

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 (Tsaneva and Van Damme, 2020) and therefore possess at least one carbohydrate-binding domain (CBD). The majority of plant lectins occur as chimerolectins 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 (Vandenborre 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*), Nictaba 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

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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).

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

Only few G-type LecRLKs have been functionally characterized. CaMBL1 from pepper (*Capsicum annuum*) 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 fiorinae* 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

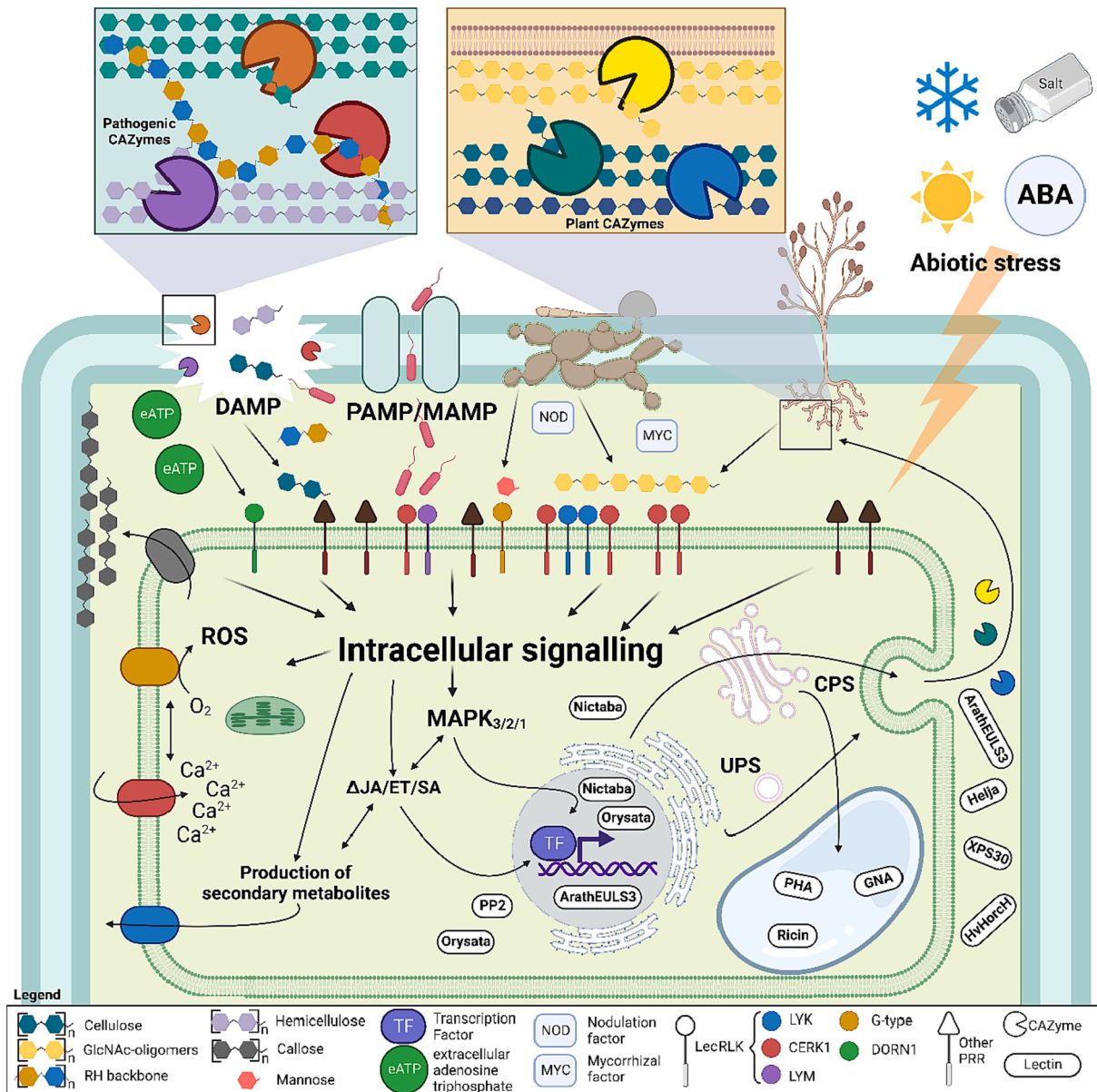


Fig. 1. Lectins at the cell surface and intracellular signalling upon exposure to elicitors. The presence of pathogens, symbionts or damage is perceived by PRRs. Ligand binding to LecRLKs or other receptors initiates a signalling cascade which often involves influx of Ca^{2+} ions, production of reactive 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 jacalin*-related lectin), JA (jasmonic acid), LecRLK (lectin receptor-like kinase), Nictaba (*Nicotiana tabacum* agglutinin), HvHorch (*Hordeum vulgare* horcolin-like), Oryсата (*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/>.

