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Review

Plant peptides in defense and signaling

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ABSTRACT

This review focuses on plant peptides involved in defense against pathogen infection and those involved in the regulation of growth and development. Defense peptides, defensins, cyclotides and anti-microbial peptides are compared and contrasted. Signaling peptides are classified according to their major sites of activity. Finally, a network approach to creating an interactomic peptide map is described.

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1. Introduction

Peptides are short chains of amino acids joined together via either eupeptide or isopeptide bonds (www.chem.qmul.ac.uk/iupac/AminoAcid). They are distinguished from proteins purely on the basis of the number of residues present, conventionally understood to be less than 50, while those shorter than 20 residues tend to be labeled as oligopeptides. A recent attempt to standardize nomenclature has suggested that molecules smaller than 10 kDa should be referred to as ribosomally synthesized and post-translationally modified peptides [7]. While plant peptides are important across the whole of cell biology, they also have a narrower, practical relevance in the context of crop improvement, the production of novel foods and the delivery of pharmaceutical products [166]. The contribution of small proteins and peptides to the functioning of the plant cell is becoming clearer, as reviewed by Farrokhi et al. [55] and Butenko et al. [20] inter alia. The term "peptidomics", coined by Clynen et al. [36], has since been trademarked by Digilab BioVisioN GmbH (Hannover, Germany). Peptidomics fills the low molecular weight gap left by the failure of conventional two dimensional gel electrophoresis to resolve species smaller than 10 kDa. The technical platforms used for peptide separation are based on liquid chromatography, followed by identification using tandem mass spectrometry. Note that proteomics differs from peptidomics not just on the basis of target molecular weight, but also because peptidomic analysis does not involve any preparatory

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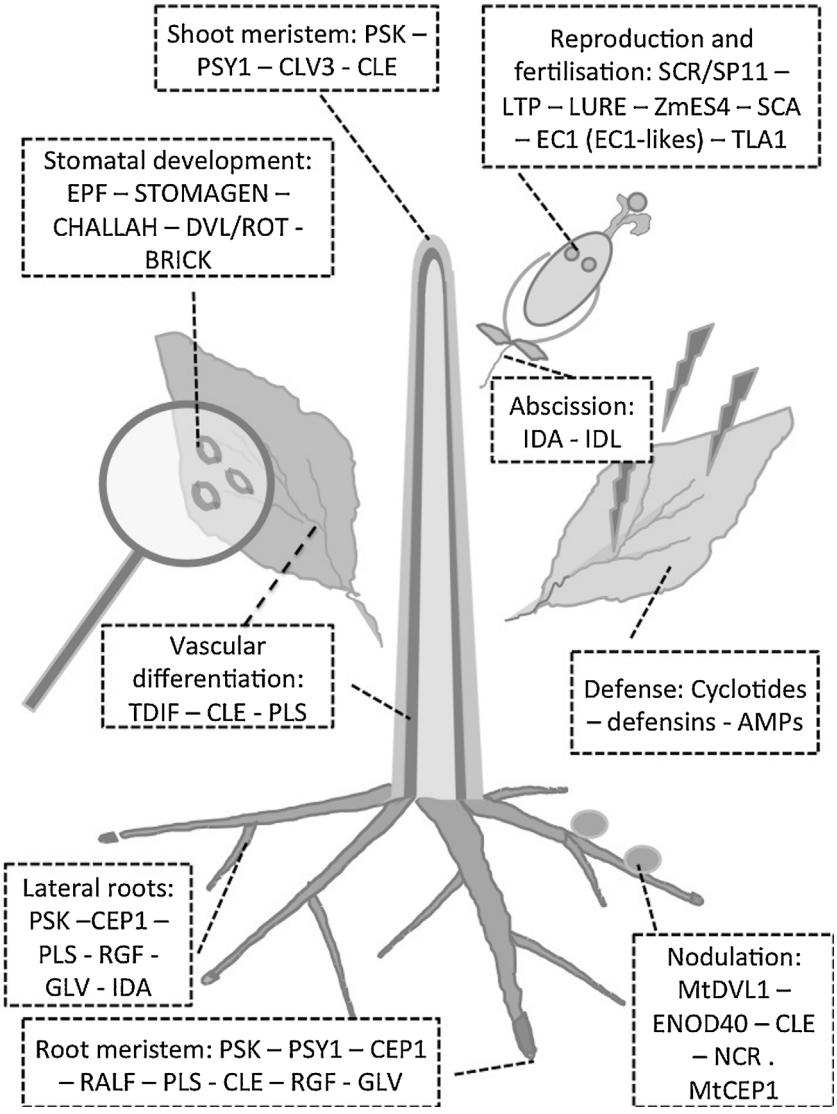

Fig. 1. Sites of action of the major known plant peptides. Abbreviations explained in the text.

chemical or enzymatic digestion – searches are based on the native molecule. Most peptides are thought to be produced via the proteolysis of precursor proteins, through the action of specific peptidases [55]. In plants, many peptides are generated as part of the process of protein turnover and degradation, and the biological role, if any, of many of these remains unclear. A small number of peptides is produced by non-ribosomal enzymatic synthesis, for instance, glutathione and the phytochelatins (PCs) (see below). Some peptides are actively secreted, and thus form part of the secretome [87]. A general scheme of the sites of action of the peptides described in this review is given as Fig. 1.

2. Methodological aspects

Few plant peptide sequences are recorded in protein databases, and those which are represented are mostly poorly (if at all) annotated, because their open reading frame is so short. A recent review illustrates the possible approaches for identifying short open reading frames in genomes [6]. Lease and Walker [91] were nevertheless able to describe more than 1000 open reading frames which potentially encoded functional peptides; these authors considered peptides all those of length ranging between 25 and 200 residues. More recently, the exploration of various legume genomes has led to the identification of several thousand short open reading frames, potentially encoding peptides shorter than 120 residues [71]. Bioactive peptides have also been found to be encoded in pseudogenes and introns [45]. Two major approaches have been taken to assign function to plant peptides:

- The *bottom-up approach* which searches for loss-of-function mutations and attempts to relate these to phenotype; this fails either where there is functional redundancy and/or where multigene families are involved. A characteristic example of this approach was the identification of CLAVATA3 [119].
- The *top-down approach* which relies either on the addition of a known peptide to a growth media, or seeks to generate transgenic plants which express a gain-of-function phenotype due to the over-expression or ectopic expression of a known gene. A relevant example relates to the CLE peptides described by Whitford et al. [183].

The conventional bioinformatics approach has contributed to the understanding of the structure of mature peptides or their post-translationally modified forms, complemented by the analysis of peptides via mass spectrometry, either on its own or in hyphenated techniques (see for instance [126]). Recent technical