Plant lectins: Handymen at the cell surface

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ABSTRACT

Lectins are carbohydrate-binding proteins and are involved in a multitude of biological functions. Lectins at the surface of plant cells often occur as lectin receptor-like kinases (LecRLK) anchored to the plasma membrane. These LecRLKs are part of the plant’s pattern-recognition receptor (PRR) system enabling the plant to perceive threats and respond adequately. Furthermore, plant lectins also occur as secreted proteins, which are associated with stress signalling and defence. The aim of this short review is to provide a general perspective on plant lectins and their role at the cell surface.

Lectin receptor-like kinases at the cell surface perceive threats

Plant lectins and plant defence

By definition, lectins are proteins devoid of enzymatic activity which can specifically recognise and reversibly bind carbohydrate structures (Taneva and Van Damme, 2020) and therefore possess at least one carbohydrate-binding domain (CBD). The majority of plant lectins occur as chimeric lectins in which the lectin domain is coupled to an unrelated domain such as a protein kinase, a glycosyl hydrolase or an F-box domain (Van Holle et al., 2017) (see Fig. 1). Lectins are widespread in the kingdoms of life. They are found in storage tissues (i.e. seeds, bulbs, bark, rhizomes), xylem and phloem, and to a lesser extent in roots, shoots, leaves and flowers (Van Damme et al., 1987). At the cellular level, lectins are present in the nucleus and/or cytoplasm, in the vacuole or at the cell surface (Table 1). Vacuolar lectins are generally very abundant and reside in protein bodies. Some examples are ricin from the castor bean (Ricinus communis), phytohaemagglutinin from common bean (Phaseolus vulgaris) and the Galanthus nivalis agglutinin from snowdrop (G. nivalis). These lectins probably fulfil a role as a nitrogen source for the growing and developing plant (Nsimba-Lubaki and Peumans, 1986; Wetzel et al., 1989) or as deterrents against predators (Vandenborne et al., 2011). Nucleocytoplasmic lectins are usually present in low quantities, but are upregulated after exposure of the plant to biotic and/or abiotic stresses. Some examples of well-studied nucleocytoplasmic lectins include Oryzata from rice (Oryza sativa), Nicotaba from tobacco (Nicotiana tabacum) and Euonymus-related (EUL) lectins in thale cress (Arabidopsis thaliana).

Lectins also occur in the vascular tissue, as demonstrated by the xylem lectin XSP30 and phloem lectin PP2 from cucumber (Cucumis sativus). The biological functions of these vascular lectins are divergent. The expression of XSP30 is regulated by the circadian rhythm and gibberellic acid (Oda et al., 2003), while PP2 is capable of binding and transporting RNA molecules throughout the plant (Gómez and Pallás, 2004).

Plants have developed a defence system to distinguish pathogen- and damage-related signals from benign signals and respond adequately to perceived threats. To do so, plants are equipped with a battery of PRRs which recognise pathogen-, microbial- and damage-associated molecular patterns (PAMP/MAMP/DAMP). These PRRs are found at the cell surface and are anchored in the plasma membrane. Upon elicitor recognition, downstream signalling is initiated, leading to either systemic acquired resistance, hypersensitive response, pathogenic colonization and/or cell death (Dangl and Jones, 2001).

Lectin receptor-like kinases

Lectin receptor-like kinases (LecRLKs) have been identified in many crops and model species (Kaur et al., 2023). LecRLKs are PRRs and distinguish themselves from other PRRs through their interaction with the matching molecular patterns. Three types of LecRLKs have been studied in detail, including: (1) G-type LecRLKs containing the GNA domain; (2) L-type LecRLKs with a legume lectin domain; (3) LysM-type LecRLK with a LysM lectin domain (Bellande et al., 2017) (Table 2). All LecRLKs share a similar topology, consisting of an apoplastic lectin domain which recognises and binds molecular patterns (carbohydrates), a transmembrane domain attaching the LecRLK to the plasma...
membrane, and an intracellular kinase domain which is crucial for the downstream signalling and pathway activation. LecRLKs rely on carbohydrate-protein interactions, whereas many other PRRs rely on protein–protein ligand-receptor interactions. However, the nature of the ligand-receptor interaction is not completely uncovered for some LecRLKs. Next to their role as PRRs, LecRLKs are also involved in other physiological processes (Bellande et al., 2017) such as seed germination (Deng et al., 2009) and pollen development (Micol-Ponce et al., 2022).

