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REVIEW

Amyloids and prions in plants: Facts and perspectives

K. S. Antonets[a,b], and A. A. Nizhnikov[a,b]

[a]All-Russia Research Institute for Agricultural Microbiology, St. Petersburg, Russian Federation;
[b]Department of Genetics and Biotechnology, St. Petersburg State University, St. Petersburg, Russian Federation

ABSTRACT. Amyloids represent protein fibrils that have highly ordered structure with unique physical and chemical properties. Amyloids have long been considered lethal pathogens that cause dozens of incurable diseases in humans and animals. Recent data show that amyloids may not only possess pathogenic properties but are also implicated in the essential biological processes in a variety of prokaryotes and eukaryotes. Functional amyloids have been identified in archaea, bacteria, fungi, and animals, including humans. Plants are one of the most poorly studied groups of organisms in the field of amyloid biology. Although amyloid properties have not been shown under native conditions for any plant protein, studies demonstrating amyloid properties for a set of plant proteins *in vitro* or in heterologous systems *in vivo* have been published in recent years. In this review, we systematize the data on the amyloidogenic proteins of plants and their functions and discuss the perspectives of identifying novel amyloids using bioinformatic and proteomic approaches.

KEYWORDS. Amyloid, prion, LD, WALTZ, SARP, PSIA, AFP, plant, yeast, A. *thaliana*, S. cerevisiae

INTRODUCTION

Amyloids are protein fibrils with a characteristic structure called "cross-β". This structure results from the formation of intermolecular β-sheets perpendicular to the axis of the amyloid fibrils[1] and is detected using two-dimensional X-ray diffraction.[2] The stacking of monomers in the fibrils results from the formation of numerous hydrogen bonds between neighboring β-chains.[3] Such spatial organization makes amyloids one of the most

Correspondence to: A. A. Nizhnikov; Podbelskogo sh., 3, St. Petersburg, Russia, 196608; Email: ant.nizhnikov@gmail.com
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stable biogenic particles and endows these macromolecules with unique physico-chemical properties: amyloids resist treatment with different detergents (like SDS and sarkosyl), proteinases, high temperatures, and several acids,[2,4-7] and can persist in the environment for years.[8] In addition, the unique spatial structure of amyloids can be specifically detected with several compounds. The binding of amyloids with Congo red diazo dye leads to apple-green birefringence in the polarized light,[9] while the interaction of amyloids with the fluorescent dye Thioflavin-T enhances the emission of its fluorescence.[10,11]

Amyloids have long been considered as pathogens for humans and animals causing incurable diseases called amyloidoses. The first pathanatomic descriptions of amyloidoses in the liver and spleen were obtained in the XVII or XVIII centuries, while the protein nature of pathological amyloid deposits was revealed only in 1858.[12] In 1854, Rudolf Virchow proposed the term "amyloid" (starch-like),[13] since amyloid deposits were stained a blue color using iodine similarly to starch granules. It has since been confirmed that the blue staining reflects the complex organization of amyloid deposits comprising, in addition to protein fibrils, proteoglycans and glycosaminoglycans.[14] To date, more than 30 proteins forming pathological or pathology-associated amyloids have been identified in humans.[15] Infectious neurodegenerative amyloidoses represent a special group of diseases caused by the amyloid state of prion (an acronym from proteinaceous infectious particle) protein (PrP), which was called PrP^{Sc} (PrP Scrapie, from scrapie disease of sheep and goats).[7,16] Presently, the term "prion" is attributed to all infectious amyloids. Nevertheless, there are prions that are unlikely to form amyloids.[17,18] In a broader sense, prions are proteins that persist under the same conditions in two or more conformations, of which at least one conformation possesses infectious properties.[19] Thus, amyloids and prions represent partially overlapping sets.

Since 2000, the paradigm of amyloids as pathogens has rapidly shifted. The formation of the amyloid structure not only leads to lethal diseases but is also necessary for essential biological functions. In different organisms, from archaea and bacteria to humans, more than 20 functional amyloids have been described, and their number is constantly growing.[20-22] In prokaryotes, at least eight groups of proteins capable of forming functional amyloids were identified. These amyloids participate in the biofilm formation,[23] overcoming the surface tension,[24] storage of toxins,[25] formation of pores in phagolysosome membrane[26] or hypersensitive response activation in plants.[27] In animals, amyloids are involved in long-term memory formation,[28,29] melanin polymerization,[30] hormone storage,[31] tooth enamel biomineralization,[32] programmed necrosis regulation[33] and the matrix formation in spermatozoid acrosome.[34]

