Biosystems Diversity

ISSN 2519-8513 (Print)
ISSN 2520-2529 (Online)
Biosyst. Divers.

Evolution of immune mechanisms in monocots and dicots in response to microbial pathogens and abiotic stressors

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Article info
Received 04.03.2025
Received in revised form 12.04.2025
Accepted 17.05.2025

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Patyka, M. V., Khablak, S. H., Patyka, T. I., Bondareva, L. M., Dolia, M. M., Spychak, V. M., & Lykholat, Y. V. (2025). Evolution of immune mechanisms in monocots and dicots in response to microbial pathogens and abiotic stressors. Biosystems Diversity, 33(2), e2531. doi:10.15421/012531

An in-depth comparative analysis of the evolutionary features of non-specific immune mechanism formation in monocotyledonous (*Triticum aestivum* L.) and dicotyledonous (*Helianthus annuus* L.) plants has been conducted. The main focus is on the differential role of key protein families – ABC transporters, lipid transfer proteins (LTPs), and wall-associated kinase receptors (WAKs) – in modulating immune signaling cascades in response to various pathogenic and stress factors. The study demonstrates that winter wheat effectively implements systemic acquired resistance (SAR) mechanisms, particularly through the functioning of ABCG transporters (e.g., Lr34), ensuring long-term, quantitative resistance to a wide range of microbial pathogens. In contrast, sunflower predominantly exhibits a localized immune response (LAR), where ROS signaling, activated via WAK receptors, plays a key role, ensuring rapid response to necrotrophic pathogens and abiotic factors. The analysis indicates significant functional divergence of orthologous proteins: in wheat, WAK receptors and LTPs are primarily involved in strengthening physical barriers, whereas in sunflower, WAKs function as primary damage sensors (DAMPs) and activators of local stress pathways, and LTPs participate in signaling processes and membrane stabilization. Different immune strategies correlate with physiological-anatomical features and evolutionary adaptation to dominant pathogen types. The obtained results underscore the importance of integrating knowledge about the molecular mechanisms of non-specific immunity into breeding programs and biotechnological approaches to create cultivars with enhanced and durable resistance. Unresolved questions, particularly regarding the precise activation mechanisms of WAK receptors, and prospects for further research are discussed.

Keywords: plant immune evolution; non-specific resistance; *Triticum aestivum*; *Helianthus annuus*; ABC transporters; lipid transfer proteins (LTPs); WAK receptors; systemic acquired resistance; localized immune response.

Evolutionary landscape of plant immunity: current challenges and core defense mechanisms in monocot and dicot plants

The plant immune system is a complex, multi-layered network of defense mechanisms that has evolved to counter a wide range of biotic (pathogens, pests) and abiotic (drought, salinity, extreme temperatures) stressors. Traditionally, two main levels of immunity are distinguished: basal immunity, or PAMP-triggered immunity (PTI), and effector-triggered immunity (ETI). PTI, the first line of defense, is activated by the recognition of conserved microbial molecules – pathogen-associated molecular patterns (PAMPs) – or endogenous damage signals (DAMPs) through pattern recognition receptors (PRRs) located on the plasma membrane, such as receptor-like kinases (RLKs) and receptor-like proteins (RLPs) (Appels et al., 2018). This level of immunity provides broad-spectrum but relatively weak resistance. For instance, DAMPs such as oligogalacturonides, which arise from cell wall degradation, can trigger basal defense responses (Badouin et al., 2017).

Pathogens that have successfully adapted to host defense systems often secrete effector proteins to suppress PTI. In response, plants have evolved intracellular immune receptors, primarily from the NLR (nucleotide-binding leucine-rich repeat) family, that detect these effectors or their activity, initiating ETI – an enhanced, often localized immune response characterized by hypersensitive response (HR) and cell death at the infection site (Appels et al., 2018). Beyond these two classical layers, a significant role is played by so-called non-specific or quantitative resistance, which is frequently associated with durable, broad-spectrum protection and mediated by genes that do not belong to the canonical NLR class (Poland et al., 2009). This type of resistance is especially critical for crop performance under the conditions of modern agroecosystems.

Contemporary agriculture faces unprecedented challenges due to production intensification, global climate change, and the emergence of novel, more aggressive pathogen races (Atkinson & Urwin, 2012; Velásquez et al., 2018). According to Bazzalo et al. (2019), climate change leads to pathogen range shifts, increased epiphytotic outbreaks, and amplified abiotic stress, all of which can modulate plant immune responses. The mounting pressure from combined biotic and abiotic stressors – as emphasized in recent 2025 studies – demands urgent development of innovative and sustainable strategies to mitigate plant stress (Herold et al., 2025; Koyama et al., 2025). This underscores the growing importance of understanding and harnessing mechanisms underlying long-lasting, non-specific resistance, which, unlike highly specific R gene-mediated immunity, is more difficult for rapidly evolving pathogens to overcome.

In this context, investigating the molecular basis of broad-spectrum, durable, non-specific resistance is of primary importance for ensuring food security. Membrane proteins, particularly receptors and transporters, play a central role in non-specific immunity by functioning at the interface between the cell and the external environment. Three protein families are of particular interest: ATP-binding cassette (ABC) transporters, lipid transfer proteins (LTPs), and wall-associated kinases (WAKs). Notably, components of non-specific immunity such as ABC transporters often have dual functions, contributing not only to pathogen defense but also to abiotic stress tolerance, such as heavy metal detoxification (Borghi et al., 2015). This duality high-

lights that these protein families operate at the intersection of multiple stress-response pathways, making them key targets for breeding crops with enhanced general resistance.

