Microcin E492	*Klebsiella pneumoniae*	Extracellular	Amyloid fibrils act as a reservoir for antimicrobial peptides	[Bieler et al., 2005; Shahnawaz and Soto, 2012]
	Prohevein	*Hevea brasiliensis*	Extracellular	Latex tree antifungal peptide	[Berthelot et al., 2016]
	Cn-AMP2	*Cocos nucifera*	Extracellular	Antimicrobial peptide from coconut	[Gour et al., 2016]
	RsAFP-19	*Raphanus sativus*	Extracellular	Antifungal peptide from radish	[Garvey et al., 2013]
Plant virulence promotion	Harpins	*Xanthomonas* species *Erwinia amylovora* *Pseudomonas syringae*	Extracellular Cell wall	Effector translocation Plant hypersensitive response Plant cell toxicity	[Oh et al., 2007; Choi et al., 2013]
	RTP1p	*Uromyces* fabae	Extracellular Haustorium	Structural and stabilizing role	[Kemen et al., 2013]
Signaling	NLR amyloids	Filamentous fungi and bacteria	Membrane and cytosolic components	Non-self recognition	[Loquet and Saupe, 2017; Dyrka et al., 2020]
Plant symbiosis promotion	RopA and RopB	*Rhizobium leguminosarum*	Outer membrane Extracellular	Soluble forms are membrane proteins	[Kosolapova et al., 2019]

NLR, Nod-like receptor.

phyllosphere and rhizosphere and are accountable for a large part of all activity of bacteria in nature [Hall-Stoodley et al., 2004]. The ECM is composed of proteins, extracellular DNA, and polysaccharides, which in addition to maintaining microbial adhesion, protects the community and mediates interaction with the environment, including the host [Branda et al., 2005]. Within biofilms, common goods can be freely shared and bacteria are protected against harmful chemical and physical events, such as antimicrobials or displacement by rain [Patel, 2005; Arnaouteli et al., 2016]. The ECM components of biofilms are diverse in function and their composition varies for different microbial species [Flemming and Wingender, 2010]. However, the protein component is often consistently comprised of a single protein which forms a mesh of functional amyloid fibrils [Erskine et al., 2018a]. The main role of these fibrils is to build the scaffold on which the stationary cells and other ECM components rest. Additionally, it gives a greater degree of resilience to the structure, as mature fibrils are resistant to thermal and chemical denaturing conditions, including proteases. This helps to maintain the integrity of biofilms in a competitive environment, such as the extracellular compartments inside of plants, where these stresses are common

[Taglialegna et al., 2016]. Functional amyloids in association with biofilms have been studied in many different microbial species, the majority of them focusing on bacteria. Herein, we summarize the well-documented ones and their involvement in plant colonization.

Curli is the most studied biofilm-associated amyloid and was the first to be described [Olsen et al., 1989]. It is produced by, among others, the enteric bacteria *Escherichia coli* and *Salmonella enterica*, which are also found in the environment and are well prepared to form biofilms on plants [Danhorn and Fuqua, 2007; Carter et al., 2016; Pruteanu et al., 2020]. The major subunit protein of curli is CsgA, composed of five repeat units with conserved glutamine and asparagine residues important for amyloid formation [Wang et al., 2010]. Curli plays an important role in the adhesion and promotion of biofilm onto different phyllosphere surfaces, including various economically important crops [Jeter and Matthysse, 2005; Boyer et al., 2016]. Moreover, curli is involved in many aspects of the biology of its producer, including virulence promotion, and it is regulated through quorum sensing [Smith et al., 2017; Saxena et al., 2019]. Curli has been determined in addition as an important virulence factor in Shigatoxigenic *E. coli* on fresh produce of crops and therefore represents a serious risk to human health through ingestion of uncooked vegetables [Merget et al., 2019]. How far curli stabilizes biofilms on plants and how much it promotes resistance to biofilms of *E. coli* to mechanical stresses and removal by solvents is still under debate and an important topic in food security.