Prions of ascomycetes represent a specific group of infectious amyloids. There are approximately ten prions in yeast *Saccharomyces cerevisiae*.[35] In contrast to non-infectious amyloids, the aggregates of prions are constantly fragmented by chaperone proteins,[36,37] providing the infectious properties and efficient transmission of prions during cell division.[38,39] The prionization of proteins may lead to heritable changes in their functional activities that cause different phenotypic manifestations. This phenomenon is referred to as protein inheritance,[40,41] i.e., an inheritance that is not determined by changes in the primary structure of genes, but rather the conformation of particular proteins. Most yeast prions have no significant effect on viability; however, some of them may be harmful under certain conditions,[42] and in contrast, some prions may increase cell survival.[43,44]

Thus, numerous amyloids involved in pathogenesis or implicated in a variety of functions have been identified in different organisms. At the same time, plants remain one of the most poorly studied group of organisms in the field of amyloid biology reflecting, on the one hand, the high complexity of working with plants as objects of research, and, on the other hand, the lack of methods for detecting amyloids at the proteomic level. In this review, we systematize the data on amyloidogenic proteins of plants, analyze their potential biological functions, and discuss the perspectives for the identification of novel amyloids in plants.

I. *Amyloids Involved in the Adhesion of Green Algae*

Life forms of green algae are diverse, and many of these organisms form biofilms attached to different surfaces. The adhesion of the spores of green algae includes two stages: initial and constant adhesion.[45] At the initial stage, preceded by a complex mechanism involving the recognition of a proper substrate, spores attach to the surface using a sticky secretion present on their shells. Subsequently, the spores actively produce special gel-like extracellular polymeric substances (EPS) comprising different proteins, glycoproteins, and proteoglycans. EPS bind Thioflavin-T and exhibit apple-green birefringence upon staining with Congo red.[46,47] Moreover, Raman spectroscopy revealed EPS peaks similar to those observed for known amyloids.[46] These data suggest that the EPS of green algae, including micro- (*Coccomyxa sp*. or *Glaphyrella trebouxiodes*)[46] and macrophytes (*Prasiola linearis*),[47] may contain protein (or proteins) in an amyloid state. These proteins might be the main determinants of the high mechanical resistance of EPS. Amyloids are involved in the biofilm formation and adhesion of different species of bacteria.[22,23] Thus, adhesive proteins represent an example of cross-kingdom conservation of biological functions of amyloids. Nevertheless, the particular amyloid-forming proteins of EPS were not identified, and a complete understanding of the role of amyloid formation for green algae adhesion requires further investigation.

Notably, amyloids are important structural elements for different biological substances. The egg envelopes (chorions) of "annual fish" *Austrofundulus limnaeus*, which lives in the annually drying reservoirs of South America, contain amyloid proteins. The amount of amyloids in these envelopes increases with dehydration, which increases the survival of embryos.[48] The matrix of mice spermatozoid acrosome contains a range of proteins forming detergent-resistant aggregates with amyloid properties.[49] The chorion of silk moth eggs bears at least two classes of amyloid-forming proteins.[50] Thus, similar to the aforementioned structures, the formation of EPS might implicate ensembles of various amyloid-forming proteins likely to co-aggregate as a result of their structural similarity.

II. *Prion-like Protein Luminidependens of* Arabidopsis thaliana

Flowering time in *Arabidopsis thaliana* is controlled by a complex molecular mechanism involving several cascades of transcriptional factors,[51] one of which is so-called Autonomous Flowering Pathway (AFP). This regulatory pathway is independent of the photoperiod and vernalization, i.e., induction of flowering as a result of a prolonged influence of low, typically positive temperatures.[52]

Recently, a paper by S. Chakrabortee and coauthors, from the laboratory of S. Lindquist demonstrated that Luminidependens (LD), an AFP protein in *A. thaliana*, has prion properties in the heterologous system of the yeast *Saccharomyces cerevisiae*.[53] Most known yeast prion proteins are rich in asparagine (N) and glutamine (Q).[54,55] LD was predicted as a potentially prion-forming protein using a recently developed bioinformatic algorithm based on a hidden Markov model,[56] as the prion-forming region of *A. thaliana* protein was closely similar to those of yeast prion proteins.[53] Notably, the fraction of proteins acting as flowering regulators was statistically significantly increased in a set of approximately 500 *A. thaliana* proteins detected using this algorithm.[53] Further experimental analysis demonstrated that LD and two other AFP proteins, Flowering Locus PA (FPA) and Flowering Locus CA (FCA), form detergent-resistant oligomers in yeast cells. Moreover, LD fused with the reporter sequences demonstrated properties typical for yeast prions: dominance, cytoplasmic infectivity, and dependence on the level of Hsp70 chaperone production.[53]