interaction with lipopolysaccharides from *Pseudomonas syringae* without showing affinity for mannose (Luo et al., 2020; Ranf et al., 2015) (Table 2).

Archetypical examples of LysM-type LecRLKs from thale cress and rice are AtCERK1 and OsCERK1 but utilize coreceptors for binding to chitin and GlcNAc oligomers (AtLYK4, AtLYK5, AtLYM2) (Cao et al., 2014; Faulkner et al., 2013; Wan et al., 2012) or peptidoglycan (AtLYM1, AtLYM3) (Willmann et al., 2011), or both (OsLYK4, OsLYK6) (Liu et al., 2012). In rice, prior binding to OsCEBiP is required for chitin or peptidoglycan recognition. The downstream signalling has not yet been uncovered completely, although several key players have been identified (Akamatsu et al., 2013; Hu et al., 2021; Yamada et al., 2016). Upon ligand recognition by LysM-type LecRLKs, the intracellular kinase domain is phosphorylated and binds other intracellular proteins. Ultimately, this leads to the activation of the mitogen-activated protein kinase cascade, formation of reactive oxygen species, altered phytohormone household, production of secondary metabolites, callose deposition in the cell wall and/or secretion of carbohydrate-active enzymes. Plant chitinases and glucanases hydrolyse the pathogen's cell wall and cause the release of MAMPs, such as β -1,3-glucans and GlcNAc-oligomers, which are in turn recognised by CERKs, LYMs and LYKs, further maintaining and instigating the pattern triggered immunity (Rovenich et al., 2016). Recently, it was shown that OsCERK1 is also involved in the perception of DAMPs, in particular cellobiosyl/triosyl-glucose units liberated from the hemicellulose fraction of the rice cell wall by the hydrolytic activity of secreted β -glucanases from *M. oryzae* (Yang et al., 2021). This is a remarkable observation, since only few DAMP receptors have been identified (Wan et al., 2021) (Table 2).

Next to sensing pathogens, some LysM-type and G-type LecRLKs, can also perceive molecular patterns from symbiotic organisms. It was shown that LjNFR1/5 and MtNFP, both LysM-type LecRLKs from Japanese trefoil (*Lotus japonicus*) and barrelclover (*Medicago truncatula*), respectively, are involved in the perception of lipochitooligosaccharide and short-chain chitin oligomers, similar to nodulation factors from nitrogen fixing bacteria as well as the interaction with arbuscular mycorrhizae (Duan et al., 2019; Gough and Jacquet, 2013; Zhang et al., 2015). Similarly, the G-type PtRLK1 from poplar (*Populus trichocarpa*) was proven to be involved in the symbiosis with *Laccaria bicolor*, an ectomycorrhizal fungus (Labbé et al., 2019) (Table 2). Interestingly, the kinase domain of LfNFR1/5 is truncated and lacks phosphorylation activity. It was demonstrated before that also pseudokinases can be part of signalling cascades (Madsen et al., 2003).

Table 1

Overview of vacuolar, nucleocytoplasmic and vascular lectins with their carbohydrate binding specificity, subcellular localization and biological function.

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.	(Patishtan 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)
ArathEULS3	Thale cress	Weak affinity towards LacNAc, Lewis A and B-antigens	Nucleus and/or cytosol	Upregulated upon drought and salt stress, ABA/ET/JA treatment. Overexpression lines show improved drought tolerance.	(Fouquaert and Van Damme, 2012; Li et al., 2014; Van Hove et al., 2011)
XSP30	Cucumber	Chitobiose	Secreted in xylem	Diurnal expression influenced by GA	(Oda et al., 2003)
PP2	Cucumber	GlcNAc, GlcNAc oligomers	Companion cells and sieve elements	Transport of RNA molecules. Deterrent action against predators.	(Gómez and Pallás, 2004)

Abbreviations: ABA (abscisic acid), ET (ethylene), GA (gibberellic acid), GalNAc (N-acetylgalactosamine), GlcNAc (N-acetylglucosamine), JA (jasmonate), LacNAc (N-acetylglucosamine), SA (salicylic acid).