The formation of *Bacillus* biofilms in the rhizosphere and phyllosphere is associated with plant growth promotion [Hashem et al., 2019]. The major proteinaceous component of this biofilm is TasA, which forms amyloid fibrils and provides integrity to the ECM [Romero et al., 2010]. Despite claims to its non-amyloidogenic nature, it is still widely considered to be a functional amyloid [Erskine et al., 2018b]. TasA was also shown initially to be antibacterial [Stöver and Driks, 1999]. However, whether this function is associated with its capacity to form an amyloid structure is not known. Recently reported functions of this amyloid not related to biofilm formation include its potential contribution to membrane stabilization during the stationary phase of the cell and its role in community signaling [Steinberg et al., 2020; Cámara-Almirón et al., 2020]. Overall, TasA promotes many aspects of the fitness and survival of plant-associated *Bacillus* species.

Biofilm formation in the roots by some members of *Pseudomonas*, like *Pseudomonas fluorescens* and *Pseudomonas putida*, is also associated with plant growth promotion [Meliani et al., 2017]. *Pseudomonas* species secrete the functional amyloid protein (Fap), which contributes to stable and robust biofilm formation and renders protection against chemical and mechanical stresses [Ueda and Saneoka, 2015; Zeng et al., 2015; Rouse et al., 2018b]. The major amyloid fibril component in *Pseudomonas*' biofilm is FapC [Dueholm et al., 2010]. It presents three imperfect repeats of a glutamine- and asparagine-rich domain that are responsible for the formation of very stable amyloid fibrils [Rasmussen et al., 2019].

All of these biofilm amyloids require unique and intricate pathways with numerous intermediate enzymes and safety stops that keep aggregation under control [Balistreri et al., 2020], as its unintended trigger in the cytoplasm would overwhelm chaperones and lead to cell death [Landreh et al., 2015]. Additionally, there are usually two or more proteins that are directly responsible for amyloid formation: the major subunit protein that makes up most of the fibril's weight but is unable to polymerize on its own, or does so slowly, and the minor subunit that acts as a nucleator. This strategy is found, for example, in curli, where CsgA and CsgB fulfill those roles, respectively [Hammer et al., 2007; Yan et al., 2020].

The dependence on amyloid fibrils for biofilm construction makes them a central target for interference by plants in order to keep infection under control. Plant polyphenols and flavonoids, in particular, have been shown to inhibit the development of bacterial biofilms through the blocking of amyloid formation in several distinct bacterial species [Najarzadeh et al., 2019; Pruteanu et al., 2020]. Interestingly, rather than a broad anti-amyloidogenic effect, they target amyloids produced by specific bacterial species. This is in accordance with the reported benefits of some bacterial biofilms in the promotion of plant fitness, which therefore may be preferred by the plant over others.

The widespread occurrence of functional amyloids in their association with biofilm-forming pathogenic and beneficial microbes emphasize their significance in microbe-microbe and microbe-host interactions. Further studies are required to decipher their role in plant-associated microbes, which could lead to the development of novel strategies for plant disease management particularly through probiotics based on mixed cultures that could gain resilience under harsh natural conditions through amyloid-stabilized surface attachment.