Only few G-type LecRLKs have been functionally characterized. CaMBL1 from pepper (Capsicum annum) and FaMBL1 from strawberry (Fragaria × ananassa) are examples of G-type LecRLKs where the lectin domain was shown to bind cell wall mannose from Xanthomonas campestris, Colletotrichum fioriniae and Botrytis cinerea (Hwang and Hwang, 2011; Ma et al., 2022). Not all identified G-type LecRLKs make use of their carbohydrate-binding properties in the interaction with pathogenic ligands. For instance, LIPOOLIGOSACCHARIDE-SPECIFIC REDUCED ELICITATION (LORE1) from thale cress is involved in the production of secondary metabolites, callose deposition and/or expression of effector proteins to counteract the attack. Effectors include several stress-inducible lectins, inhibitors and CAZymes. Abbreviations: ABA (abscisic acid), ArathEULS3 (Arabidopsis thaliana EULS3), CAZyme (carbohydrate-active enzyme), CERK1 (CHITIN ELICITOR RECEPTOR KINASE 1), CPS (conventional protein secretion), DORN1 (DOES NOT RESPOND TO NUCLEOTIDES1), ET (ethylene), GNA (Galanthus nivalis agglutinin), Helja (Helianthus j acalin-related lectin), JA (jasmonic acid), LecRLK (lectin receptor-like kinase), Nictaba (Nicotiana tabacum agglutinin), HvHorcH (Hordeum vulgare horcolin-like), Orysata (Oryza sativa agglutinin), PHA (phytohaemagglutinin), PP2 (phloem protein 2), PRR (pattern-recognition receptor), ROS (reactive oxygen species), SA (salicylic acid), UPS (unconventional protein secretion), XSP30 (xylem sap protein 30). This figure was created using https://app.biorender.com/.

G-type and LysM-type LecRLKs interact with friends and foes

Fig. 1. Lectins at the cell surface and intracellular signalling upon exposure to elicitors. The presence of pathogens, symbionts or damage is perceived by PRRs. Ligand binding to LecRLKs or other receptors initiates a signalling cascade which often involves influx of Ca$^{2+}$ ions, production of reactive oxygen species, mitogen-activated protein kinases and altered phytohormone household. The downstream signalling triggers a plant defence response which eventually leads to the production of secondary metabolites, callose deposition and/or expression of effector proteins to counteract the attack. Effectors include several stress-inducible lectins, inhibitors and CAZymes. Abbreviations: ABA (abscisic acid), ArathEULS3 (Arabidopsis thaliana EULS3), CAZyme (carbohydrate-active enzyme), CERK1 (CHITIN ELICITOR RECEPTOR KINASE 1), CPS (conventional protein secretion), DORN1 (DOES NOT RESPOND TO NUCLEOTIDES1), ET (ethylene), GNA (Galanthus nivalis agglutinin), Helja (Helianthus j acalin-related lectin), JA (jasmonic acid), LecRLK (lectin receptor-like kinase), Nictaba (Nicotiana tabacum agglutinin), HvHorcH (Hordeum vulgare horcolin-like), Orysata (Oryza sativa agglutinin), PHA (phytohaemagglutinin), PP2 (phloem protein 2), PRR (pattern-recognition receptor), ROS (reactive oxygen species), SA (salicylic acid), UPS (unconventional protein secretion), XSP30 (xylem sap protein 30). This figure was created using https://app.biorender.com/.
L-type LecRLKs are devoid of carbohydrate-binding properties

All L-type LecRLKs from thale cress are devoid of carbohydrate-binding properties. Nevertheless many L-type LecRLKs are involved in plant-pathogen interactions, in the defence response or the resistance against pathogens, as illustrated by LecRLKs from cucumber (C. sativus), tomato (Solanum lycopersicum), pepper (C. annuum), thale cress (A. thaliana) and Dassypyrus villosum (Table 2).