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 *Dasyphyrum 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., 2013).

A few years ago, a novel L-type LecRLK named DORN1 (DOES NOT RESPOND TO NUCLEOTIDES1) 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, 16, 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

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 apoplasmic 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 OsSaT are two mannose-binding lectins from rice (*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).

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 <i>Xanthomonas campestris</i> .	(Hwang and Hwang, 2011)	
	FaMBL1	Strawberry	Mannose	Recognition of cell wall mannose from <i>Colletotrichum fioriniae</i> and <i>Botrytis cinerea</i> .	(Ma et al., 2022)	
	LORE1	Thale cress	Lipopolysaccharides	Biotic interaction with <i>P. syringae</i> .	(Luo et al., 2020)	
L	SD1-29	Thale cress	Lipopolysaccharides	Biotic interaction with <i>P. syringae</i> .	(Ranf et al., 2015)	
	PtRLK1	Poplar	Not confirmed	Symbiotic interaction with <i>Laccaria bicolor</i>	(Labbé et al., 2019)	
	CsLecRK6.1	Cucumber	Not confirmed	Resistance against <i>Phytophthora melonis</i> and <i>P. capsica</i> .	(Wu et al., 2014)	
	SpSRLK-5	Tomato	Not confirmed	Resistance against <i>Fusarium oxysporum</i>	(Catanzariti et al., 2015)	
	CaLecRK-S.5	Pepper	Not confirmed	Recognition of <i>Phytophthora</i> effectors.	(Woo et al., 2020)	
	LecRK-I.8	Thale cress	Not confirmed	Perception of <i>Pieris brassicae</i> eggs.	(Gouhier-Darimont et al., 2019)	
	LecRK-IX.1	Thale cress	Not confirmed	Defensive response to <i>Phytophthora</i>	(Wang et al., 2015)	
	LecRK-IX.2	Thale cress	Not confirmed	Defensive response to <i>Phytophthora</i>	(Wang et al., 2015)	
	LecRK-I.9	Thale cress	Not confirmed	Defensive response to <i>Phytophthora</i>	(Balagué et al., 2017)	
	LecRK-V.5	Thale cress	Not confirmed	Resistance against <i>P. syringae</i>	(Desclos-Theveniau et al., 2012)	
	HvLecRK-V	<i>Dasyphyrum villosum</i>	Not confirmed	Resistance against <i>Blumeria graminis</i>	(Wang et al., 2018)	
	GhLecRK-2	Cotton	Not confirmed	Upregulation after exposure to <i>Verticillium dahliae</i> glycoconjugate cell wall fraction.	(Phillips et al., 2013)	
	LysM	DORN1	Thale cress	Extracellular ATP	Perception of cell wall damage.	(Tripathi et al., 2018)
		AtCERK1	Thale cress	Chitin	Perception of chitin from <i>Alternaria brassicola</i>	(Yamada et al., 2016)
		AtLYK4	Thale cress	Chitin and GlcNAc oligomers	Perception of chitin from <i>Alternaria brassicola</i>	(Wan et al., 2012)
AtLYK5		Thale cress	Chitin and GlcNAc oligomers	Perception of chitin from <i>Alternaria brassicola</i>	(Cao et al., 2014)	
AtLYM2		Thale cress	Chitin and GlcNAc oligomers	Perception of chitin from <i>Botrytis cinerea</i>	(Faulkner et al., 2013)	
AtLYM1		Thale cress	Peptidoglycan	Perception of peptidoglycan from <i>P. syringae</i>	(Willmann et al., 2011)	
AtLYM3		Thale cress	Peptidoglycan	Perception of peptidoglycan from <i>P. syringae</i>	(Willmann et al., 2011)	
OsCERK1		Rice	Cellobiosyl/triosyl glucose units	Perception of cellobiosyl and cellotriosyl glucose units from <i>M. oryzae</i>	(Yang et al., 2021)	
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)	
OsCEBiP		Rice	Chitin oligomers	Perception of chitin oligomers	(Akamatsu et al., 2013)	
LjNFR1/5		Japanese trefoil	Lipochito-oligosaccharides and short chitin oligomers	Interaction with nitrogen fixing bacteria and arbuscular mycorrhizae.	(Duan et al., 2019; Zhang et al., 2015)	
MtNFP/LYK3		Barrelclover	Lipochito-oligosaccharides and short chitin oligomers	Interaction with nitrogen fixing bacteria and arbuscular mycorrhizae.	(Gough and Jacquet, 2013; Zhang et al., 2015)	