Hydrophobic Surface Formation

Another class of structural modifications that are related to microbial survival in the plant holobiont includes hydrophobic layer formation by surface-active proteins. Surface-active proteins modify the properties of physical interfaces and are often linked to an amyloid structure [Sunde et al., 2016]. In fungi, these are called hydrophobins and are known to play an active role in plant-fungi interactions that favor virulence [Teertstra et al., 2009]. Proteins with a similar function as fungal hydrophobins have also been described in some filamentous bacteria. In *Streptomyces coelicolor*, the protein family of chaplins is composed of amyloids that play a role in the formation of aerial mycelia and attachment to surfaces [Elliot et al., 2003]. They respectively perform these roles in two distinct amyloid morphologies, the first formed at water-air interfaces, and the second formed in solution [Bokhove et al., 2013]. In *Bacillus subtilis*, the protein BslA is known to coat TasA-formed biofilm in a thin hydrophobic layer, which helps maintain impermeability and repellency [Kobayashi and Iwano, 2012; Bromley et al., 2015]. BslA is self-assembling, but in contrast to fungal hydrophobins, is not described as amyloidogenic in nature [Liu et al., 2017]. Both *Streptomyces* and *Bacillus* species are soil-dwelling bacteria associated with plants and have been shown to promote their growth and protect them against phytopathogens [Hashem et al., 2019; Kim et al., 2019].

Some Streptomyces species such as *S. scabies* have become serious crop pathogens where the ability to colonize plant niches including the secretion of plant hormones has become a virulence factor [Li et al., 2019]. The role of functional amyloids in such lifestyle shifts has been poorly studied and might in the future become an important target to study the transition from symbionts and facultative pathogens to obligate pathogens. In the obligate biotrophic plant pathogenic fungus *Ustilago maydis* two secreted candidate effectors Hum3 and Rsp1, a hydrophobin and a hydrophobic repeat-rich protein, are tightly bound to the cell wall and form amyloid-like fibrils that influence the surface hydrophobicity [Müller et al., 2008]. It was proposed that they play a role in shielding the fungal hyphae from the plant immune system [Lanver et al., 2017]. For obligate biotrophic fungi, the integrity of the host is crucial for their successful manifestation and the completion of their pathogen life cycle. The obligate rust fungus, *Uromyces fabae*, delivers the filament-forming protein RTP1p, via sub-compartments of the haustorium into the host cytoplasm where it plays a structural and stabilizing role [Kemen et al., 2005, 2013]. RTP1p has therefore been hypothesized to be a haustorial cell wall protein that extends the intracellular lifespan of the pathogen. Amyloid effector proteins may therefore represent a tool for extending the biotrophic phase and protecting the haustorium from the plant defenses even under conditions where cell death has been initiated by the host. If and how this is related to the green islands that can be observed when endophytes colonize plant leaves is a future topic of debate [Wemheuer et al., 2019].

In other filamentous phytopathogenic fungi, hydrophobin functions that promote virulence and pathogenicity include spore dispersal, attachment to hydrophobic surfaces, and immune evasion. Hydrophobins act as surfactants that break surface water tension and maintain a hydrophobic exterior to allow aerial hyphae to develop and prevent its desiccation [Linder et al., 2005]. This also helps with better dissemination as dry spores are lighter and carried farther away [Beever and Dempsey, 1978; Wessels, 1996]. Hydrophobins also contribute to surface detection and spore attachment to the hydrophobic leaf surface. Such is the case of the hydrophobin MPG1 from the pathogen *Magnaporthe oryzae* in rice [Kershaw et al., 1998], whose amyloid aggregation is triggered by a surface-driven mechanism [Pham et al., 2016]. Hydrophobins may also help mask spore epitopes recognized by the plant and thus evade immune detection [Aimanianda et al., 2009; Carrion et al., 2013; Marcos et al., 2016].

These hydrophobic coatings can also be understood as a way to prevent bacterial colonization from water droplets. They discourage accumulation and adsorption onto the surface, therefore effectively inhibiting bacterial adhesion and thus biofilm formation onto the hyphae, spores, or other biofilm surfaces [Wick et al., 2007; Artini et al., 2017]. In fact, new developments in antibacterial surfaces with application in, for example, medical devices, include the use of recombinant hydrophobins to prevent biofilm attachment [Wang et al., 2017; Berger and Sallada, 2019; Devine et al., 2019; Sorrentino et al., 2020].

