



Plant elicitor peptides in induced defense against insects

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Over 20 years ago the peptide systemin was discovered to be an integral regulator of anti-herbivore defense responses in Solanaceous plants. However, other peptides of similar function have remained elusive. Plant Elicitor Peptides (Peps) were initially discovered in Arabidopsis as mediators of basal immune responses protective against invading pathogens. Recently a Pep from maize, ZmPep3, was demonstrated to be a potent regulator of anti-herbivore defenses. ZmPep3 was as active as the Lepidopteran elicitor N-linolenoyl-L-glutamine (Gln-18:3) in stimulating volatile emission and accumulation of defense transcripts and metabolites, resulting in both attraction of the parasitoid *Cotesia marginiventris* and suppressed growth of *Spodoptera exigua* larvae. Orthologues of Peps in Solanaceous and Fabaceous plants also trigger emission of herbivore-associated volatiles, indicating that Peps have a conserved role as regulators of plant defense against herbivores in diverse species. This conservation of a peptide signal and cognate receptor for activation of plant defense responses reveals a widespread regulatory motif and provides opportunities for manipulation of plant resistance.

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Introduction

To minimize damage by herbivores, plants respond to attack with extensive transcriptional and metabolic reprogramming. Plants accumulate defense proteins that primarily act to sequester or prevent assimilation of essential nutrients, including proteinase inhibitors, threonine deaminase, arginase and polyphenol oxidase, which limit amino acid acquisition [1–4]. These are complemented by a diversity of small molecules that are toxic or feeding deterrents, such as Brassicaceous glucosinolates, Poaceous benzoxazinoids, Solanaceous alkaloids or phytoecdysteroids

found in a number of plant species [3–6]. In addition to molecules that act directly on attackers, plants also produce volatile chemicals that attract natural enemy predators and parasitoids of herbivorous pests [7,8]. Many of these induced defenses are protective against pathogens as well as herbivores and likely have signaling roles as well [9,10]. To mount this complex protective response, plants recognize herbivores through both damage and herbivore-associated molecular patterns (HAMPs) and must subsequently initiate and coordinate defensive reprogramming, both at the site of attack and in systemic tissues [11–13].

Systemin

The study of systemically-induced plant defense against herbivores was initiated by the discovery that proteinase inhibitors accumulate in both damaged and undamaged leaves of Solanaceous plants after wounding or attack by Colorado potato beetle larvae [1]. This observation raised the question of which plant molecules act systemically as Proteinase Inhibitor-Inducing Factors (PIIFs). Cell wall oligogalacturonic acid fragments (OGAs) were initially implicated as PIIFs, but subsequently shown to be contributors to local rather than systemic responses [14]. The continued search for PIIFs uncovered systemin, an 18 amino acid peptide derived from the carboxyl terminus of prosystemin, a 200 amino acid precursor protein [15,16]. Systemin had potent PIIF activity, inducing PI accumulation when applied at femtomolar concentrations, and antisense-mediated silencing of the prosystemin gene resulted in severely diminished herbivore resistance. Moreover, radiolabeled systemin applied to wound sites was phloem-mobile, implying that systemin was the sought-after systemic signal [17].

The contributions of the octadecanoid pathway to plant defense signaling also were discovered in the context of the tomato anti-herbivore response. Jasmonic acid (JA) was found to promote PI accumulation in tomato and to be required for systemin-induced defenses [18]. A series of elegant grafting experiments using 35S::Prosystemin rootstock demonstrated that JA perception was required in aerial tissues, but not JA biosynthesis [19]. These results established that JA, or some derivative thereof, is the mobile signal, not systemin [20]. While no longer considered the mobile signal, systemin is critical to tomato systemic anti-herbivore defense. The peptide acts in an amplification loop with JA; application of JA increases abundance of prosystemin protein and in turn, systemin treatment promotes JA biosynthesis [21]. The localization

of prosystemin to phloem parenchyma cells indicates that the peptide is suitably located for release to the proximal phloem companion cells, where JA is preferentially biosynthesized and readily translocatable [20,22,23]. Systemin also coordinates synthesis of many other immunoregulatory signals including ethylene (ET), OGAs, hydrogen peroxide, cytosolic calcium ion influx and plasma membrane depolarization [24]. While the identity of the systemin receptor remains a mystery, upon perception the peptide triggers MAP kinase signaling, activation of phospholipase activity and calmodulin, while deactivating a proton-pumping ATPase in the plasma membrane [24,25]. Together this results in transcriptional and metabolic reprogramming.