Recently, a large set of unconventionally 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

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 ArathEULS3, 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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References

- Akamatsu, A., Wong, H.L., Fujiwara, M., Okuda, J., Nishide, K., Uno, K., Imai, K., Umemura, K., Kawasaki, T., Kawano, Y., Shimamoto, K., 2013. Article module is an essential early component of chitin-induced rice immunity. *Cell Host Microbe* 13, 465–476. <https://doi.org/10.1016/j.chom.2013.03.007>.
- Balagué, C., Gouget, A., Bouchez, O., Souriac, C., Haget, N., Boutet-Mercery, S., Govers, F., Roby, D., Canut, H., 2017. The Arabidopsis thaliana lectin receptor kinase LecRK-I.9 is required for full resistance to *Pseudomonas syringae* and affects jasmonate signalling. *Mol. Plant Pathol.* 18, 937–948. <https://doi.org/10.1111/mpp.12457>.
- Bellande, K., Bono, J.J., Savelli, B., Jamet, E., Canut, H., 2017. Plant lectins and lectin receptor-like kinases: How do they sense the outside? *Int. J. Mol. Sci.* 18, 1164. <https://doi.org/10.3390/ijms18061164>.
- Boraston, A.B., et al., 2004. Carbohydrate-binding modules: fine-tuning polysaccharide recognition. *The Biochemical Journal* 15 (382), 769–781. <https://doi.org/10.1042/BJ20040892>.
- Cao, Y., Liang, Y., Tanaka, K., Nguyen, C.T., Jedrzejczak, R.P., Joachimiak, A., Stacey, G., 2014. The kinase LYK5 is a major chitin receptor in Arabidopsis and forms a chitin-induced complex with related kinase CERK1. *Elife* 3, e03766. <https://doi.org/10.7554/eLife.03766>.
- Catanzariti, A.M., Lim, G.T.T., Jones, D.A., 2015. The tomato I-3 gene: A novel gene for resistance to Fusarium wilt disease. *New Phytol.* 207, 106–118. <https://doi.org/10.1111/nph.13348>.
- Chen, Y., Peumans, W.J., Hause, B., Bras, J., Kumar, M., Proost, P., Barre, A., Rougé, P., Van Damme, E.J.M., 2002. Jasmonic acid methyl ester induces the synthesis of a cytoplasmic/nuclear chito-oligosaccharide binding lectin in tobacco leaves. *FASEB J.* 16, 905–907. <https://doi.org/10.1096/fj.01-0598fje>.
- Dangl, J.L., Jones, J.D.G., 2001. Plant pathogens and integrated defence responses to infection. *Nature* 411, 826–833. <https://doi.org/10.1038/35081161>.
- Delporte, A., De Zaeytjij, J., De Storme, N., Azmi, A., Geelen, D., Smaghe, G., Guisez, Y., Van Damme, E.J.M., 2014. Cell cycle-dependent O-GlcNAc modification of tobacco histones and their interaction with the tobacco lectin. *Plant Physiol. Biochem.* 83, 151–158. <https://doi.org/10.1016/j.plaphy.2014.07.021>.
- Deng, K., Wang, Q., Zeng, J., Guo, X., Zhao, X., Tang, D., Liu, X., 2009. A lectin receptor kinase positively regulates ABA response during seed germination and is involved in salt and osmotic stress response. *J. Plant Biol.* 52, 493–500. <https://doi.org/10.1007/s12374-009-9063-5>.
- Desclos-Théveniau, M., Arnaud, D., Huang, T.Y., Lin, G.J.C., Chen, W.Y., Lin, Y.C., Zimmerli, L., 2012. The Arabidopsis lectin receptor kinase LecRK-V.5 represses stomatal immunity induced by *Pseudomonas syringae* pv. tomato DC3000. *PLoS Pathog.* 8, e1002513. <https://doi.org/10.1371/journal.ppat.1002513>.
- Duan, L., Pei, J., Ren, Y., Li, H., Zhou, X., Zhu, H., Duanmu, D., Wen, J., Mysore, K.S., Cao, Y., Zhang, Z., 2019. A dihydroflavonol-4-reductase-like protein interacts with NFR5 and regulates rhizobial infection in *Lotus japonicus*. *MPMI* 32, 401–412. <https://doi.org/10.1094/MPMI-04-18-0104-R>.
