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Role of the proteome in phytohormonal signaling☆

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ABSTRACT

Phytohormones are orchestrators of plant growth and development. A lot of time and effort has been invested in attempting to comprehend their complex signaling pathways but despite success in elucidating some key components, molecular mechanisms in the transduction pathways are far from being resolved. The last decade has seen a boom in the analysis of phytohormone-responsive proteins. Abscisic acid, auxin, brassinosteroids, cytokinin, ethylene, gibberellins, nitric oxide, oxylipins, strigolactones, salicylic acid — all have been analyzed to various degrees. For this review, we collected data from proteome-wide analyses resulting in a list of over 2000 annotated proteins from *Arabidopsis* proteomics and nearly 500 manually filtered protein families merged from all the data available from different species. We present the currently accepted model of phytohormone signaling, highlight the contributions made by proteomic-based research and describe the key nodes in phytohormone signaling networks, as revealed by proteome analysis. These include ubiquitination and proteasome mediated degradation, calcium ion signaling, redox homeostasis, and phosphoproteome dynamics. Finally, we discuss potential pitfalls and future perspectives in the field. This article is part of a Special Issue entitled: Plant Proteomics — a bridge between fundamental processes and crop production, edited by Dr. Hans-Peter Mock.

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1. Introduction

The phytohormones are small-molecule regulators that collectively regulate all aspects of the life of a plant cell. Growth and development, integration of environmental cues including biotic and abiotic stressors, regulation of circadian clock output, seed formation, and senescence — these are just few examples from a long list of important functions. Phytohormones have been intensively studied, but the signaling mechanisms underlying their complex modes of action are a long way from being resolved. In this review we summarize recent advances in the characterization of phytohormone signaling pathways, with a focus on phytohormone-responsive proteome analyses.

1.1. Signaling mechanisms

In general, any signaling cascade comprises the perception, transduction and response processes. The fastest responses, which are mediated via allosteric control, occur within milliseconds (Fig. 1). This reversible binding of small signal molecules is an important means by which the activity of many proteins is controlled. For example, a metabolic pathway product can bind to a key enzyme and inhibit its activity by inducing conformational changes that are transmitted to the enzyme's active site. A calcium ion flux can act as a regulator in this way, as can a number of other small molecules. In fact, over fifty ions and over 70,000 organic compounds have been annotated as being allosteric modulators (AlloSteric Database, [1]). The second level of regulation is governed by post-translational modifications (PTMs). The time required for PTM regulation to take place is typically minutes, and these forms of regulations are highly complex and far from being fully understood. We have previously reviewed in detail the more important PTMs and the methods of choice for isolation of modified proteins [2]; the most common PTMs in plant hormonal signaling are phosphorylation, ubiquitination and redox modifications and these will be addressed in the relevant parts of this review. The final level of regulation is that mediated by gene expression and the transcription-translation machinery. Though it is the slowest process, with an effective time span of hours, it is the best understood component of plant hormone signaling, and most of the current signaling pathway models described below are based predominantly on transcriptional analyses and studies of candidate gene mutants.

2. Phytohormone-responsive proteome

For this review, we have collected data from over one hundred proteome analyses conducted in the last fifteen years (i.e. since the year 2000), and nearly 6000 protein entries from diverse plant species are

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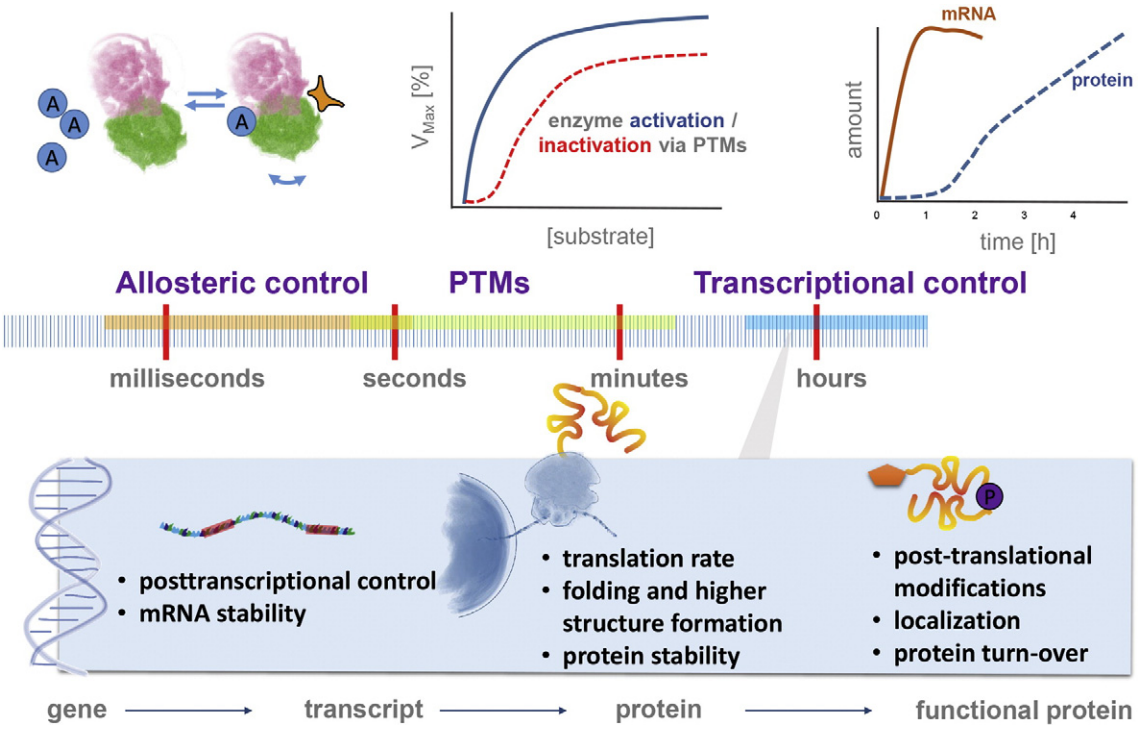