Winter wheat (*Triticum aestivum* L.), a representative monocotyledonous cereal, and sunflower (*Helianthus annuus* L.), a dicotyledonous member of the Asteraceae family, are important agricultural crops with distinct evolutionary trajectories and, likely, different strategies for adapting to pathogens and stressors. Wheat exemplifies effective systemic acquired resistance (SAR), mediated by genes such as Lr34 (Krattinger et al., 2009), while sunflower, which is frequently attacked by necrotrophs, tends to develop localized responses and enhanced abiotic stress tolerance. Research has shown that systemic resistance can also be induced by beneficial microbes such as *Pseudomonas fluorescens*, highlighting the potential for modulating plant non-specific immunity (Ivanova & Patyka, 2023).

The central hypothesis of this review is that the evolutionary divergence between monocots and dicots, along with their adaptation to distinct pathogen spectra and environmental conditions, has led to functional specialization of conserved components of non-specific immunity – such as ABC transporters, LTPs, and WAK receptors. The aim of this work is to conduct a comparative cellular and molecular analysis of the roles these protein families play in shaping non-specific resistance in winter wheat and sunflower, to identify shared and distinct features of their function, and to evaluate their contributions to various immune strategies. Understanding these mechanisms is key to developing novel approaches for breeding resilient crop varieties and optimizing agronomic practices in the face of modern agricultural challenges.

Molecular architecture and functional repertoires of key immune modulators: ABC transporters, LTPs, and WAKs

Plant innate immunity largely depends on the function of conserved protein families that act as sensors, transporters, and modulators at the cellular level. Among these, ATP-binding cassette (ABC) transporters, lipid transfer proteins (LTPs), and wall-associated kinases (WAKs) stand out due to their versatility and remarkable functional plasticity.

WAKs (Wall-Associated Kinases) are transmembrane proteins characterized by an extracellular WAK domain, believed to interact with cell wall components (primarily pectins), a transmembrane segment, and an intracellular serine/threonine kinase domain (Dangl et al., 2013). They function as cell wall integrity (CWI) sensors, recognizing damage-associated molecular patterns (DAMPs), such as oligogalacturonides (OGs), which are released upon cell wall degradation by pathogenic enzymes or mechanical injury (Badouin et al., 2017). WAK activation initiates signaling cascades involving MAPK activation, reactive oxygen species (ROS) production, and the induction of defense genes, as well as reinforcement of the cell wall itself. In sunflower, specific WAK-RLKs have been identified that are closely associated with ROS signaling. WAKs are found in all land plants and have expanded notably in monocots (Dodds & Rathjen, 2010). However, recent studies have challenged the central role of WAKs as primary OG receptors in *Arabidopsis*. CRISPR-generated mutants lacking all five WAK genes demonstrated that WAKs are not essential for OG-triggered signaling or immunity in this model plant (Dodds & Rathjen, 2010). This fundamental finding necessitates a reevaluation of WAK activation mechanisms. WAKs may function as co-receptors, recognize alternative pectic structures, or respond to broader disruptions in cell wall integrity rather than specific OG motifs. This has significant implications for our understanding of DAMP signaling, especially given that WAKs are still considered key CWI sensors (Jones & Dangl, 2006). Despite this controversy, WAKs remain important players in plant immunity, as evidenced by the identification of 44 NtWAK genes in tobacco, many of which respond to abiotic stresses and phytohormones and are predominantly localized to the plasma membrane (Dangl et al., 2013).

ABC transporters (ATP-Binding Cassette transporters) represent a large superfamily of membrane proteins divided into several subfamilies (ABCA–ABCI, though ABCI is not always recognized in plants). In the context of immunity and stress tolerance, subfamilies ABCB (MDR/TAP), ABCC (MRP), and particularly ABCG (PDR/WBC) are of greatest interest (Borghi et al., 2015). They have a characteristic structure consisting of one or two nucleotide-binding domains (NBDs) and one or two transmembrane domains (TMDs) (Kelley et al., 2015). The functions of ABC transporters are highly diverse: they transport phytohormones (salicylic acid [SA], abscisic acid [ABA], jasmonic acid [JA], auxins), secondary metabolites (phytoalexins, flavonoids, glycosides), lipids, and detoxify endogenous and exogenous toxins, including herbicides and heavy metals (Borghi et al., 2015). The Lr34/Yr18/Sr57/Pm38 and Lr46/Sr58 genes in wheat encode ABCG transporters that confer durable, broad-spectrum systemic acquired resistance (SAR) (Krattinger et al., 2009). Research by Kang et al. (2011) confirmed that Lr34 transports sinapyl alcohol, a lignin precursor, strengthens the cell wall against fungal pathogens. In sunflower, ABCG transporters (e.g., ABCG31, ABCG25, ABCG29) have also been identified and are associated with ROS regulation, defense compound transport, and stress responses. The ABC gene family has undergone significant expansion via tandem and whole-genome duplications, highlighting their evolutionary significance (Kelley et al., 2015).

LTPs (lipid transfer proteins) are small (9–10 kDa), predominantly secreted proteins containing a conserved eight-cysteine motif (PR-14 domain) that forms a hydrophobic cavity for lipid binding (Kourelis & Van der Hoorn, 2018). They are localized in the apoplast, cell wall, and cuticle (Krattinger et al., 2009). Their functions are diverse: they participate in cuticle and wax layer formation, transport lipid monomers, carry lipid signaling molecules (e.g., DIR1 in SAR), exhibit direct antimicrobial activity against fungi and bacteria, and play roles in osmoregulation and abiotic stress responses (Kourelis & Van der Hoorn, 2018). Numerous LTP genes have been identified in wheat and sunflower (LTP1, LTP2, LTP4, LTP5 in wheat; LTP3, LTP10 in sunflower), emphasizing their importance in both species. Interestingly, some LTPs, such as Ha-AP10 in sunflower, can dynamically relocate from the apoplast to the cell interior during germination, indicating broader roles than previously thought, possibly functioning as fatty acid shuttles (Mistry et al., 2021). Additionally, LTPs like NbLTPVAS in *Nicotiana benthamiana* can modulate the hypersensitive response (HR) by affecting ROS signaling and inducing antioxidant gene expression (Kourelis & Van der Hoorn, 2018).