- Dubiel, M., De Coninck, T., Osterme, V.J.S., Verbeke, I., Van Damme, D., Smaghe, G., Van Damme, E.J.M., 2020. The ArathEULS3 lectin ends up in stress granules and can follow an unconventional route for secretion. *Int. J. Mol. Sci.* 21. <https://doi.org/10.3390/ijms21051659>.
- Faulkner, C., Petutschnig, E., Benitez-Alfonso, Y., Beck, M., Robatzek, S., Lipka, V., Maule, A.J., 2013. LYM2-dependent chitin perception limits molecular flux via plasmodesmata. *Proc. Natl. Acad. Sci. U. S. A.* 110, 9166–9170. <https://doi.org/10.1073/pnas.1203458110>.
- Fouquaert, E., Van Damme, E.J.M., 2012. Promiscuity of the *Euonymus* carbohydrate-binding domain. *Biomolecules* 2, 415–434. <https://doi.org/10.3390/biom2040415>.
- Gómez, G., Pallás, V., 2004. A long-distance translocatable phloem protein from cucumber forms a ribonucleoprotein complex in vivo with hop stunt viroid RNA. *J. Virol.* 78, 10104–10110. <https://doi.org/10.1128/jvi.78.18.10104-10110.2004>.
- Gough, C., Jacquet, C., 2013. Nod factor perception protein carries weight in biotic interactions. *Trends Plant Sci.* 18, 566–574. <https://doi.org/10.1016/j.tplants.2013.06.001>.
- Gouhier-Darimont, C., Stahl, E., Glauser, G., Reymond, P., 2019. The Arabidopsis lectin receptor kinase lecrk-i.8 is involved in insect egg perception. *Front. Plant Sci.* 10, 623. <https://doi.org/10.3389/fpls.2019.00623>.
- He, X., Li, L., Xu, H., Xi, J., Cao, X., Xu, H., Rong, S., Dong, Y., Wang, C., Chen, R., Xu, J., Gao, X., Xu, Z., 2017. A rice jacalin-related mannose-binding lectin gene, OsJRL, enhances *Escherichia coli* viability under high salinity stress and improves salinity tolerance of rice. *Plant Biol.* 19, 257–267. <https://doi.org/10.1111/plb.12514>.
- Hu, S.P., Li, J.J., Dhar, N., Li, J.P., Chen, J.Y., Jian, W., Dai, X.F., Yang, X.Y., 2021. Lysin motif (Lysm) proteins: Interlinking manipulation of plant immunity and fungi. *Int. J. Mol. Sci.* 22, 1–12. <https://doi.org/10.3390/ijms22063114>.
- Hwang, I.S., Hwang, B.K., 2011. The pepper mannose-binding lectin gene CaMBL1 is required to regulate cell death and defense responses to microbial pathogens. *Plant Physiol.* 155, 447–463. <https://doi.org/10.1104/pp.110.164848>.
- Jung, I.J., Ahn, J., Jung, S., Hwang, J.E., Hong, M.J., Choi, H., 2019. Overexpression of rice jacalin-related mannose-binding lectin (OsJAC1) enhances resistance to ionizing radiation in Arabidopsis. *BMC Genomics* 19, 1–16.
- Kaur, A., Sharma, A., Madhu, Upadhyay, S.K., 2023. Analysis of lectin receptor-like kinases and their functions in higher plants, Plant Receptor-Like Kinases. INC. <https://doi.org/10.1016/b978-0-323-90594-7.00008-9>.
- Labbé, J., Muchero, W., Czarnecki, O., Wang, J., Wang, X., Bryan, A.C., Zheng, K., Yang, Y., Xie, M., Zhang, J., Wang, D., Meidl, P., Wang, H., Morrell-Falvey, J.L., Cope, K.R., Maia, L.G.S., Ané, J.M., Mewalal, R., Jawdy, S.S., Gunter, L.E., Schackwitz, W., Martin, J., Le Tacon, F., Li, T., Zhang, Z., Ranjan, P., Lindquist, E., Yang, X., Jacobson, D.A., Tschaplinski, T.J., Barry, K., Schmutz, J., Chen, J.G., Tuskan, G.A., 2019. Mediation of plant–mycorrhizal interaction by a lectin receptor-like kinase. *Nat. Plants* 5, 676–680. <https://doi.org/10.1038/s41477-019-0469-x>.
