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Review

Microbial signature-triggered plant defense responses and early signaling mechanisms

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ABSTRACT

It has long been observed that microbial elicitors can trigger various cellular responses in plants. Microbial elicitors have recently been referred to as pathogen or microbe-associated molecular patterns (PAMPs or MAMPs) and remarkable progress has been made on research of their corresponding receptors, signaling mechanisms and critical involvement in disease resistance. Plants also generate endogenous signals due to the damage or wounds caused by microbes. These signals were originally called endogenous elicitors and subsequently renamed damage-associated molecular patterns (DAMPs) that serve as warning signals for infections. The cellular responses induced by PAMPs and DAMPs include medium alkalinization, ion fluxes across the membrane, reactive oxygen species (ROS) and ethylene production. They collectively contribute to plant pattern-triggered immunity (PTI) and play an important role in plant basal defense against a broad spectrum of microbial infections. In this review, we provide an update on multiple PTI responses and early signaling mechanisms and discuss its potential applications to improve crop disease resistance.

Contents

1. Introduction

In nature, plant resistance to microbial infections is the rule rather than the exception. Besides the preformed physical barriers, plants have evolved an innate immune system to recognize

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microbial invasion and launch effective defense responses to fend off pathogen attacks. As the first line of innate immune response, plant pattern-triggered immunity (PTI) was initiated upon perception of evolutionarily conserved microbial signatures, termed pathogen- or microbe-associated molecular patterns (PAMPs or MAMPs) [1,2]. PAMPs or MAMPs are often only present in the microbes and not the hosts. Endogenous damage-associated molecular patterns (DAMPs) are released from plants due to pathogen wounding or damage and serve as warning signals to trigger or amplify plant defense responses [3,4]. Perception of PAMPs/DAMPs is mediated through cell surface-resident pattern recognition receptors (PRRs), which are often encoded by receptor-like kinases (RLKs) or receptor-like proteins (RLPs) in plants [1,2]. Upon specific recognition of PAMP by the cognate PRR, the host elicits a series of cellular responses and physiological changes, such as a Ca^{2+} spike, extracellular alkalinization, membrane potential depolarization, ion effluxes, production of nitric oxide (NO), reactive oxygen species (ROS), and phosphatidic acid (PA), activation of an evolutionarily conserved MAP kinase (MPK) cascade, ethylene biosynthesis, callose deposition, and profound gene transcriptional reprogramming, which collectively results in plant resistance to pathogen attacks [1,2].

The signaling events that lead to these cellular and physiological responses in the plant have been a major focus of the studies in the plant–microbe interaction. Despite the detailed mechanisms that remain elusive; the framework underlying PAMP perception, signaling and responses is emerging. The understanding of PAMP-triggered plant basal resistance not only advances our general knowledge on the host immune signaling mechanisms but also holds significant promise to provide genetic resources and improve broad-spectrum and durable disease resistance in economically important crops. The yield loss caused by various diseases is one of the key challenges in crop production worldwide. In this review we summarize various physiological responses triggered by PAMPs/DAMPs and the recent advances in PTI signaling mechanisms.

2. Physiological responses triggered by PAMPs

As described in its original name, microbial elicitors, also called PAMPs, are the molecules from microbes capable of triggering plant defense responses [5]. The full repertoire of microbial elicitors remains unknown. Various PAMPs have been identified, such as the bacterial flagellin or its derived peptides flg22 and flgII-28, harpins, elongation factor Tu (EF-Tu) or its derived peptides elf18 and elf26, peptidoglycan (PGN), lipopolysaccharide (LPS), cold shock protein (CSP) and fungal chitin, Oomycete necrosis-inducing Phytophthora proteins (NPPs), cryptogein and elicitins [1]. Plant cell wall fragments or peptides derived from cleaved and degraded products, including oligogalacturonides (OG), prosystemin, hydroxyproline-rich systemins, proPeps and phytosulphokines, have been considered to be DAMPs [4,6]. Some PAMPs elicit responses in a wide range of plant species while others seem to be specific to certain plant species. Various distinct and overlapping physiological responses have been observed in diverse host systems depending upon the different PAMPs perceived. A series of typical cellular responses have been established to serve as useful bioassays to monitor plant defenses upon PAMP perception. Some responses are initiated rapidly upon pathogen infection or elicitor treatment (within minutes) whereas some occur relatively late (within hours to days) [1].