Although ABC transporters, LTPs, and WAKs are ancient and conserved protein families, their functional roles exhibit both convergence (e.g., participation in stress responses) and divergence (e.g., substrate specificity in ABC transporters, signaling and structural roles in LTPs, specific cell wall interactions in WAKs). This suggests that a shared molecular toolkit has been differentially adapted and refined throughout plant evolution. For instance, a possible functional link between LTPs involved in transporting lipid signals for SAR (e.g., DIR1) (Krattinger et al., 2009) and ABC transporters responsible for shuttling phytohormones (SA, ABA, JA), which are key in SAR/LAR signaling, represents an underexplored but promising area of research (Borghi et al., 2015).

Divergent strategies of non-specific immunity: systemic acquired resistance (SAR) versus localized immune responses (LAR) in different plant lineages

Plants have evolved diverse strategies of non-specific immunity to counter pathogens. Two main paradigms – systemic acquired resistance (SAR) and localized immune response (LAR) – represent different defense philosophies, which become especially evident when comparing evolutionarily distant groups such as monocots (e.g., wheat) and dicots (e.g., sunflower).

Systemic acquired resistance (SAR) is a form of induced resistance that is activated throughout the plant following an initial localized exposure to a pathogen or elicitors (Bazzalo et al., 2019). This "priming" process prepares the plant for a faster and stronger response to subsequent attacks (Poland et al., 2009). Key components of SAR include the accumulation of salicylic acid (SA) and the function of the NPR1 (non expressor of PR1) protein (Poland et al., 2009).

Mobile signals such as methyl salicylate (MeSA) and the DIR1 lipid-transfer protein complexed with lipids or their derivatives play a crucial role in systemic signal transmission (Krattinger et al., 2009). SAR is characterized by a long-lasting effect, accumulation of pathogenesis-related (PR) proteins, and the ability to confer cross-resistance to a broad spectrum of pathogens (Osuna-Cruz et al., 2018). Evidence exists for epigenetic regulation and even transgenerational transmission of SAR (Poland et al., 2009).

Table 1
Comparative molecular characteristics and immune functions of ABC transporters, LTPs, and WAKs in plants

Feature	ABC transporters	LTPs (lipid transfer proteins)	WAKs (wall-associated kinases)
Key structural domains	Nucleotide-binding domain (NBD), transmembrane domain (TMD)	PR-14 domain (8 conserved cysteines), signal peptide	Extracellular WAK/GUB (pectin-binding), EGF-like domains, transmembrane domain (TM), intracellular serine/threonine kinase domain (STK)
General localization	Plasma membrane, tonoplast, organelle membranes (ER, mitochondria, chloroplasts)	Apoplast, cell wall, cuticle; possible intracellular localization (e.g., Ha-AP10)	Plasma membrane, closely associated with the cell wall
Primary biochemical function	ATP-dependent transport of diverse substrates	Binding and transport of lipids and hydrophobic molecules	Receptor kinase activity; sensors of cell wall integrity (CWI)
Known ligands/substrates	Phytohormones (SA, ABA, JA, auxins), secondary metabolites, lipids, ions, toxins, lignin precursors (e.g., Lr34)	Fatty acids, phospholipids, cutin monomers, lipid signal molecules (e.g., DIR1)	Pectins, oligogalacturonides (OGs), possibly other cell wall components or degradation products
General immune roles	Detoxification, transport of defense compounds and signaling molecules (PTI, SAR, LAR), resistance to abiotic stress	Formation of the cuticular barrier, direct antimicrobial activity, lipid signal transport (SAR), DAMP/PAMP response, ROS modulation	Recognition of DAMPs/PAMPs (indirect via wall changes), activation of PTI, ROS induction, cell wall reinforcement, regulation of growth and stress responses
Examples (wheat / sunflower)	Wheat: Lr34/Sr57, Lr46/Sr58 (SAR) Sunflower: ABCG31, ABCG25 (ROS regulation, stress)	Wheat: LTP1, LTP2 (barrier formation) Sunflower: LTP3, LTP10 (antifungal), Ha-AP10 (dynamic localization)	Wheat: TaWAKs (cell wall strengthening) Sunflower: HaWAK-RLKs (ROS signaling, DAMP perception)
Recent updates / controversies	Role in transport of lignin precursors (e.g., Lr34); involvement in symbiosis (e.g., STR)	Dynamic intracellular relocalization (e.g., Ha-AP10); HR modulation via ROS (e.g., NbLTPVAS)	WAKs not essential for OG-induced immunity in *Arabidopsis*, questioning their role as primary OG receptors

Winter wheat actively employs SAR mechanisms, as demonstrated by the presence and function of the Lr34/Sr57 and Lr46/Sr58 genes, which encode ABCG transporters. These genes provide durable, broad-spectrum resistance and are likely involved in transporting signaling molecules such as SA and abscisic acid (ABA). SAR induction can also be achieved by rhizosphere bacteria such as *Pseudomonas fluorescens* (Camacho et al., 2009), or by applying elicitors that stimulate the accumulation of protective phenolic compounds (Ramírez-González et al., 2018), typical manifestations of SAR or Induced Systemic Resistance (ISR).

Localized immune response (LAR), by contrast, is characterized by rapid and concentrated defense at the site of infection or damage (Salcedo et al., 2007). LAR is often associated with effector-triggered immunity (ETI) and may include the hypersensitive response (HR). Current research suggests that LAR may be a key mechanism of ETI, in which a strong defense response is observed at the boundary of the infected zone, effectively limiting pathogen spread (Harrison et al., 2024). In sunflower, SAR is much less pronounced or even absent; instead, rapid LAR dominates, especially effective against necrotrophic pathogens.