- Li, D., Wang, X., Yuan, D., Zhang, L., Jiang, X., Tao, Z., Li, Y., Wang, J., Li, X., Yang, Y., 2014. Over-expression of ArathEULS3 confers ABA sensitivity and drought tolerance in Arabidopsis. *Plant Cell. Tissue Organ Cult.* 117, 431–442. <https://doi.org/10.1007/s11240-014-0453-0>.
- Liu, T., Liu, Z., Song, C., Hu, Y., Han, Z., She, J., Fan, G., Wang, J., Jin, C., Chang, J., Zhou, J.M., Chai, J., 2012. Chitin-induced dimerization activates a plant immune receptor. *Science* (80-) 336, 1160–1164. <https://doi.org/10.1126/science.1218867>.
- Luo, X., Wu, W., Liang, Y., Xu, N., Wang, Z., Zou, H., Liu, J., 2020. Tyrosine phosphorylation of the lectin receptor-like kinase LORE regulates plant immunity. *EMBO J.* 39, e102856. <https://doi.org/10.15252/emboj.2019102856>.
- Ma, L., Haile, Z.M., Sabbadini, S., Mezzetti, B., Negri, F., Baraldi, E., 2022. Functional characterization of FaMBL1, a G-type lectin gene family member, in response to fungal pathogens of strawberry. *J. Exp. Bot.* 152–160. <https://doi.org/10.1093/jxb/erac396>.
- Madsen, E.B., Madsen, L.H., Radutoiu, S., Sato, S., Kaneko, T., Tabata, S., Sandal, N., 2003. A receptor kinase gene of the LysM type is involved in legume perception of rhizobial signals. *Nat. Lett.* 425, 637–640.
- Micol-Ponce, R., García-Alcázar, M., Lebrón, R., Capel, C., Pineda, B., García-Sogo, B., Alché, J., Ortiz-Ateiza, A., Bretones, S., Yuste-Lisbona, F., Moreno, V., Capel, J., Lozano, R., 2022. The tomato POD2 encodes a G-type lectin receptor kinase required for viable pollen grain formation Micol-Ponce. *J. Exp. Bot.* <https://doi.org/10.1093/jxb/erac419>.
- Nsimba-Lubaki, M., Peumans, W.J., 1986. Seasonal Fluctuations of Lectins in Barks of Elderberry (*Sambucus nigra*) and Black Locust (*Robinia pseudoacacia*). *Plant Physiol.* 80, 747–751. <https://doi.org/10.1104/pp.80.3.747>.
- Oda, A., Sakuta, C., Masuda, S., Mizoguchi, T., Kamada, H., Satoh, S., 2003. Possible involvement of leaf gibberellins in the clock-controlled expression of XSP30, a gene encoding a Xylem Sap Lectin, in cucumber roots. *Plant Physiol.* 133, 1779–1790. <https://doi.org/10.1104/pp.103.030742>.
- Osman, M.E., fadil M., Dirar, A.I., Konozy, E.H.E., 2022. Genome-wide screening of lectin putative genes from Sorghum bicolor L., distribution in QTLs and a probable implications of lectins in abiotic stress tolerance. *BMC Plant Biol.* 22, 1–15. <https://doi.org/10.1186/s12870-022-03792-6>.
- Patishtan, J., Hartley, T.N., Fonseca de Carvalho, R., Maathuis, F.J.M., 2018. Genome-wide association studies to identify rice salt-tolerance markers. *Plant Cell Environ.* 41, 970–982. <https://doi.org/10.1111/pce.12975>.
- Phillips, S.M., Dubery, I.A., van Heerden, H., 2013. Identification and molecular characterisation of a lectin receptor-like kinase (GhLecRK-2) from cotton. *Plant Mol. Biol. Report.* 31, 9–20. <https://doi.org/10.1007/s11105-012-0470-2>.
- Ranf, S., Gisch, N., Schäffer, M., Illig, T., Westphal, L., Knirel, Y.A., Sánchez-Carballo, P. M., Zähringer, U., Hüchelhofen, R., Lee, J., Scheel, D., 2015. A lectin S-domain receptor kinase mediates lipopolysaccharide sensing in Arabidopsis thaliana. *Nat. Immunol.* 16, 426–433. <https://doi.org/10.1038/ni.3124>.
- Regente, M., Pinedo, M., Clemente, H.S., Balliau, T., Jamet, E., De La Canal, L., 2017. Plant extracellular vesicles are incorporated by a fungal pathogen and inhibit its growth. *J. Exp. Bot.* 68, 5485–5495. <https://doi.org/10.1093/jxb/erx355>.