As signal transduction mechanisms regulating anti-herbivore defense responses became more widely studied in a diversity of species, a high degree of conservation was observed. JA is critical for defense in every species examined, as is calcium signaling, plasma membrane depolarization, reactive oxygen species production and kinase cascades [26–29]. Simultaneously, other diverse signal amplification components have come to light. Numerous receptors have been identified as contributing to immune activation upon damage, including glutamate receptor-like proteins required for rapid electrical signal propagation and JA biosynthesis, a Wall Associated Kinase (WAK) responsible for OGA perception and the lectin receptor kinase DORN1 which binds extracellular ATP [30,31,32].

However, the involvement of a peptide mediator such as systemin was not readily identifiable across plant species. Prior to the discovery of systemin, plants were thought to utilize only small molecules as signals, not peptides. Since that time a plethora of endogenous bioactive peptides have been characterized in plants and regulate many developmental processes [33]. Still, systemin was an outlier as a mediator of anti-herbivore defense: it is only active in the Solanoideae subfamily of Solanaceous plants and no orthologues are readily identifiable by sequence homology in unrelated species [34]. Similar peptides in other plants were thought to be either nonexistent or to have such divergent amino acid sequences that they were rendered unrecognizable.

The search for other peptide mediators of plant anti-herbivore defense

Because sequence homology did not reveal systemins in other plants, similar peptides were sought through bioassay-driven purification. Like microbe-associated molecular pattern (MAMP) elicitors such as flg22 and elf18, systemin causes a marked alkalinization of suspension-cultured cell medium within minutes of application — a result of the transient deactivation of a plasma membrane proton-pumping ATPase as part of the initial signaling cascade [35–38]. This response was used to guide isolation

of the hydroxyproline-rich systemins (HypSys) from non-Solanoideae plants such as tobacco, and excitingly, *Ipomoea batatas*, a Convulvoalaceous plant [39–41]. HypSys peptides contain polyproline motifs like systemin, but because the proHypSys precursor passes through the secretory pathway en route to the apoplast rather than being retained in the cytosol like prosystemin, HypSys prolines are hydroxylated and subsequently glycosylated [39]. In some species HypSys stimulate expression of pathogen defense genes, whereas in others they induce proteinase inhibitor accumulation [41]. They act in tomato to coordinate anti-herbivore defenses with systemin [41]. However, with the exception of *I. batatas*, HypSys have yet to be discovered in other non-Solanaceous species.

The alkalinization response also led to purification of other bioactive peptides, but none were immediately demonstrated to activate anti-herbivore defenses. One family, the Rapid Alkalinization Factors (RALFs), regulates cell expansion associated with developmental processes [42,43]. Several other peptides were found to trigger pathogen defense responses. GmSubPep and GmPep914 and 890 were isolated from soybean and promote expression of genes encoding chitinases and glyceollin biosynthetic enzymes [44,45]. Orthologues for all of these peptides are apparent only in the Fabaceae and closely-related Cucurbitaceae [44,45]. In contrast, the Plant Elicitor Peptides (Peps) isolated from Arabidopsis are family-specific in their ability to induce defense responses, but have readily identifiable sequence orthologues throughout Angiosperm plants [46].

Plant elicitor peptides

Arabidopsis thaliana Pep1 (AtPep1) was the first endogenous peptide signal found to regulate plant anti-microbial defenses and is one of an eight member gene family encoding related peptides (AtPEP2-8) [46–48]. Each is derived from the carboxyl terminus of AtPROPEP precursor proteins, and each interacts with one or both of two LRR-RLKs, AtPEPR1 and AtPEPR2, to initiate signal transduction [48,49]. AtPROPEP1 is expressed in response to application of JA, ET or MAMPs such as flg22 or chitin [46,47]. As might be expected given this transcriptional pattern, AtPep1 does not trigger expression of Vegetative Storage Protein 2 (VSP2) or other genes associated with the canonical Arabidopsis wound/herbivory response pathway mediated by JA activation of the MYC2 transcription factor [46]. However, the peptide does activate marker genes regulated by JA in conjunction with ET, including the defensin PDF1.2 as well as a number of other pathogenesis related (PR) genes [46]. Plants constitutively expressing AtPROPEP1 have enhanced resistance to root necrosis by the oomycete, *Pythium irregulare*, and AtPep signaling through AtPEPRs is required for both local and systemic immunity to *Pseudomonas syringae* pv. *tomato* DC3000 (Pst DC3000) [46,49,50].

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