Fig. 1. Signaling mechanisms. Based on [3,4].

listed in the supplementary material. Where available, the *Arabidopsis* gene identifier was used. In total, there are 2157 reported *Arabidopsis* phytohormone-responsive proteins which represent a wide range of functions and cover all major metabolic pathways, with nearly four hundred unique enzymes (on the basis of EC numbers) (Fig. S1). The stress-related hormones abscisic acid, jasmonic acid and salicylic acid have been the most intensively studied substances, together representing more than 50% of all experiments (Table 1), and this is reflected in the number of *Arabidopsis* proteins annotated as being responsive to specific phytohormones: abscisic acid (955), cytokinin (690), brassinosteroids (375), jasmonic acid/oxylipins (336), auxin (137), salicylic acid (100), strigolactone (38), ethylene (13). The average overlap between the different phytohormone treatments among the identified *Arabidopsis* proteins is relatively high (13%), ranging up to 29% (jasmonates/abscisic acid). The shared biological processes include carbohydrate metabolism and photosynthesis, energy metabolism, response to stress and redox processes, and amino acid and protein metabolism (Fig. 2A). To provide an interspecies overview and utilize the whole dataset, we manually filtered the data and combined individual protein entries into protein families. The resulting list contains 70 protein families, each of which was found at least once in response to more than four different phytohormones (Fig. 2B, Supplementary tables). As well as the similarities identified from *Arabidopsis* annotations, this list highlights the common roles of cytoskeletal components (tubulin, actin), protein phosphorylation (kinases, phosphatases), membrane transport (ABC transporters), and the proteasome (26S regulatory subunit). The whole set is available from the Supplementary material.

Although the majority of the analyses employed a gel-based proteomics approach (Table 1), nearly half of the reported phytohormone-responsive entries were identified *via* a gel-free shotgun LC–MS protocol. 2-DE is still the method of choice for the analysis of PTMs, especially in redox proteomics, but the increased availability of state-of-the-art mass spectrometry is shifting the field towards peptide-based analyses. The efficiency of the LC–MS platform seemingly outperforms that of 2-DE separation, but its sensitivity is still compromised by loss

Table 1
Phytohormone proteomics overview. Numbers indicate the number of proteome-wide analyses that have been published since the year 2000; two-dimensional gel electrophoresis, 2-DE; liquid chromatography–mass spectrometry, LC–MS; two-dimensional liquid chromatography, 2D-LC.

Stimulus	Response			Method			
	Early 0–30 min	Delayed 1–8 h	Long-term >12 h	2-DE	LC–MS	2D-LC	PTM analysis
Abscisic acid (ABA)	4	12	18	20	13	1	8
Auxin (AUX)	0	4	5	6	3	0	2
Brassinosteroids (BR)	0	3	6	6	1	1	1
Cytokinin (CK)	3	2	9	11	3	0	3
Ethylene	0	1	3	3	1	0	1
Gibberellins (GA)	0	1	11	10	1	1	1
Nitric oxide, protein nitration (NO)	0	2	3	4	1	0	2
Oxylipins (jasmonates) (OL, JA)	0	5	14	15	2	0	3
Polyamines (PA)	0	0	1	1	0	0	1
Salicylic acid (SA)	0	2	14	14	1	0	0
Strigolactone (SL)	0	0	2	1	1	0	1

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