Noteworthy, GhLecRK-2 from cotton (Gossypium hirsutum) was thought to be involved in the signalling of Verticillium dahliae. GhLecRK-2 is highly upregulated after treatment with the glycoconjugate cell wall fraction of V. dahliae. Sequence alignment with functionally characterized legume lectins resulted in 30% similarity with conservation of amino acid residues making up the carbohydrate binding site. However, lectin activity was not functionally proven (Phillips et al., 2015).

A few years ago, a novel L-type LecRLK named DORN1 (DOES NOT RESPOND TO NUCLEOTIDES) was discovered. Similar to other L-type LecRLKs, it is devoid of lectin activity. However, DORN1 can interact with pathogenic signals through protein–protein interactions. Furthermore, DORN1 binds extracellular ATP (eATP) which is associated with damage to the cell wall. The downstream signalling of eATP shows tight linkages with mitogen-activated protein kinase and JA signalling (Balagué et al., 2017; Tripathi et al., 2018).

Secreted plant lectins and stress signalling

Secreted lectins are involved in biotic interactions

A large group of lectin sequences are synthesized without a signal peptide and localize to the nucleus and/or cytosol. However, examples have emerged of unconventionally secreted lectins in the extracellular vesicles (EV) of e.g. imbibed sunflower seeds. Proteomics analyses showed that the largest share of these imbibed seed proteins was secreted conventionally. However, there were also examples of enriched unconventionally secreted plant lectins, such as the leaderless Helja lectin, and PRRs which are usually found attached/anchored to the plasma membrane. Quite interestingly, these EVs also contained proteins which were annotated with a lectin domain (GNA, Ricin-B, ConA) and a glycosyl hydrolase domain (family 5, 13, 27, 32, 35). Gene ontology analyses suggested that the majority of the identified proteins inside the apoplastic EVs are related to cell wall metabolism and plant defence (Regente et al., 2017). These observations generated the hypothesis that the catalytic domain and the carbohydrate-binding domain

| Lectin | Organism | Carbohydrate binding specificity | (Subcellular) localization | Biological function | Reference |
|--------|----------|---------------------------------|---------------------------|---------------------|-----------|
| Ricin  | Castor bean | Galactose and GalNAc; complex N-glycans | Vacuole | Nitrogen source for growing plantlets. Deterrent action against predators. | (Youle and Huang, 1976) |
| PHA    | Common bean | Galactose, GalNAc; complex N-glycans | Vacuole | Nitrogen source for growing plantlets. Deterrent action against predators. | (Sturm et al., 1988) |
| GNA    | Snowdrop | Mannose, high mannose N-glycans | Vacuole | Nitrogen source for growing plantlets. Deterrent action against predators. | (Van Damme et al., 1987) |
| Oryzata | Rice | Mannose, high mannose N-glycans | Nucleus and/or cytosol | Upregulated upon drought and salt stress, ABA/JA/SA treatment. Overexpression lines show improved salt tolerance. | (Patishan et al., 2018) |
| Nictaba | Tobacco | Chitin oligomers and N-glycans | Nucleus and/or cytosol | Upregulated upon JA treatment and herbivory. Interaction with core histones in an O-GlcNAc and cell-cycle dependent way. | (Chen et al., 2002; Delporte et al., 2014) |
| ArathEUL53 | Thale cress | Weak affinity towards LacNAc, Lewis A and B-antigens | Nucleus and/or cytosol | Upregulated upon drought and salt stress, ABA/JA treatment. Overexpression lines show improved drought tolerance. | (Fougaut and Van Damme, 2012; Li et al., 2014; Van Hove et al., 2011) |
| XSP30 | Cucumber | Chitohiose, GlcNAc, GlcNAc oligomers | Secreted in xylem Companion cells and sieve elements | Diurnal expression influenced by GA Transport of RNA molecules. Deterrent action against predators. | (Oda et al., 2003; Gómez and Pallás, 2004) |
| PP2    | Cucumber | GalNAc, GlcNAc oligomers | Secreted in xylem Companion cells and sieve elements | Secreted in xylem Companion cells and sieve elements | |

Abbreviations: ABA (abscisic acid), ET (ethylene), GA (gibberellic acid), GalNAc (N-acetylgalactosamine), GlcNAc (N-acetylgluosamine), JA (jasmonate), LacNAc (N-acetylactosamine), SA (salicylic acid).
of chimeric lectins may display a synergistic activity, and fulfil a potential function in plant-pathogen interactions.