The role of ROS signaling is central in both strategies but with different emphases. In sunflower, reactive oxygen species (ROS) play a key role in LAR by activating MAPK cascades via WAK receptors and other sensors. This ensures a rapid response to damage and necrotroph attacks. In wheat, ROS signaling is also present but is integrated into SAR as a secondary component that supports long-term responses and may be part of the priming process. ROS are critical signaling molecules and direct effectors in plant defense, involved in basal resistance, HR, and SAR. Their production is tightly regulated, and they interact with phytohormones such as SA, jasmonic acid (JA), and ethylene (ET) to fine-tune immune responses (UniProt, 2023). Phosphatidic acid (PA) homeostasis, regulated by DGK5, is closely linked to ROS signaling in both PTI and ETI (Velásquez et al., 2018).

Functional specialization of WAK and LTP proteins also reflects these divergent strategies. Although both protein families are conserved, their roles are differentiated. In wheat, WAK receptors and LTPs are primarily involved in reinforcing physical barriers – remodeling the cell wall (WAK) and forming the cuticle (LTP). In sunflower, WAKs function as key DAMP receptors that activate ROS and local signaling, while LTPs participate in signaling pathways and membrane stabilization under stress. The ability of some LTPs, such as NbLTPVAS, to modulate ROS production and HR (Kourelis & Hoorn, 2018) highlights their role in fine-tuning the intensity and spread of local responses. This modulation may be critical for determining whether the response remains localized (LAR) or contributes to broader systemic signaling (SAR), which may vary between monocots and dicots.

The divergence of ABC transporters provides another striking example. In both species, they are involved in hormone and lipid transport, as well as detoxification. However, in wheat, they are closely associated with the induction and maintenance of SAR (notably the ABCG subfamily, such as Lr34), whereas in sunflower, their role is more focused on local membrane protection, transport of defensive compounds, and detoxification of oxidative stress byproducts – important for resistance to necrotrophs and abiotic factors.

The dominance of SAR in wheat – a monocot plant that frequently encounters biotrophic and hemibiotrophic rusts and powdery mildews, where systemic preparedness is advantageous – contrasts with the dominance of LAR in sunflower, a dicot plant often attacked by necrotrophs, where rapid local containment and damage limitation are paramount. This likely represents an evolutionary adaptation driven by prevailing pathogen pressures and different resource allocation strategies. The differential deployment of ABC transporters, LTPs, and WAK receptors underlies these divergent strategies. The concept of LAR as a core outcome of ETI, in which defense is spatially confined to the infection boundary (Harrison et al., 2024), refines our understanding of how plants achieve resistance without excessive self-damage – especially relevant for LAR-reliant species like sunflower.

The evolutionary arms race: pathogen lifestyle as a driving force of functional specialization in plant immune components

Interaction between plants and pathogens is a dynamic process characterized by a continuous evolutionary "arms race." Pathogens produce effector molecules to overcome the defense mechanisms of the host plant and facilitate colonization (Kang et al., 2011), while plants evolve new strategies to recognize and neutralize these threats. Basal (non-specific) immunity, mediated by such conserved components as ABC transporters, lipid transfer proteins (LTPs), and wall-associated kinases (WAKs), provides a fundamental level of protection.

The functional specialization of these components is largely determined by the type of pathogens the plant most frequently encounters.

Table 2
Comparison of the characteristics of systemic acquired resistance (SAR) and localized immune response (LAR)

Trait	Systemic acquired resistance (SAR)	Localized acquired resistance (LAR)
Inducing stimulus	Local infection by a pathogen (often biotrophic), PAMPs, certain chemical elicitors, beneficial microbes (e.g., *P. fluorescens*)	Local infection (often necrotrophic or strong biotrophic attack), ETI, DAMPs, strong PTI
Onset speed	Relatively slow (days)	Rapid (hours)
Spatial distribution	Systemic (throughout the plant)	Localized (at the infection site and nearby, ~2 mm zone)
Duration	Long-lasting (weeks, months), may have "memory"	Usually short-term, associated with active infection
Key signaling molecules	SA, NPR1, MeSA, DIR1-lipid complex, G3P, ROS (secondary signal), ABA (modulation)	ROS (primary signal), MAPK, JA, ET, DAMPs, often associated with HR
Involvement of ABC/LTP/WAK	ABCG (e.g., Lr34 – transports SA/ABA/lignin precursors), LTP (DIR1 – lipid signal transport), WAK (integration into systemic response)	WAK (DAMP recognition, ROS activation), LTP (membrane stabilization, antimicrobial action, ROS modulation), ABC (detoxification, transport)
Target pathogens	Broad spectrum, especially biotrophs and hemibiotrophs	Necrotrophs, strong localized biotrophic infections
Example plant system	Wheat (Lr34-mediated SAR)	Sunflower (ROS-dependent LAR against necrotrophs)

Against biotrophic pathogens (e.g., *Blumeria graminis*, *Puccinia* spp. in wheat; *Plasmopara halstedii* in sunflower), which require living host cells for nutrition and often form specialized structures such as haustoria, plants deploy strategies aimed at restricting pathogen growth and spread while avoiding widespread cell death (i.e., hypersensitive response, HR), which could be detrimental to the plant itself. In this context, LTPs play an important role by reinforcing the cuticle and cell walls, forming a hydrophobic barrier that limits pathogen penetration (Krattinger et al., 2009). ABCG transporters, such as Lr34 in wheat, mediate systemic acquired resistance (SAR) by transporting signaling molecules (e.g., salicylic acid, SA) and precursors of defense compounds (e.g., sinapyl alcohol for lignification), which make cell walls more resistant to biotroph colonization. Wheat, with its well-developed SAR, exhibits effective defense against many biotrophic fungi.