Antimicrobial Properties of Amyloids

Many already known antimicrobials have been associated in their activity with their capacity to assemble amyloid structures, including mammalian Protegrin-1 and amphibian Uperin 3.5 [Jang et al., 2011; Martin et al., 2018; Salinas et al., 2020]. The bacterial microcin E492 produced by *Klebsiella pneumoniae,* a soil and plant dwelling bacterium, has been described as amyloid. This microcin is an antibacterial peptide that kills bacteria through the formation of channels that disrupt mem-

brane permeability and mannose metabolism [Biéler et al., 2010]. Another interesting aspect of this amyloid is that mature fibrils act as an inert reservoir for the toxic peptide. After triggering through external factors, such as low pH, small soluble oligomers are released, which are then responsible for its toxicity [Bieler et al., 2005; Shahnawaz and Soto, 2012].

On the plant side, certain defense-related peptides have been shown to exhibit amyloid-like properties in vitro. These include prohevein from *Hevea brasiliensis*, a wound-induced peptide whose C-terminus exhibits agglutination of pathogenic organisms [Berthelot et al., 2016]. Other antimicrobial amyloid peptides from plants include Cn-AMP2 from *Cocos nucifera*, an antimicrobial from coconut water effective against gram-positive and gram-negative bacteria, and RsAFP-19, an antifungal defensin from *Raphanus sativus* [Mandal et al., 2009; Gour et al., 2016]. Interestingly, the fungicidal activity of the latter is negatively correlated with its aggregation level. This seems to suggest that one of its roles is to act as a decoy for the inactivation of toxic oligomeric intermediates from competitors into non-active fibrils [Caughey and Lansbury, 2003; Bieler et al., 2005].

The antimicrobial nature of amyloids is a topic of research with many implications for their potential use in human health. Particularly interesting would be the applications of such antimicrobial peptides against multidrug-resistant bacteria, for which targeted antibiotic resistance is an increasing problem [Wise et al., 1998]. Since the mechanism of most antimicrobial peptides, including antimicrobial amyloids, is not linked to a specific target but rather to irreversible binding and disruption of membranes, mechanisms of resistance are less likely to evolve [Mwangi et al., 2019]. Additionally, there is a need for antimicrobial compounds with little environmental impact for their use in agriculture [Montesinos and Bardají, 2008]. However, their applicability in both of these branches is hindered by the lack of understanding of what makes some antimicrobial amyloids more cytotoxic than others [Voth et al., 2020].

How antimicrobial amyloid producers defend against their own peptides is not known and probably varies among specific amyloids. As already mentioned, a complex system of chaperones ensures that there is no aggregation in the cytoplasm and the protein is in a state ready for translocation across the membrane [Sugimoto et al., 2018]. Additionally, external conditions also trigger amyloid-dependent antimicrobial activity and therefore may help to direct its action through two main mechanisms. The first is conformational change into an amyloid structure that leads to a more toxic protein, for example, human Serum amyloid A, which is active only at the skin surface because of its sensitivity to lower pH [Zheng et al., 2020]. The second is due to the shedding of soluble oligomers from mature fibrils that may themselves be toxic, as is the case of microcin E492 [Shahnawaz and Soto, 2012]. Very little is known about toxic amyloid proteins in the plant microbial community. Such as microbes on the human skin, microbes in the plant apoplast face a low pH (healthy skin pH 5.4 to 5.9, plant apoplast pH 5 to 6) that can quickly get more alkaline upon stress [Geilfus, 2017]. These changes might have a severe impact on amyloid toxicity and functionality as described above for human Serum amyloid A and require a high degree of adaptation by the microbes [Zheng et al., 2020]. Identifying antimicrobial amyloids that react to pH shifts in plants might be key to identify novel antimicrobial compounds that do not harm the natural microbiota but do protect from specific pathogens.