- Rovenich, H., Zuccaro, A., Thomma, B.P.H.J., 2016. Convergent evolution of filamentous microbes towards evasion of glycan-triggered immunity. *New Phytol.* 212, 896–901. <https://doi.org/10.1111/nph.14064>.
- Sahid, S., Roy, C., Shee, D., Datta, R., Paul, S., 2021. Jacalin domain-containing protein Os SaIT interacts with Os DREB2A and Os NAC1 to impart drought stress tolerance in planta. *Environ. Exp. Bot.* 183.
- Sturm, A., Voelker, T.A., Herman, E.M., Chrispeels, M.J., 1988. Planta to protein bodies of the vacuolar protein phytohemagglutinin in transgenic tobacco. *Planta* 175, 170–183.
- Tripathi, D., Zhang, T., Koo, A.J., Stacey, G., Tanaka, K., 2018. Extracellular ATP acts on jasmonate signaling to reinforce plant defense. *Plant Physiol.* 176, 511–523. <https://doi.org/10.1104/pp.17.01477>.
- Tsaneva, M., Van Damme, E.J.M., 2020. 130 years of plant lectin research. *Glycoconj. J.* 37, 533–551. <https://doi.org/10.1007/s10719-020-09942-y>.
- Van Damme, E.J.M., Allen, A.K., Peumans, W.J., 1987. Isolation and characterization of a lectin with exclusive specificity towards mannose from snowdrop (*Galanthus nivalis*) bulbs. *FEBS* 215, 140–144.
- Van Holle, S., De Schutter, K., Eggermont, L., Tsaneva, M., Dang, L., Van Damme, E.J.M., 2017. Comparative study of lectin domains in model species: New insights into evolutionary dynamics. *Int. J. Mol. Sci.* 18, 1136. <https://doi.org/10.3390/ijms18061136>.
- Van Hove, J., Fouquaert, E., Smith, D.F., Proost, P., Van Damme, E.J.M., 2011. Lectin activity of the nucleocytoplasmic EUL protein from *Arabidopsis thaliana*. *Biochem. Biophys. Res. Commun.* 414, 101–105. <https://doi.org/10.1016/j.bbrc.2011.09.031>.
- Vandenborre, G., Smaghe, G., Van Damme, E.J.M., 2011. Plant lectins as defense proteins against phytophagous insects. *Phytochemistry* 72, 1538–1550. <https://doi.org/10.1016/j.phytochem.2011.02.024>.
- Wan, J., Tanaka, K., Zhang, X.C., Son, G.H., Brechenmacher, L., Nguyen, T.H.N., Stacey, G., 2012. LYK4, a lysin motif receptor-like kinase, is important for chitin signaling and plant innate immunity in *Arabidopsis*. *Plant Physiol.* 160, 396–406. <https://doi.org/10.1104/pp.112.201699>.
- Vuong, U.T., et al., 2022. Engineering plant immune circuit: walking to the bright future with a novel toolbox. *Plant biotechnology journal*. <https://doi.org/10.1111/pbi.13916>. Submitted for publication.
- Wan, J., He, M., Hou, Q., Zou, L., Yang, Y., Wei, Y., Chen, X., 2021. Cell wall associated immunity in plants. *Stress Biol.* 1 <https://doi.org/10.1007/s44154-021-00003-4>.
- Wang, Z., Cheng, J., Fan, A., Zhao, J., Yu, Z., Li, Y., Zhang, H., Xiao, J., Muhammad, F., Wang, H., Cao, A., Xing, L., Wang, X., 2018. LecRK-V, an L-type lectin receptor kinase in *Haynaldia villosa*, plays positive role in resistance to wheat powdery mildew. *Plant Biotechnol. J.* 16, 50–62. <https://doi.org/10.1111/pbi.12748>.