Thus, LD forms a chimeric prion in yeast cells. Does this finding suggest that LD has prion properties in *A. thaliana* cells? Indeed, drawing this conclusion would be at least premature. The fact that LD forms detergent-resistant oligomers in a heterologous system at an

increased level of production confirms neither amyloid fibril formation nor prion-like properties under native conditions in *A. thaliana*. Nevertheless, the role of epigenetic regulation in flowering induction in *A. thaliana* has been demonstrated in a number of studies. Vernalization results in the silencing of the *FLOWERING LOCUS C* (FLC), the product of which is a protein that represses flowering.[52] The *FLC* gene is also a target for LD with a nuclear localization[57] and inhibits the expression of *FLC* in meristems via histone modification[58] and the negative regulation of the *SUF4* activator of FLC expression.[59] Prionization typically entails the functional inactivation of prion-forming protein;[60] therefore, according to the hypothesis of Y. Chernoff, the most likely phenotype of LD prionization would be the delay of the flowering.[61] Notably, temperature is not only a factor controlling vernalization in plants but also affects both the induction[62] and stability of prions.[63] Thus, the influence of temperature on flowering could also be modulated through changes in the induction frequency or the effectiveness of LD prion propagation.

III. *Plant Proteins with Amyloid Properties* in Vitro

Several plant proteins possess amyloid properties *in vitro*. The monellin protein of the tropical fruit *Dioscoreophyllum cumminsii* irreversibly denatures when boiled at 85°C in acidic (pH 2.5) buffer. The consequent addition of 100 mM sodium chloride induces the formation of monellin fibrils that bind Congo red.[64] Unfortunately, birefringence upon binding of Congo red with monellin fibrils was not analyzed, therefore it is impossible to draw a conclusion concerning the amyloid nature of this protein, even *in vitro*.

Maize transglutaminase (TGZ) forms insoluble inclusions when overproduced under the control of the strong *psbA* promoter *in vivo* in the transplastomic tobacco plants.[65] These inclusions contain fibrillar aggregates of TGZ resistant to SDS treatment.[65] *In vitro*, the TGZ protein forms detergent-resistant aggregates of a fibrillar structure showing birefringence upon binding with Congo red. The fibrils of the short C-terminal (aa 466–477) region of TGZ have similar properties *in vitro*.[65] Therefore, maize TGZ forms amyloid-like fibrils *in vitro* and in the transplastomic tobacco plants.

Prohevein protein is the precursor of hevein, a key component of *Hevea brasiliensis* latex, and has an evolutionarily conserved C-terminal region, which, in contrast to the full-length protein, forms fibrils *in vitro*.[66] These fibrils exhibit a pattern typical for amyloids in two-dimensional X-ray diffraction and apple-green birefringence upon binding with Congo red.[66] Notably, the C-terminal region of progevein is also present in the latex of the hevea and exhibits agglutination.[67] Thus, the amyloid properties of the C-terminal region of progevein could enhance its stability *in vivo* and the agglutination of pathogenic microorganisms and fungi, facilitating their destruction by the enzymes of the lutoid fraction of latex.[66]

Several defense peptides of plants were recently demonstrated as exhibiting amyloid properties *in vitro.* For example, the antimicrobial peptide Cn-AMP2 from coconut (*Cocos nucifera*) liquid endosperm contains bioinformatically predicted amyloidogenic regions and demonstrates amyloid properties *in vitro*, including the formation of fibrils detectable using electronic microscopy and the enhancement of the fluorescence of Thioflavin-T dye.[68] Another example is defensins, which are short plant proteins involved in protection from various pathogens. The RsAFP-19 peptide is a C-terminal fragment (19 residues) of RsAFP1 and RsAFP2 defensins of the radish *Raphanus sativus*. This peptide exhibits fungicidal activity. Freeze-thaw cycles induce RsAFP-19 aggregation *in vitro*. These aggregates have a fibrillar structure and exhibit a cross-β pattern in X-ray diffraction typical for amyloids.[69] It is not known whether the full-length defensins RsAFP1 and RsAFP2 form amyloid aggregates *in vivo*, but the fungicidal activity of RsAFP-19 is negatively correlated with the level of its aggregation.[69] A similar effect has been reported for the amyloids of bacterial microcin E492.[25] Thus, one of the

potential biological roles of amyloid formation by plant defense proteins might be the sequestration of the toxic intermediates of these proteins into the functionally inactive fibrils.[25,70]

Taken together, the studies conducted to date show that several plant proteins or their fragments have amyloid properties *in vitro* or in heterologous systems (Table 1). Whether these molecules have amyloid properties in the native conditions remains unclear and should be analyzed in additional studies. Further, is it likely that plants have other amyloid-forming proteins?

