

Extracellular DNA as DAMPs in Plants: A Mini-Review

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ABSTRACT

Crustaceans, insects and plants do not have an adaptive immune system like higher vertebrates. Instead they use only their innate immune system for protection against infection and these pathways are activated in response to pattern recognition receptor (PRR) activation. The PPRs perception of host-derived endogenous molecules called DAMPs (Damage Associated Molecular Patterns) activates the 'damaged-self recognition' pathway, whereas exogenous molecules called HAMPs (Herbivore Associated Molecular Patterns), MAMPs (Microbe Associated Molecular Patterns) and PAMPs (Pathogen Associated Molecular Patterns) activate the 'non-self-recognition' pathway.

INTRODUCTION

Crustaceans, insects and plants do not have an adaptive immune system like higher vertebrates. Instead they use only their innate immune system for protection against infection and these pathways are activated in response to pattern recognition receptor (PRR) activation. The PPRs perception of host-derived endogenous molecules called DAMPs (Damage Associated Molecular Patterns) activates the 'damaged-self recognition' pathway, whereas exogenous molecules called HAMPs (Herbivore Associated Molecular Patterns), MAMPs (Microbe Associated Molecular Patterns) and PAMPs (Pathogen Associated Molecular Patterns) activate the 'non-self-recognition' pathway [1,2]. Recently DAMPs have been categorized as elicitors that have effect in the activation of the plant immune system. They have been proposed as "vaccines" that enhance plant resistance in an environmentally friendly way [3], as well as their use in other agricultural approaches [4]. This is the case of extracellular fragmented DNA (eDNA), recently considered as a type of DAMP in plants. The aim of this work is to review some molecules considered as DAMPs in plants focusing on eDNA and its effect in activation of different pathways related with the plant immune system.

DAMPs in plants

In plants a few number of molecules has been identified acting as a DAMP in comparison with metazoans. Gust et al. [2] proposed that molecular patterns passively released from injured plant tissue ('debris') should be termed primary endogenous danger signals or classical DAMPs. Molecularly defined signaling peptides, which are processed and released in response to damage, are analogous to immunomodulatory metazoan cytokines and are thus more appropriately called phytocytokines. Some of these molecules identified on

different plant species are cellobiose, cellodextrins, cutin, extracellular ATP, lectin-RK, eDNA, extracellular NAD (P), GLV (green leaf volatile)/VOC (volatile organic compound), High-mobility group protein B3 (HMGB3), methanol, oligogalacturonides.

Effects of extracellular DNA in plants

Experiments in laboratory conditions showed that the application of total DNA purified fragments on seeds of nine plants (*Acanthus mollis*, *Ampelodesmos mauritanicus*, *Arabidopsis thaliana*, *Hedera helix*, *Lepidium sativum*, *Medicago sativa*, *Pinus halepensis*, *Quercus ilex*, *Quercus pubescens*) have an inhibitory effect on their root growth [5]. This effect occurs in a conspecific and concentration-dependent manner. On one hand, a lower concentration of eDNA is required to cause an inhibitory effect when this is extracted from the same plant species (self-eDNA) that the target plant, increasing the effect with the increase of the concentration. On the other hand, the effect caused by eDNA extracted from different species (non-self-eDNA) is low compared with the self-DNA at a same concentration and in

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some cases the inhibitory effect is not shown [5]. Barbero et al. [6] demonstrated in their experiments that plants of *Phaseolus lunatus* and *Zea mays* also respond to fragmented extracellular DNA (300-700 bp) but not to integrate DNA in a conspecific manner confirming the results obtained by Mazzoleni et al. [5]. Additionally, they observed that this response induces a plasma membrane potential depolarization and calcium signaling in the leaves. In both plant species, self-eDNA prompted a sustained calcium elevation. Duran-Flores and Heil [7] elaborated a series of experiments that suggest that eDNA has activity as a DAMP, they observed that fragments of self-DNA triggers various immunity-related responses in bean plants and the effects of self-versus non self-eDNA were conspecifics.

The results of the experiments showed the formation of ROS and the activation of MAPKs, the reduction of a bacterial infection and an effect in the extra floral nectar production caused by the self-eDNA in *Phaseolus vulgaris*. More recently, a study to elucidate the role of eDNA as a DAMP analyzing the changes in CpG DNA methylation and defense-related responses was performed by Vega-Munoz et al. [8]. The use of lettuce (*Lactuca sativa*) as a target plant and *Capsicum chinense* and *Acaciella angustissima* as source of non-self-DNA. In this study, the effect of self-eDNA caused also an inhibition of growth and germination in lettuce. The plants *L. sativa* and *C. chinense* belong to the Asterids clade but to different orders (Asterales and Solanales, respectively), whereas *A. angustissima* belongs to the clade Rosids I and the order Fabales. Thus *C. chinense* is closer phylogenetically to *L. sativa* than *A. angustissima*, and this situation might explain the similar effects of self-eDNA and nsDNA from *C. chinense* on the lettuce plants evaluated and the significant CpG DNA hypomethylation at similar eDNA concentrations in their study. This latter result is the first experimental demonstration that phylogenetic closeness is an important feature for plant responses to DAMPs along an epigenetic pathway. With these results they suggests that if the epigenetic pathway is a possible mechanism in DAMP signaling, high doses of self-eDNA, at least in lettuce, induces a switch (on-off) in several epigenetic mechanisms, unlike to CpG DNA methylation (i.e., methylation in CHH and CHG, or changes in the methylation and acetylation of histones); although it might be also possible that the induction of genetic mechanisms to control gene expression under these stress conditions.

Vega-Munoz et al. [8] also mentioned that probably, the DNA excreted by plants and further metabolized to sequences 50-2000 bp long have a very specific signature for each species to be recognized as self-DNA by the plant. Through DNA restriction-modification, bacteria distinguish the same from the strange through DNA methylation. The same effect is observed for TLR9, which specifically recognizes unmethylated CpGs [9]; in plants, specific responses depend on DNA fragmentation [9]. Thus, DNA methylation patterns could be one possible mechanism for

self-eDNA recognition in plants, although more research should be undertaken on this topic. This discovery opens new opportunities for exploiting the best characteristics of self-eDNA in the agricultural, horticultural and pharmacological industries, as highly species-specific inhibitory products, limiting effects on other species, as suggested elsewhere [4].

Agricultural approaches

A concept that has received increasing interest over the last years is the vaccination of plants, using natural or synthetic molecules that act as resistance elicitors: they stimulate the plant's own immune system. The responses that are elicited by individual DAMPs range from early signaling cascades (e.g. Ca²⁺ influxes, H₂O₂ formation and MAPK activation) to phenotypic resistance responses [2]. The biotechnological exploitation of eDNA as a selective pesticide may be an option to reduce the use of chemicals in agriculture due to the selective phytotoxic effect observed in different plant models as well as a product that stimulate the plant immune system.

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