Against necrotrophic pathogens (e.g., *Sclerotinia sclerotiorum*, *Botrytis cinerea*, *Alternaria* spp.), which kill host cells through the secretion of toxins and cell wall–degrading enzymes (CWDEs) and feed on dead tissue, HR activation is counterproductive, as it can facilitate pathogen spread. Instead, rapid, localized, non-specific responses play a key role. WAK receptors detect damage-associated molecular patterns (DAMPs), such as oligogalacturonides (Badouin et al., 2017) – although recent studies question direct OG binding by WAKs in *Arabidopsis* – and trigger a PTI-like response, including ROS production, cell wall reinforcement, and synthesis of PR proteins. LTPs aid in restoring damaged barriers and may exhibit direct antifungal activity (Krattinger et al., 2009). ABC transporters are involved in detoxifying pathogen-derived toxins and removing oxidative stress products generated during ROS bursts. Sunflower, with its strong ROS-mediated local response and active WAK receptors, demonstrates an effective defense strategy against necrotrophs.

Against hemibiotrophic pathogens (e.g., *Zymoseptoria tritici*, *Fusarium graminearum*), which combine an initial biotrophic phase (growth in living tissue) with a later necrotrophic phase (cell killing), the plant response must be both flexible and balanced. It should integrate defense elements effective against both lifestyles. Activation of PTI mechanisms (barrier strengthening, local production of defense compounds) is accompanied by SAR induction (especially in wheat). ABCG transporters are crucial for transporting phytohormones (SA/JA), antioxidants, and for detoxifying mycotoxins. WAK receptors, by sensing cell wall damage, activate defense cascades tailored to the current infection stage. The cellular response involves modulation of hormone balance, deposition of callose and flavonoids, and stabilization of the cell wall. Effective defense requires coordinated action of WAKs, ABCs, and LTPs.

The functional specialization of ABC transporters, LTPs, and WAK receptors is not only an adaptation by the plant but also a direct result of the co-evolutionary arms race. Pathogens constantly evolve to produce new effectors to bypass host defenses, while plants evolve new recognition and defense mechanisms. For example, fungal pathogens themselves use ABC transporters to export toxins or protect against plant antimicrobial compounds, highlighting a molecular "arms race" employing similar tools (Yang et al., 2015). The lifestyle of dominant pathogens acts as a powerful selective force shaping specific types of immune responses and, accordingly, specific functional roles for ABCs, LTPs, and WAKs. For instance, against necrotrophs that destroy tissues, mechanisms for rapid DAMP recognition by WAKs and detoxification by ABC transporters will be strongly selected – as observed in sunflower. The evolution of defense strategies is also shaped by internal trade-offs. For example, the GhSTR1 gene (an ABCG transporter in cotton) mediates resistance to *Verticillium*, but this is associated with growth penalties (Kang et al., 2011). This indicates that natural selection optimizes not for maximal resistance per se, but for a balance that maximizes overall plant fitness in a specific environment with its characteristic pathogen pressure.

The cell periphery as an immunological battlefield: anatomical determinants of defense strategies in monocot and dicot plants

Differences in immune strategies between monocot and dicot plants are not accidental, but are closely linked to structural features of their cell walls, epidermis, and cuticle. These anatomical characteristics determine not only the passive barrier properties but also influence the types of molecular signals generated during interactions with pathogens, as well as the efficiency of defense mechanisms mediated by ABC transporters, LTPs, and WAK receptors.

The cell wall is the first line of defense and an important source of damage-associated molecular patterns (DAMPs). In dicots such as sunflower, the cell wall is typically rich in pectins and cellulose, which provides relative flexibility but also makes it more susceptible to the action of pectinases secreted by many necrotrophic pathogens. This explains the abundance and functional importance of WAK receptors in dicots, which have traditionally been considered sensors of pectic fragments (oligogalacturonides – OGs) (Dangl et al., 2013). Even though direct recognition of OGs by WAKs in *Arabidopsis* is now under debate (Dodds & Rathjen, 2010), WAKs are undoubtedly key cell wall integrity (CWI) sensors, and their role in pectin-rich walls of dicots remains critical (Jones & Dangl, 2006). In contrast, the cell wall of monocots, such as wheat, is more rigid, contains significantly more hemicelluloses (e.g., arabinoxylans), lignin, and is often silicified. This structure makes it less sensitive to pectinases, and thus WAK receptors in grasses have likely evolved to recognize other types of DAMPs (e.g., hemicellulose fragments) or to respond to mechanical stress and general wall disruption. The rigidity of the wheat cell wall itself serves as an effective physical barrier against pathogen penetration, especially necrotrophs, but it may limit flexibility and speed of the local immune response. This difference in wall composition is a primary determinant of the types of DAMPs generated and, consequently, a driving force for the evolution of specialized WAKs with different ligand specificities, resulting in divergent signaling pathways.

The epidermis and cuticle form the outer protective layer. The epidermis of dicot plants generally has a thinner cuticle and less lignified cell walls compared to monocots. This necessitates intensive secretion of waxes and cutin mediated by LTPs to form an effective hydrophobic barrier, particularly important for protection against

necrotrophic pathogens that often enter through wounded surfaces. In wheat, the epidermis is thicker and the cuticle is more robust, often enriched with phenolic compounds that provide additional protection. LTPs in wheat are also involved in transporting phytoalexins and lipid signaling molecules into the apoplast in response to biotrophic pathogen attacks. The role of LTPs in cuticle formation is not limited to creating a passive barrier. The integrity and composition of the cuticle shaped by LTPs can directly affect the efficiency of apoplastic defense signaling, including the movement of lipid-derived systemic signals such as DIR1, which are also transported by LTPs. Thus, differences in the cuticles of monocots and dicots influence this level of defense (Krattinger et al., 2009).