2.1. Increase of Ca^{2+} concentration

A rapid increase of plant cell cytosolic Ca^{2+} concentration $[Ca^{2+}]_{cyt}$ in response to various PAMPs has been observed and represents an essential and common early event in PTI responses [7,8]. Treatment of parsley cells with the *Phytophthora sojae*-derived oligopeptide elicitor, Pep-13, induced a rapid increase in $[Ca^{2+}]_{cyt}$ concentration within 4 min, which peaked at ~1 mM and subsequently declined to sustained values of 300 nM. Interestingly, sustained increasing concentrations of $[Ca^{2+}]_{cyt}$ but not the transiently induced $[Ca^{2+}]_{cyt}$ are required for Pep-13-mediated activation of defense-associated responses [7]. Flg22 treatment induced a strong and rapid increase of $[Ca^{2+}]_{cyt}$ starting after a 30–40 s lag phase and peaking after ~2–3 min, followed by a plateau phase of elevated $[Ca^{2+}]_{cyt}$, whereas PGN activated a much weaker and slower $[Ca^{2+}]_{cyt}$ increase [9]. Apparently, different PAMPs/DAMPs induce specific $[Ca^{2+}]_{cyt}$ elevations with flg22 having the highest $[Ca^{2+}]_{cyt}$ amplitude [8]. Nuclear Ca^{2+} concentration $[Ca^{2+}]_{nuc}$ is also elevated upon different PAMP treatments [10]. It appears that different PAMPs also induce specific spatial and temporal signatures of $[Ca^{2+}]_{nuc}$. Proteinaceous elicitors, including elicitins, flg22 and harpin, induced a pronounced and sustainable $[Ca^{2+}]_{nuc}$ elevation, whereas oligosaccharidic elicitors, such as the OG β-1,3-glucan laminarin induced little $[Ca^{2+}]_{nuc}$ elevation [10]. The significance of $[Ca^{2+}]_{nuc}$ rise and how it is perceived and transduced in plant defenses awaits to be elucidated in the future.

PAMP-induced cytosolic Ca^{2+} spike is most likely generated through two sources: the influx of extracellular Ca^{2+} and the release of Ca^{2+} from intracellular organelle stores, such as endoplasmic reticulum (ER) and vacuole [11]. Interestingly, the influx of extracellular Ca^{2+}, not intracellular Ca^{2+}, is essential for Pep-13-triggered immune responses as Pep-13-treated parsley cells maintained the normal defense responses in the presence of Ruthenium Red (RR) which inhibits Ca^{2+} release from intracellular compartments [7]. So far, the Ca^{2+} channels and how Ca^{2+} signals are sensed and transduced upon pathogen attacks or elicitor treatments still remain largely unknown. It has been suggested that cyclic nucleotide-gated channels (CNGCs) function in conducting Ca^{2+} to mediate plant immune responses [12,13]. There are three major types of Ca^{2+} sensors in plants, including calmodulin (CAM), calcineurin B-like proteins (CBLs) and calcium-dependent protein kinases (CDPKs) [14–16]. Recently, four *Arabidopsis* CDPKs (CDPK4, 5, 6 and 11) have been identified to play important roles, together with the MAPK cascades, in relaying primary flg22 and likely other PAMP signaling [17]. In addition to specific CDPKs, CAMs, CAM-like proteins (CMLs) and NO also mediate Ca^{2+} signaling and plant immune responses [12,13]. Future studies may identify other Ca^{2+} channels and elucidate the precise functions of Ca^{2+} sensors in mediating distinct and overlapping Ca^{2+} signatures triggered by different PAMPs.

2.2. Extracellular alkalinization, membrane potential depolarization and ion fluxes

All plant cells have the capacity to maintain an electrochemical proton gradient across the plasma membrane (PM), generated by the PM-resident H^+-ATPases, which pump H^+ from the cytosol to the extracellular space in an ATP-dependent fashion and maintain a negative membrane potential and a transmembrane pH gradient (acidic outside) [18]. The H^+ gradient plays an essential role in many physiological processes including ion uptake, solute transport, and cell wall growth [19]. Rapid and transient changes in extracellular or intracellular concentration of H^+, often accompanied by PM potential depolarization, have been observed during various biotic and abiotic stress responses [19]. Medium alkalinization due to altered ion fluxes across the plasma membrane, is one of the earliest responses observed in elicitor-treated plant cells. Bacterial flagellin and fungal chitin induce medium alkalinization of *Arabidopsis*, tomato, tobacco and potato cell cultures within minutes [20]. A similar pattern but slightly weaker amplitude than flagellin was

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