**Secreted lectins are involved in abiotic stress signalling and tolerance**

Nucleocytoplasmic plant lectins are highly associated with abiotic stress signalling (Table 1). However, only few secreted lectins have been functionally characterized. Two major examples are the EUL lectin ArathEULS3 from thale cress and the jacalin-related mannose-binding lectin HvHorcH from barley (Hordeum vulgare). ArathEULS3 is induced when exposed to osmotic stress, salt stress, treatment with abscisic acid and *P. syringae* infection (Dubiel et al., 2020). HvHorcH shows a high degree of sequence similarity towards the salinity-related lectin horcolin from barley (Witzel et al., 2021). Interestingly, both lectins are nucleocytoplasmic lectins under non-stressed conditions. Upon application of heat stress and salt stress, the localization of ArathEULS3 and HvHorcH shifted towards apoplastic stress granules and the extracellular space respectively (Dubiel et al., 2020; Witzel et al., 2021). Furthermore, overexpression of ArathEULS3 and HvHorcH in thale cress resulted in increased drought and salinity tolerance (Li et al., 2014; Witzel et al., 2021).

The importance of jacalin-related mannose-binding lectins for salinity tolerance and salt stress signalling was studied in rice. OsJRL and OsSalT are two mannose-binding lectins from *O. sativa* which interact with several important salinity-related transcription factors and proteins (He et al., 2017; Sahid et al., 2021). Finally, it was shown that the jacalin-related mannose-binding lectin OsJAC1 from rice plays a role in DNA damage repair after exposure to ionizing radiation. Overexpression of OsJAC1 resulted in hyper-resistant rice plants, thriving in conditions with radiation doses up to 100 Gray (Jung et al., 2019).

Recently, a large set of conventionally secreted lectins with a potential function in abiotic stress signalling, was identified in sorghum (*Sorghum bicolor*), based on the identification of quantitative trait loci known to be important for abiotic stress signalling. These analyses revealed a potential association with cold and drought stress signalling (Osman et al., 2022).

The above examples illustrate that several lectins fulfil a role in abiotic stress signalling and confer resistance to abiotic stress, next to their proven role as PRRs in plant-pathogen interactions.

**Concluding remarks**

Plant lectins are versatile and can be considered as Jack-of-all-trades with a major function in biotic interactions. Many lectins reside inside plant cells, some lectins occur as LecRLKs or as secreted proteins. The role of LecRLKs in biotic stress signalling is evident through their receptor function towards molecular patterns. At present, the lectin-carbohydrate interaction has only been proven for LysM-type and several G-type LecRLKs. L-type LecRLKs act through protein–protein interactions. Despite the technological progress in the last decade, there are many unknowns in the field of LecRLKs. Much attention has focused on the identification of novel receptors and the corresponding elicitors. However, the underlying mechanisms of post-elicitor recognition are far from being understood. One way to expand the research field of LecRLKs could be to apply novel genome editing and silencing technologies, thereby modifying the carbohydrate-binding properties of LecRLKs and other PRRs in planta (Vuong, 2022). This could yield increased knowledge about biotic interactions and potential agronomic applications. Furthermore, the significance of secreted plant lectins remains enigmatic. Some secreted plant lectins, such as Helja display toxicity towards

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**Table 2**

Overview of characterized LecRLK examples with their ligands and biological functions.

