doi: 10.13241/j.cnki.pmb.2014.30.053

生物逆境和共生状态下植物的蛋白质组学研究 *

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摘要：蛋白质组技术已广泛应用于植物遗传、发育和生理生态等诸多生物学领域，主要研究植物的遗传多样性、植物发育、组织分化、植物对非生物逆境(包括高温、低温、高盐和干旱等)和生物逆境(病虫害)的适应机制和植物与微生物(根瘤共生体)相互作用机制。本文综述了微生物与植物互作的蛋白质组研究进展，包括有害和有益的相互作用，同时对植物蛋白质组学的发展前景进行了讨论。

关键词：蛋白质组；植物蛋白；发育相关蛋白组；生物逆境；共生体

中图分类号：Q943.2；Q946 **文献标识码：**A **文章编号：**1673-6273(2014)30-5995-06

The Study of Vegetable Proteome Under Biotic Stress and Symbionic State*

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ABSTRACT: Proteome techniques have been widely applied to the fields of plant genetics, plant development, plant physiology and ecology to investigate plant genetic diversity, plant development, differentiation of plant tissue, mechanisms of plant adapted to abiotic or biotic stresses including high temperature, low temperature, high salt, drought, and plant pathogens and pests, and interaction of plant with microbe. In the paper, proteome progression on the interaction of plant with microbe are summarized and the prospects of plant proteomics are discussed.

Key words: Proteome; Vegetable proteome; Development proteome; Biotic stress; Symbiont

Chinese Library Classification(CLC): Q943.2; Q946 Document code: A

Article ID: 1673-6273(2014)30-5995-06

相对于对动物和微生物蛋白质组的研究，植物蛋白质组的研究较为滞后，主要是由于植物细胞中蛋白质相对较少，且植物中存在的粘液质等影响了植物总蛋白的分离，进而影响了蛋白质组的研究。目前，植物蛋白质组学研究主要集中于少数测序的植物如水稻、拟南芥。虽然一些未测序的植物种如玉米、苜蓿、大麦、小麦等也有相关蛋白组的研究，但是大部分蛋白未能得到有效鉴定。除对植物总蛋白的蛋白质组研究之外，植物亚细胞(或细胞器)蛋白质组的研究也日益增多，通过对叶绿体、线粒体等细胞器在植物不同生长发育时期、逆境响应、激素应答、植物与微生物互作等过程差异蛋白质的分析与鉴定，不仅有利于确定差异蛋白质的功能及亚细胞定位，而且可以进一步明确这些细胞器在上述过程中的重要作用。目前拟南芥、水稻等模式植物的蛋白质组数据库以及一些亚细胞蛋白质组数据库已建立，为进一步研究植物与微生物相互作用、揭示诸如微生物作用方式、防御系统的平衡、营养交换方式及植物的发育改变等提供了新的研究方法和新的视角。本文综述了针对病原菌与植物相互作用、共生体研究方面的最新研究进展，相信随着蛋白质组技术的发展，植物与微生物相互作用机理会越来越为人们所了解。

1 病害应激相关蛋白质组研究

病害发生时植物会出现局部坏死等表观症状，在出现症状前植物的防御系统已诱导产生了一些抗逆物质，包括一些信号分子、激素、化学物质和蛋白质等。为考察病害诱导产生的植物抗逆蛋白，Rep M 等 [1] 研究了感染维管束萎蔫真菌(Fusarium oxysporum)的番茄木质部液的蛋白含量变化，出现 5 条受菌诱导的蛋白带，其中之一为 PR-5 家族新成员，主要在互作早期积累。Colditz F 等用比较蛋白质组学方法鉴定在卵菌病原 Aphanomyces euteiches 感染苜蓿属 Medicago truncatula 后 6 小时到 21 天中差异表达的诱导蛋白，有多个 PR-10 蛋白、一个查耳酮 -O- 甲基转移酶同工型、一个脯氨酸丰富蛋白、一个甘氨酸丰富蛋白、一个热激蛋白被证实与病原诱导相关[2]，经进一步研究，Colditz F 等发现 PR-10 蛋白的表达水平与病原菌感染 M. truncatula 水平之间与植物的抗性水平呈现出一定的相关性[3]，并且发现，早期的菌根真菌感染可以保护植物免受其它病原菌的进一步感染，这一过程可诱导一些苯丙醇途径相关蛋白和水解蛋白酶的表达，这些均与植物抗病性相关。随后的 RNAi 研究证实特定的 PR-10 基因的沉默可增加植物对 A. euteiches 的