Table 3
The role of ABC transporters, LTPs, and WAK receptors in plant defense against pathogens with different lifestyles

Pathogen lifestyle	Key plant defense strategy	Dominant role of ABC transporters	Dominant role of LTPs	Dominant role of WAK receptors	Example in wheat / sunflower
Biotrophs	SAR, reinforcement of barriers, restriction of nutrient access	Transport of SA, ABA, lignin precursors (e.g., Lr34 in wheat), induction of SAR	Formation of cuticular barrier, transport of signaling lipids (e.g., DIR1), direct antimicrobial action	Detection of cell wall alterations, induction of local wall strengthening (e.g., callose, papillae deposition)	Wheat: Lr34 (SAR), LTP (cuticle) Sunflower: LTP (cuticle), WAK (local reinforcement)
Necrotrophs	Rapid LAR, ROS production, detoxification, cell wall reinforcement	Export of pathogen toxins, ROS products, transport of defense compounds (e.g., phytoalexins)	Barrier repair, antifungal action, membrane stabilization, modulation of ROS (e.g., NbLTPVAS)	Recognition of DAMPs (cell wall degradation products), activation of PTI-like response, ROS induction, wall reinforcement	Sunflower: WAK (DAMP sensors, ROS), ABC (detoxification), LTP (antifungal) Wheat: WAK (cell wall remodeling), ABC (detoxification)
Hemibiotrophs	Flexible combination of PTI, LAR, and SAR depending on infection phase	Transport of SA/JA, antioxidants, detoxification of mycotoxins, hormone balance modulation	Barrier reinforcement, signaling lipid transport, antimicrobial activity	Detection of wall damage, activation of adaptive defense cascades, hormone signaling modulation	Wheat: Lr34 (SAR), WAK (remodeling) Sunflower: WAK (DAMP sensors), ABC (detoxification), LTP (signaling)

Anatomical and structural features of the cell periphery have likely imposed constraints or directed the evolution of functional roles of ABC transporters, LTPs, and WAK receptors. For example, the need for transport of lignin precursors such as sinapyl alcohol (carried out by Lr34 in wheat) (Kang et al., 2011) is more pronounced in plants with highly lignified walls like grasses, which has driven the selection of specific ABC transporter functions. Similarly, the types of lipids that LTPs need to mobilize for cuticle repair or signaling will differ depending on membrane and cuticle composition characteristic of monocots or dicots. Comparative genomic studies of receptor kinase families, such as BRI1 or WAK, reveal structural and evolutionary differences between monocots and dicots, which likely reflect adaptations to different cellular architectures and signaling needs (Dodds & Rathjen, 2010; Huang et al., 2023).

Thus, physiological and anatomical features define the "architecture" of nonspecific immunity. The more flexible, pectin-rich cell wall of dicots has likely driven the evolution of a broader spectrum of WAK receptors and LTPs focused on rapid local response and barrier repair. In contrast, the rigid, multi-component cell wall of monocots relies on reinforcing existing barriers (e.g., via lignification) and systemic signals to contain infection, reflected in the functional specialization of their immune components.

Table 4
Anatomical features of the cell periphery in monocots (wheat) and dicots (sunflower) and their impact on non-specific immune mechanisms

Anatomical feature	Monocots (wheat)	Dicots (sunflower)	Predicted role/ specialization of WAKs	Predicted role/ specialization of LTPs	Predicted role/specialization of ABC transporters
Primary cell wall composition	Rich in hemicelluloses (arabinoxylans), (1,3;1,4)-β-glucans; less pectin	Rich in pectins and cellulose; lower hemicellulose content	Wheat: recognition of DAMPs from hemicellulose, mechanical stress; Sunflower: detection of pectin-related changes (not necessarily OGs), general CWI signaling	Wheat/sunflower: involvement in wall integrity maintenance, lipid component transport	Wheat/sunflower: transport of wall-modifying compounds (e.g., phenolics)
Lignification	High, especially in secondary walls and vascular tissues	Moderate, mainly in vascular tissues and sclerenchyma	Wheat: indirect role in lignification-related responses; sunflower: less prominent direct involvement	Wheat/sunflower: indirect impact via signaling that can trigger lignification	Wheat: transport of lignin precursors (e.g., Lr34); sunflower: less specialized lignin precursor transport for defense
Cuticle (thickness/ composition)	Usually thicker and stronger; may contain more phenolics and long-chain waxes	Usually thinner, more elastic; wax composition may differ	Indirect role via signaling upon cuticular damage	Wheat: transport of phytoalexins/signaling lipids, formation of strong cuticle; Sunflower: active secretion of waxes/cutin to build barrier	Wheat/sunflower: transport of cuticular waxes and cutin monomers (some ABCG-type)
Epidermal structure	Often contains specialized cells (e.g., silica cells, cork cells), tightly packed	Less specialized; may have trichomes, more dispersed stomata	Detection of epidermal cell damage	Protection of epidermal cells, sealing of intercellular spaces	Transport of defense compounds to the epidermis, detoxification

Harnessing non-specific immunity: biotechnological horizons and multi-omics approaches for enhancing crop resistance

Understanding the molecular mechanisms of non-specific immunity opens up significant opportunities for developing new strategies to enhance crop resistance to biotic and abiotic stressors. Genes that control durable, broad-spectrum resistance, such as Lr34 in wheat, are extremely valuable in breeding because they are harder for pathogens to overcome compared to R-genes that confer race-specific resistance (Kohorn & Kohorn, 2012). Modern multi-omics technologies and genetic engineering tools provide powerful means for identifying, characterizing, and precisely modifying key components of non-specific immunity, including ABC transporters, LTPs, and WAK receptors.

Multi-omics approaches for gene identification and mechanistic insight. Transcriptomics, proteomics, and metabolomics have become indispensable tools for studying plant responses to stress and identifying candidate genes involved in immune responses (Bechtold & Field, 2018). Genomic analyses of gene families such as ABC transporters in Rosaceae, WAK receptors in tobacco (Dangl et al., 2013), or RLKs in wheat (Harvey et al., 2024), enable the discovery of evolutionary patterns, identification of stress-responsive genes, and prediction of their functions. Integrative analysis of multi-omics data is particularly crucial for understanding complex responses to combined

stresses (Ivanova & Patyka, 2023), which is becoming increasingly relevant under climate change. For example, a systems analysis of the transcriptome and metabolome in sunflower under salt stress and melatonin treatment revealed key genes and metabolic pathways involved in enhanced stress resistance (Smetanska et al., 2021).