| Type | Example | Organism | Ligand | Function | Reference |
|------|---------|----------|--------|----------|-----------|
| G    | CaMBl1  | Pepper   | Mannose| Recognition of cell wall mannose from *Xanthomonas campestris*. | (Hwang and Hwang, 2011) |
|      | FaMBl1  | Strawberry| Mannose| Recognition of cell wall mannose from *Colletotrichum luteum* and *Botrytis cinerea*. | (Ma et al., 2022) |
|      | LORE1   | Thale cress| Lipopolysaccharides| Biotic interaction with *P. syringae*. | (Luo et al., 2020) |
|      | SDI-29  | Thale cress| Lipopolysaccharides| Biotic interaction with *P. syringae*. | (Rafat et al., 2015) |
|      | PriLRK1 | Poplar   | Not confirmed | Symbiotic interaction with *Laccaria bicolor*. | (Labbé et al., 2019) |
|      | HvLecRK-V | Dasyxylon villatum | Not confirmed | Resistance against *Rubus idaeus*. | (Wang et al., 2018) |
| L    | CoLecRK6.1 | Cucumber | Not confirmed | Resistance against *Phytophora capsici*. | (Wu et al., 2014) |
|      | SpLecRK5.5 | Tomato   | Not confirmed | Resistance against *Fusarium oxysporum*. | (Catananzari et al., 2015) |
|      | LecRK-I.8 | Thale cress| Not confirmed | Perception of *Pisum sativum* eggs. | (Gobert-Darimont et al., 2019) |
|      | LecRK-I.9 | Thale cress| Not confirmed | Defensive response to *Phytophora*. | (Wang et al., 2015) |
|      | LecRK-V.5 | Thale cress| Not confirmed | Defensive response to *Phytophora*. | (Balag et al., 2017) |
|      | HvLecRK-V | Dasyxylon villatum | Not confirmed | Resistance against *Blumeria graminis*. | (Descolle-Theniau et al., 2012) |
|      | GlLecRK-V | Cotton   | Not confirmed | Upregulation after exposure to *Verticillium dahliae* glycoconjugate cell wall fraction. | (Phillips et al., 2013) |
|      | LysM    | AtCERK1  | Thalia | Perception of cell wall damage. | (Tripathi et al., 2018) |
|      | A1LYK4  | Thale cress| Chitin and GlcNAc oligomers| Perception of chitin from *Alternaria brassicola*. | (Yamada et al., 2016) |
|      | A1LYK5  | Thale cress| Chitin and GlcNAc oligomers| Perception of chitin from *Alternaria brassicola*. | (Wan et al., 2012) |
|      | A1LYM2  | Thale cress| Chitin and GlcNAc oligomers| Perception of chitin from *Botrytis cinerea*. | (Cao et al., 2014) |
|      | A1LYM3  | Thale cress| Peptidoglycan| Perception of peptidoglycan from *P. syringae*. | (Faulkner et al., 2013) |
|      | OsCERK1 | Rice     | Celllobiosyl/triosyl glucose units| Perception of peptidoglycan from *P. syringae*. | (Willmann et al., 2011) |
|      | OsLYP4  | Rice     | Chitin, GlcNAc oligomers and peptidoglycan| Perception of chitin, GlcNAc oligomers and peptidoglycan. | (Liu et al., 2012) |
|      | OsLYP6  | Rice     | Chitin, GlcNAc oligomers and peptidoglycan| Perception of chitin, GlcNAc oligomers and peptidoglycan. | (Liu et al., 2012) |
|      | OsCEBP  | Rice     | Chitin oligomers| Perception of chitin oligomers | (Akamatsu et al., 2013) |
|      | LnNFR1/5 | Japanese trefoil| Lipochito-oligosaccharides and short chitin oligomers| Interaction with nitrogen fixing bacteria and arbuscular mycorrhizae. | (Du et al., 2019; Zhang et al., 2015) |
|      | MnNFP/  | Barrelclover| Lipochito-oligosaccharides and short chitin oligomers| Interaction with nitrogen fixing bacteria and arbuscular mycorrhizae. | (Gough and Jacquet, 2013; Zhang et al., 2015) |
|      | LK3     |         |         |         |           |
pathogens. Chimeric lectins comprised of a carbohydrate-binding and a catalytic domain could also be involved in biotic stress signalling by hydrolysing pathogenic cell walls. It is speculated that carbohydrate-binding and catalytic domains could uphold a synergistic relationship (Boraston, 2004). The involvement of plant lectins to fight abiotic stress is far less studied. Only anecdotal examples, such as ArabEULS3, illustrate a possible function for secreted plant lectins in abiotic stress signalling.

CRediT authorship contribution statement

Tibo De Coninck: Conceptualization, Visualization, Writing – original draft. Els J.M. Van Damme: Conceptualization, Funding acquisition, Project administration, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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