IV. *Perspectives for the Identification of Novel Amyloids and Prions in Plants*

The identification of novel prions and amyloids remains arduous and time-consuming. Significant progress in this field of biology can be provided using novel bioinformatic and

TABLE 1. Amyloidogenic proteins in plants.

Protein	Function	Species	Amyloid properties were shown:*		Reference
			in vivo	*in vitro*	
Proteins of algae extracellular polymeric substances (EPS)**	Attachment to surface	*Coccomyxa sp.*, *Glaphyrella trebouxiodes* и *Prasiola linearis* (algae)	+	–	46, 47
Luminidependens (LD)	Autonomous Flowering Pathway (AFP) component	*Arabidopsis thaliana* (rockcress), *Saccharomyces cerevisiae* (yeast)***	±	–	53
Flowering Locus PA (FPA)	AFP component	*Arabidopsis thaliana* (rockcress), *Saccharomyces cerevisiae* (yeast)***	±	–	53
Flowering Locus CA (FCA)	AFP component	*Arabidopsis thaliana* (rockcress), *Saccharomyces cerevisiae* (yeast)***	±	–	53
Pro-hevein C-terminal domain	Latex component, protective function	*Hevea brasiliensis* (rubber tree)	–	+	66
Monellin	Unknown, has a sweet taste for human	*Dioscoreophyllum cumminsii*	–	±	64
Maize transglutaminase (TGZ)	Posttranslational modification of proteins	*Zea mays* (corn), *Nicotiana tabacum* (tobacco)****	±	+	65
RsAFP-19 peptide	RsAFP1 and RsAFP2 defensins fragment, fungicide	*Raphanus sativus* (radish)	–	+	69
Cn-AMP2 peptide	Antimicrobial peptide of liquid endosperm	*Cocos nucifera* (coconut tree)	–	+	68
Peptides resulting after the limited proteolysis of the seed storage proteins**	Nutrient storage	*Glycine max* (soybean), *Pisum sativum* (pea), *Triticum aestivum* (wheat)	±	–	91–93

*«+» Amyloid properties were completely validated; «±» at least one of the amyloid properties was shown (formation of detergent-resistant aggregates *in vivo*, fibril formation *in vitro*, apple-green birefringence upon Congo red binding, or increase in Thioflavin-T fluorescence); «-» amyloid properties were not shown.

**Particular proteins were not identified.

***Amyloid properties of these *A. thaliana* proteins were investigated in the heterologous *S. cerevisiae* system.

****Amyloid properties of *Z. mays* TGZ protein were shown under overexpression in transplastomic *N. tabacum* plants.

proteomic methods. The methodology of proteomic analysis of amyloids is currently at the very dawn of its development. The first attempts to apply proteomics for studying amyloids[71-73] were associated with the identification of proteins sequestered by pathological amyloids that form large deposits and can be isolated from fixed tissue by laser capture microdissection (LCM).[74] A proteome-wide method for the identification of candidates for novel amyloid-forming proteins, called TAPI (Technique for Amyloid Purification and Identification), was proposed in 2013.[75] TAPI uses polyacrylamide gel electrophoresis for the ultrafiltration of detergent-treated amyloid-rich protein fractions, followed by HPLC combined with mass spectrometry to identify candidate proteins.[75] In 2014, another method called PSIA (Proteomic Screening and Identification of Amyloids) was developed.[76] This method uses differential ultracentrifugation combined with treatment using ionic detergents[77] to obtain protein fractions rich in amyloid proteins. These fractions are solubilized, and the proteins (peptides) are separated either by two-dimensional gel electrophoresis[76] or HPLC[78,79] coupled with mass spectrometry, which provides high resolution sufficient to identify the most minor amyloid-forming proteins.[79] Nevertheless, to date, proteomic methods have not been applied for the identification of amyloid proteins in plant species. Is it possible to assess the amyloid properties of plant proteins by other methods?