Virulence, Signaling, and Symbiosis in Microbial Amyloids

Finally, we describe three classes of amyloids that are not directly related to structural or antimicrobial functions that have been described in plant-associated microbial communities. These include plant toxicity and hypersensitive response promotion by harpins, non-self recognition in filamentous fungi and bacteria, and root symbiosis promotion.

The harpins are a family of heat-stable proteins produced by the phytopathogenic bacteria *Xanthomonas* spp., *Erwinia amylovora*, and *Pseudomonas syringae* [Oh et al., 2007]. These proteins are associated with the promotion of virulence through several amyloid-related mechanisms: bacterial effector translocation, induction of plant hypersensitive response, and cytotoxicity against plant cells [Choi et al., 2013]. Harpin's ability to induce hypersensitive response was correlated to its capacity to form amyloid fibrils in vitro [Oh et al., 2007]. The cytotoxicity mechanism is believed to be due to the formation of beta sheet-rich pores that bind to membranes and cause depolarization in plant cells [Pike et al., 1998].

The role for non-self-recognition and programmed cell death of amyloids has been described in filamentous fungi [Glass and Dementhon, 2006]. Small amyloid motifs act as a signaling mechanism that works by linking receptor and activator protein domains through a templating fold, leading ultimately to cell death [Loquet and

Saupe, 2017]. Nod-like receptor-associated amyloid signaling motifs have been recently discovered in filamentous bacteria, termed BELL and BASS [Dyrka et al., 2020]. They are loosely homologous to the animal, plant, and fungi Nod-like receptors and are proposed to act through similar amyloid-templating mechanisms [Saupe, 2020]. Non-self-recognition plays a role in maintaining pathogen diversity and therefore promoting the exchange of pathogenic traits important for survival against an ever-evolving plant immune system [Ishikawa et al., 2012].

There are fewer reports of functional amyloids concerning symbiotic interactions, probably because research effort is biased toward pathogenic and virulence-promoting mechanisms. RopA and RopB are two recently described proteins from *Rhizobium leguminosarum,* which display amyloid formation linked to microbe-host symbiosis [Kosolapova et al., 2019]. These proteins show structural similarity and are predicted to be outer membrane porins in their soluble forms. Their expression correlates with the formation of capsules, extracellular structures associated with stationary growth, in this root nodule bacterium. Kosolapova et al. [2019] speculate on its role in the establishment of plant-microbial symbiosis through the observation of enhanced expression after the addition of a plant flavonoid.

Conclusion

Amyloid proteins have crucial properties that make them suitable to fill diverse roles in the bacterial and fungal survival of plant-associated communities. Their capacity to polymerize into very resistant fibrils helps them withstand the stresses associated with plant colonization. This is highlighted by the many amyloid biofilm-forming proteins, including curli, Fap, and TasA. Additionally, the tendency of small soluble oligomers to interact with membranes and depolarize them makes them a common structure among antimicrobial and cytotoxic peptides. In this mini-review, we have also discussed amyloids that take part in symbiosis, signaling, and virulence mechanisms. Such a plethora of functions, with what is at the core the same fold, hints at yet to be discovered interactions. Potential cross-seeding among different amyloids in microbial communities, like the plant microbiome, may have a big impact on bacterial survival and disease. Recent examples from human health about the involvement of bacterial amyloids in the seeding of pathogenic amyloids give us a hint of this untapped potential [Javed et al., 2020; Sampson et al., 2020]. All in all, understanding proteins in the context of their amyloid structure and cross-interactions will improve our understanding of the ecology of plant-associated microbial communities and help to develop new methods relevant to human medicine and pest biocontrol.

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Conflict of Interest Statement

The authors have no conflicts of interest to declare.

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Author Contributions

D.G.-P. conceived the idea for the review, drafted the manuscript, and designed the illustrations. V.C. contributed to the biofilm section. A.K. contributed to the hydrophobic surface section. E.K. contributed to the overall discussion. All authors reviewed and approved the final manuscript.

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