Biotechnological tools for improving crop resistance. Genome editing technologies, particularly CRISPR/Cas, open the door to precise modifications of immunity-related genes, allowing targeted regulation of ABC transporters, LTPs, and WAK receptors (Appels et al., 2018). This can include upregulation of resistance-associated genes or knockout of genes that negatively regulate defense responses. The development of molecular markers for non-specific resistance genes can accelerate the breeding of resistant varieties (Bechtold & Field, 2018).

Regarding specific protein families:

– ABC transporters: enhancing expression of genes like Lr34, which confer broad-spectrum resistance, is a promising strategy. Research on GhSTR1 in cotton, where gene silencing improved disease resistance and growth, points to the potential of fine-tuning genes that mediate the trade-off between defense and productivity. However, manipulation of such genes requires caution due to their involvement in developmental processes, to avoid unwanted pleiotropic effects (Kang et al., 2011).

– LTP proteins: increasing the expression of LTPs involved in cuticular barrier formation or specific signaling pathways (e.g., associated with DIR1) is a viable strategy. Understanding the mechanisms of dynamic relocalization of certain LTPs (such as Ha-AP10) may uncover novel targets for engineering (Mistry et al., 2021).

– WAK receptors: given new evidence that WAKs in *Arabidopsis* may not be primary receptors for oligogalacturonides (OGs), biotechnological strategies should shift from simply enhancing OG binding to identifying and engineering interactions with true ligands or co-receptors, or modulating their kinase activity to strengthen perception of cell wall integrity. Although more complex, this approach may prove more effective if the actual activation mechanisms are taken into account (Dodds & Rathjen, 2010).

Induced resistance and biostimulants. Beyond genetic modification, the use of biocontrol agents and elicitors for priming or enhancing non-specific immunity is a promising strategy. The effectiveness of *Pseudomonas fluorescens* in inducing systemic resistance in plants has been well documented (Camacho et al., 2009). Application of elicitors such as yeast extract or jasmonic acid can stimulate the accumulation of protective phenolic compounds (Ramírez-González et al., 2018). Biostimulants, including microalgae extracts, also show potential in enhancing plant resistance to abiotic stresses (Boller & Felix, 2009).

The most effective strategies for improving crop resistance will likely involve a combination of genetic improvements (e.g., optimized alleles of ABC/LTP/WAK genes achieved through genome editing) and the use of resistance inducers or beneficial microorganisms. This integrated approach creates multilayered protection, reinforcing non-specific immunity.

Table 5

Biotechnological strategies and multi-omics approaches to enhance non-specific immunity via ABC transporters, LTPs, and WAK receptors

Target protein family	Potential biotechnological strategy	Specific molecular target/mechanism	Relevant omics tools for discovery/validation	Potential outcome for crop resistance
ABC transporters	Gene editing (upregulation/function modification), marker-assisted selection (MAS), RNA interference (RNAi) for negative regulators	Enhancement of Lr34-like gene activity; modulation of growth-defense trade-off regulators (e.g., GhSTR1 analogs); improved transport of phytoalexins/detoxification compounds	Transcriptomics (differential gene expression), proteomics (protein abundance), metabolomics (transported substrates), GWAS (allele identification)	Increased broad-spectrum disease resistance, enhanced tolerance to abiotic stress (e.g., toxins, herbicides)
LTP proteins	Gene editing, MAS, expression induction via elicitors	Optimization of DIR1-related signaling; enhancement of barrier-forming LTPs; modulation of ROS-related LTPs (e.g., NbLTPVAS analogs); exploration of relocalized LTP functions (e.g., Ha-AP10)	Transcriptomics, proteomics (especially secretome), lipidomics, structural biology (lipid-binding mechanisms)	Strengthened physical barriers (cuticle), enhanced systemic signaling, improved antimicrobial activity, better membrane-stress adaptation
WAK receptors	Gene editing (ligand/co-receptor affinity tuning, kinase activity modulation), MAS	Modulation of cell wall integrity (CWI) perception; identification and engineering of novel ligand/co-receptor interactions; enhancement of downstream signaling cascade	Genomics (WAK gene identification), transcriptomics, phosphoproteomics (kinase activity), protein-protein interaction (partner screening)	Improved cell wall damage detection, enhanced PTI, increased resistance to cell wall-degrading pathogens

Synthesis, outstanding questions, and future perspectives in plant non-specific immunity research

The analysis of the evolutionary features shaping immune mechanisms in monocotyledonous (exemplified by winter wheat) and dicotyledonous (exemplified by sunflower) plants has highlighted both conserved aspects and significant functional divergence of key protein families – ABC transporters, lipid transfer proteins (LTPs), and wall-associated kinases (WAKs). These components play central roles in non-specific resistance, providing protection against a broad spectrum of pathogens and enabling adaptation to abiotic stressors.

Winter wheat exhibits a strategy heavily reliant on systemic acquired resistance (SAR), particularly mediated by ABCG-type transporters such as Lr34. This strategy ensures long-lasting, quantitative defense, especially effective against biotrophic and hemibiotrophic pathogens, and is closely associated with hormonal signaling (SA, ABA) and the reinforcement of physical barriers. In contrast, sunflower predominantly deploys a localized acquired resistance (LAR), where rapid ROS signaling, activated via WAK receptors, plays a key role. This strategy is optimized for countering aggressive necrotrophic pathogens and rapidly adapting to abiotic stress.