The primary structure of proteins is the key determinant of their amyloidogenic properties. In 1997, the polyglutamine tracts capable of forming amyloids involved in the development of neurodegenerative diseases in humans were described.[80] Subsequently, it was noted that the common feature of different structural proteins of infectious yeast amyloids (prions) is the presence of regions rich in Q or N residues.[81] Homopeptides formed by several other amino acids, particularly E, also form amyloids.[82] Such amyloidogenic regions (type I amyloidogenic regions) are rich in one or similar (such as Q and N) residues. To identify these regions, several bioinformatic algorithms were developed.[54,83] Notably, the relative content of the biased residues is more important for the formation of type I amyloidogenic regions than the positions of the particular residues.[84]

QN-rich proteins are widely spread throughout plant proteomes. Thus, in *Arabidopsis thaliana*, approximately 200 such proteins were detected,[54] three of which, the transcriptional regulators LD, FPA, and FCA discussed above (see Section II, Table 1), showed some properties of amyloids.[53] Enrichment in Q and N is a characteristic feature of transcription factors, and of other DNA- and RNA-binding proteins of various organisms.[54] Moreover, polyasparagine and polyglutamine tracts display transcriptional activity.[85,86] Transcription factors are abundant in the actively dividing cells of plant meristems. These tissues are promising for identifying novel plant amyloids likely to be involved in regulatory processes and having prion-like properties.

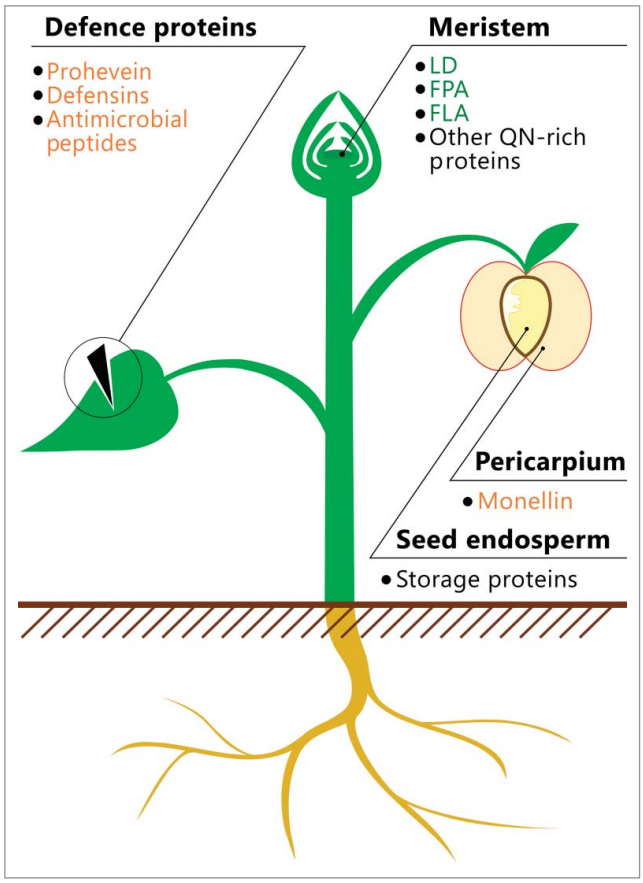
The enrichment in Q and E is a common feature of many plant seed storage proteins. For example, seed storage proteins of maize (*Zea mays*), rye (*Secale sereale*), wheat (*Triticum aestivum*), oat (*Avena sativa*), and other important crops are rich in Q and P,[87] and the storage proteins of legumes are rich in E and D.[88] The ability to form fibrils, which are widely used in biotechnology, is well known for maize prolamins (zeins).[89] In addition, studies on the structure of zein fibrils did not demonstrate characteristic signals in X-ray diffraction inherent in amyloids.[90] The fractions enriched with seed storage proteins of pea (*Pisum sativum*)[91] and soy (*Glycine max*)[92] were subjected to the limited proteolysis at a temperature of more than 80°C and pH = 2, and the resulting peptides formed fibrils with enhanced fluorescence of Thioflavin-T dye, suggesting an amyloid structure.[92] Similar results were obtained with peptide mixtures formed after trypsin digestion of the wheat gliadin and gluten storage proteins.[93] Unfortunately, the amyloid properties of the full-length seed storage proteins were never tested, and specific peptides capable of forming amyloids were not identified.[91-93] Notably, a significant portion of proteins contain bioinformatically predicted amyloidogenic peptides, which are capable of forming

amyloid-like fibrils at high concentrations and under special conditions,[94] but this fact does not indicate that the corresponding full-length proteins have amyloid properties.