- Wang, Y., Cordewener, J.H.G., America, A.H.P., Shan, W., Bouwmeester, K., Govers, F., 2015. Arabidopsis lectin receptor kinases LecRK-IX.1 and LecRK-IX.2 are functional analogs in regulating *Phytophthora* resistance and plant cell death. *Mol. Plant-Microbe Interact.* 28, 1032–1048. <https://doi.org/10.1094/MPMI-02-15-0025-R>.
- Wetzel, S., Demmers, C., Greenwood, J.S., 1989. Seasonally fluctuating bark proteins are a potential form of nitrogen storage in three temperate hardwoods. *Planta* 178, 275–281. <https://doi.org/10.1007/BF00391854>.
- Willmann, R., Lajunen, H.M., Erbs, G., Newman, M.A., Kolb, D., Tsuda, K., Katagiri, F., Fliegmann, J., Bono, J.J., Cullimore, J.V., Jehle, A.K., Götz, F., Kulik, A., Molinaro, A., Lipka, V., Gust, A.A., Nürnberger, T., 2011. Arabidopsis lysin-motif proteins LYM1 LYM3 CERK1 mediate bacterial peptidoglycan sensing and immunity to bacterial infection. *Proc. Natl. Acad. Sci. U. S. A.* 108, 19824–19829. <https://doi.org/10.1073/pnas.1112862108>.
- Witzel, K., Matros, A., Bertsch, U., Aftab, T., Rutten, T., 2021. The Jacalin-Related Lectin HvHorch Is Involved in the Physiological Response of Barley Roots to Salt Stress. *Int. J. Mol. Sci.* 22.
- Woo, J.Y., Kim, Y.J., Paek, K.H., 2020. CaLecRK-S.5, a pepper L-type lectin receptor kinase gene, accelerates *Phytophthora* elicitor-mediated defense response. *Biochem. Biophys. Res. Commun.* 524, 951–956. <https://doi.org/10.1016/j.bbrc.2020.02.014>.
- Wu, T., Wang, R., Xu, X., He, X., Sun, B., Zhong, Y., Liang, Z., Luo, S., Lin, Y., 2014. *Cucumis sativus* L-type lectin receptor kinase (CsLecRK) gene family response to *Phytophthora melonis*, *Phytophthora capsici* and water immersion in disease resistant and susceptible cucumber cultivars. *Gene* 549, 214–222. <https://doi.org/10.1016/j.gene.2014.07.058>.
- Yamada, K., Yamaguchi, K., Shirakawa, T., Nakagami, H., Mine, A., Ishikawa, K., Fujiwara, M., Narusaka, M., Narusaka, Y., Ichimura, K., Kobayashi, Y., Matsui, H., Nomura, Y., Nomoto, M., Tada, Y., Fukao, Y., Fukamizo, T., Tsuda, K., Shirasu, K., Shibuya, N., Kawasaki, T., 2016. The Arabidopsis CERK1-associated kinase PBL 27 connects chitin perception to MAPK activation. *EMBO J.* 35, 2468–2483. <https://doi.org/10.15252/embj.201694248>.
- Yang, C., Liu, R., Pang, J., Ren, B., Zhou, H., Wang, G., Wang, E., Liu, J., 2021. Poaceae-specific cell wall-derived oligosaccharides activate plant immunity via OsCERK1 during Magnaporthe oryzae infection in rice. *Nat. Commun.* 12, 2178. <https://doi.org/10.1038/s41467-021-22456-x>.
- Youle, R.J., Huang, A.C., 1976. Protein bodies from the endosperm of castor bean. *Plant Ph* 58, 703–709.
- Zhang, X., Dong, W., Sun, J., Feng, F., Deng, Y., He, Z., Oldroyd, G.E.D., Wang, E., 2015. The receptor kinase CERK1 has dual functions in symbiosis and immunity signalling. *Plant J.* 81, 258–267. <https://doi.org/10.1111/tbj.12723>.