The functional divergence of orthologous proteins is a striking example of evolutionary adaptation. WAK receptors in wheat are mainly involved in structural remodeling of the cell wall, while in sunflower they function as primary damage sensors and activators of local stress signaling pathways. LTPs contribute to barrier formation in wheat, whereas in sunflower, they are more involved in signaling processes and membrane stabilization. ABC transporters exhibit perhaps the greatest divergence: in wheat, they orchestrate SAR, while in sunflower, they act as local "sanitizers," ensuring detoxification and membrane protection. These differences correlate not only with pressures from different pathogen types but also with fundamental physiological and anatomical distinctions between monocots and dicots – particularly in cell wall and epidermal structures.

Despite considerable progress, several unresolved questions and promising avenues for future research remain:

1. Limited knowledge of WAK receptor activation: recent data challenge the role of WAKs as primary oligogalacturonide receptors in *Arabidopsis*, creating a significant gap in our understanding. A priority for future studies is the definitive identification of WAK ligands or specific cell wall features perceived by WAKs in both monocots and dicots. This may require novel biochemical approaches to identify interacting molecules and detailed structural biology analyses of WAK extracellular domains.

2. Complexity of signaling networks: the interplay among phosphatidic acid, ROS, MAP kinases, and other kinases like DGK5 in immunity regulation highlights the existence of complex signaling networks that are yet to be fully deciphered. How ABC transporters, LTPs, and WAKs integrate into these broader networks, and how they interact with hormonal pathways to fine-tune immune responses – especially under combined stresses – remains a key question. Sys-

tems biology approaches are needed to model these dynamic interactions (Velásquez et al., 2018).

3. Novel functions and dynamics of LTPs: the discovery of intracellular relocalization of LTPs, such as Ha-AP10 in sunflower, suggests potential non-canonical roles beyond the apoplast. Further studies are needed to determine whether other LTPs exhibit similar dynamic behavior and what their intracellular roles might be (Mistry et al., 2021).

4. Trade-offs and pleiotropy: many non-specific immunity genes, such as GhSTR1 in cotton, can impact both defense and plant growth/development. Understanding these trade-offs is critical for biotechnology. How can beneficial defense traits be enhanced while minimizing adverse effects on yield and other agronomically important traits? This calls for detailed functional analyses of individual members within the large ABC, LTP, and WAK gene families (Kang et al., 2011).

5. Evolution of gene families: comparative genomics of ABC transporters, LTPs, and WAKs across a wide range of monocots and dicots will continue to shed light on the pathways of their expansion and functional specialization. What specific selective pressures (pathogens, environmental conditions, anatomical features) have shaped the observed evolutionary patterns (Dangl et al., 2013)?

6. Complexity of systemic signaling: SAR involves a multitude of signals (MeSA, the DIR1-lipid complex, G3P, etc.) (Krattinger et al., 2009). How are these signals integrated, transported, and perceived systemically? What are the precise roles of ABC transporters and LTPs in orchestrating this complex systemic communication?

7. Harnessing natural variation: natural plant populations display significant variability in defense responses (Kohorn & Kohorn, 2012). The identification and characterization of non-specific immunity gene alleles that confer enhanced resistance is a promising direction for breeding programs.

8. Impact of climate change: how will the functions and interactions of these immune components change under multifactorial stress conditions triggered by future climate shifts? Understanding this is essential for developing adaptive strategies (Bazzalo et al., 2019).

Integrating knowledge of the molecular mechanisms underlying non-specific immunity into breeding programs, leveraging advanced biotechnological tools such as genome editing, and applying resistance inducers – including beneficial microorganisms – open the path to developing crop varieties with enhanced, durable, and broad-spectrum resistance (Camacho et al., 2009). This is of strategic importance for ensuring food security in the face of global challenges. Continued fundamental and applied research in the fields of phytopathology, microbiology, molecular biology, genetics, plant breeding, and agronomy will help unlock the full potential of plant non-specific immunity.

Conclusions

A comparative analysis of non-specific resistance in winter wheat (*Triticum aestivum*) and sunflower (*Helianthus annuus*) revealed that both crops utilize conserved protein families – ABC transporters, lipid transfer proteins (LTPs), and WAK receptors – for pathogen defense and stress adaptation. However, their functional implementation differs significantly, reflecting evolutionary adaptation.

Winter wheat exhibits a strategy of systemic acquired resistance (SAR), mediated by ABCG transporter genes (e.g., Lr34/Sr57, Lr46/Sr58), which provide long-term, broad-spectrum protection, particularly effective against biotrophic and hemibiotrophic pathogens. This strategy is associated with systemic signal transduction and reinforcement of physical barriers.

Sunflower predominantly implements a localized acquired resistance (LAR) response, where rapid ROS signaling plays a key role, activated via WAK receptors functioning as damage-associated molecular pattern (DAMP) sensors. This strategy is optimized to counteract necrotrophic pathogens and abiotic stresses.

A high degree of functional specialization was observed among orthologous proteins: in wheat, WAK receptors and LTPs are mainly involved in strengthening physical barriers (cell wall, cuticle), whereas in sunflower, WAK receptors act as primary DAMP sensors and local stress signal activators, and LTPs participate in signaling pathways and membrane stabilization. ABC transporters show the greatest divergence: in wheat, they are central to SAR; in sunflower – to local detoxification and membrane protection.

Differences in immune strategies closely correlate with physiological and anatomical characteristics (particularly cell wall and epidermis structure) and evolutionary adaptation to dominant pathogen types and environmental conditions typical of monocots and dicots.

These findings underscore the importance of in-depth study of non-specific resistance mechanisms and the necessity for a differentiated approach to using genes encoding ABC transporters, LTPs, and WAK receptors in breeding programs aimed at developing crop varieties with enhanced and durable resistance – a strategic priority in the context of global climate change and increasing pathogen pressure. Further research, especially considering emerging insights into the function of WAK receptors, is of critical importance.

The authors declare that they have no potential conflict of interest.

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