Notably, natural dehydration occurs during maturation of plant seeds. This process is accompanied by the compaction of genetic material, a decrease in metabolic rate, and a change in the structure of proteins.[95,96] This process is similar to the dehydration of the eggs of the "annual fish" *Austrofundulus limnaeus* leading to the amyloidogenesis of the proteins in its envelopes, which increases the survival of embryos.[48] It can be assumed that seed storage proteins during dehydration also form amyloids, which increase their stability, and subsequently, under favorable conditions, these proteins revert to a monomeric or oligomeric state that can easily be metabolized by the growing embryo.

QN-rich proteins represent approximately one-third of the currently known amyloids.[97] For other amyloid-forming proteins, strict patterns of the primary structure have not been identified. However, various amino acids have different amyloidogenic propensities. For example, hydrophobic aromatic (W, F) and some aliphatic monoamino monocarboxylic (I, V, L) amino acids have the highest amyloidogenic propensity (i.e., the ability to induce

FIGURE 1. Location of potentially amyloidogenic proteins in plants. A schematic illustration of the plant is shown. The names of proteins or peptides, whose amyloid properties were partially characterized *in vivo* (green) and *in vitro* (orange), and proteins, whose fragments have amyloidogenic properties (black), are indicated. The data on these proteins and peptides are summarized in Table 1.



amyloid formation).[98] The amyloidogenic regions formed by these amino acids (type II amyloidogenic regions), unlike type I regions, do not have one prevalent amino acid. The specific position of the corresponding amino acids is of particular importance for the formation of type II regions. Removing or changing the position of only one amino acid in such amyloidogenic regions can lead to a complete loss of amyloid properties.[99] Approximately ten different bioinformatic algorithms have been developed for the prediction of type II amyloidogenic regions.[98]

Defense proteins and peptides of plants are structurally and functionally heterogeneous groups that are not characterized by the enrichment of Q and N; however, many of these molecules are hydrophobic[100] and thus may contain type II amyloidogenic regions. Plants produce a wide range of various defense peptides and proteins.[101,102] As previously discussed, the amyloid properties for some of these molecules are shown, but are still not entirely clear (Table 1, Fig. 1). Since amyloids represent one of the most stable variants of the quaternary structure of a protein, we propose that adopting an amyloid state by defense proteins could not only promote the inactivation of toxic intermediates but also increases the effectiveness of these proteins against various pathogens.

CONCLUSION

To date, amyloid properties were shown for several plant proteins or their fragments *in vitro* or in heterologous systems *in vivo*. However, no plant proteins were shown to form amyloids under native conditions. Based on the data obtained in previous studies (Fig. 1, Table 1), we distinguished four groups of plant proteins promising for the identification of novel amyloids: (i) QN-rich proteins, particularly those capable of binding nucleic acids; (ii) defense proteins and peptides containing hydrophobic regions; (iii) seed storage proteins containing Q- and E-rich regions; and (iv) proteins involved in the adhesion of algal cells to the surfaces. Based on the methodology developed to date, we can propose two main strategies to reveal candidates for functional amyloids in the proteomes of plants: (i) bioinformatic prediction of potentially amyloidogenic proteins and (ii) proteomic screenings of proteins resistant to treatment with ionic detergents. In both cases, the amyloid properties of candidate proteins should be verified by analyzing their ability to form fibrils and adopt cross-β structure. Further studies on the bioinformatic prediction and experimental identification of amyloid proteins in the proteomes of different species are required to elucidate the biological roles and functions of plant amyloids.

ABBREVIATIONS

AFP	Autonomous Flowering Pathway
EPS	Extracellular Polymeric Substances
HPLC	High Performance Liquid Chromatography
LPS	Lowest Probability Subsequences
PSIA	Proteomic Screening and Identification of Amyloids
SDS	Sodium Dodecyl Sulfate
Sarkosyl	Sodium lauroyl sarcosinate
SARP	Sequence Analysis Based on the Ranking of Probabilities
TAPI	Technique for Amyloid Purification and Identification; The standard single-letter amino acid code is used

DISCLOSURE OF POTENTIAL CONFLICTS OF INTEREST

Authors declare no potential conflicts of interest.

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ORCID

A. A. Nizhnikov http://orcid.org/0000-0002-8338-3494

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