* 基金项目：武警后勤学院青年基金项目(WYQ201106)

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(收稿日期：2013-12-04 接受日期：2013-12-26)

抗性，而病原可诱导根中不同种类 PR 蛋白的表达[4]。

植物抵抗病原真菌的机制有多种，其中一种是根冠生长点的细胞分泌蛋白，有研究确定了大约 100 种根冠细胞分泌蛋白与病原真菌 Nectria haematococca 感染后的植物的抗性增加相关[5]，这些蛋白包括 14-3-3 蛋白、钙调蛋白、抗病应答蛋白、脂氧合酶、呼吸作用相关酶、代谢酶以及核糖体蛋白等。同时，真菌在感染植物时也分泌其自身蛋白，包括可消化植物细胞壁的水解酶及信号蛋白等[6]，在根表面这些分泌蛋白是如何作用的是个很有趣的问题。有关根与病原菌相互作用的蛋白质组研究结果总结于表 1。

2 植物与微生物共生体的蛋白组研究

表 1 根 - 病原体相互作用的蛋白质组研究

Table1 The study of the proteome on the interaction of root- pathogen vegetable

种类(Genus)	研究目标(Objective)	发现(Found)	方法(Method)
宿主研究(Study on host)			
Arabidopsis thaliana (Arabidopsis thaliana)	Proteomic research of roots infected by Plasmodiophora brassicae	Differentially expressed protein was found, 46 of which was defined	2DE, MALDI-TOF
Brassica napus (Arabidopsis thaliana)	Proteomic research of roots infected by Plasmodiophora brassicae	Differentially expressed protein was found, 20 of which was defined	2DE, LC/MS/MS
Medicago truncatula (Medicago)	Proteomic research of roots infected by Aphanomyces euteiches	Differentially expressed protein was found, 12 of which was defined2DE,	MALDI-TOF
M. truncatula	Proteomic research of infection on A. euteiches by sensitive and resistant varieties M. truncatula and mycorhizaunder the action of abscisic acid	Differentially expressed protein was found, 20 of which was defined	2DE, MALDI-TOF
M. truncatula	Proteomic research of roots infected by A. euteiches and the changes on PR10	Differentially expressed protein was found, 7 of which was defined	2DE, MALDI-TOF
Pisum sativum (pea)	Proteomic research of Root cell wall body secretion infected by Nectria haemotacocca	100 Extracellular protein were found	MudPIT
P. sativum	Proteomic research of roots infected by Orobranche crenata	Differentially expressed protein was found, 7 of which was defined	2DE, MALDI-TOF
病原体研究(Study on pathogen)			
Heterodera schachtii	Pharyngeal gland secretory protein	4 Nematode secreted protein were found	2DE, LCQ-MS/MS
Meloidogyne incognita	To find sting secretory protein	7 sting secretory protein were found	2DE, internal micro- sequencing
Phytophthora sojae and P. ramorum	Proteome of protein in Infection and vegetative period	3897 P. ramorumprotein and 2970 P.sojae protein were found	MudPIT

2DE - 2-Dimensional gel Electrophoresis;
LC-MS/MS - Liquid Chromatography/tandem mass spectrometry;
LCQ-MS/MS - Liquid Chromatography Quadrupole/ tandem mass spectrometry;
MALDI-TOF - Matrix-Assisted Laser Desorption/Ionization Time Of Flight mass spectrometry;
MudPIT - Multidimensional Protein Identification Technology.

多种微生物与植物形成共生关系，它们能协助植物吸收营养、增强抗性、促进植物生长，同时植物也为它们的生长提供养分和生长空间，它们与植物的关系是相互利用、相互制约、取长补短、协调生长。

2.1 豆科植物与根瘤菌的相互作用

研究根与微生物相互作用的最好材料之一就是根瘤菌，植物释放出特有的黄酮类物质进入土壤，根瘤菌通过一种蛋白与黄酮类物质结合而识别其宿主，进而诱导一系列结瘤基因的表达。在对 S. meliloti 与其宿主 Rhizobium leguminosarum 的蛋白质组分析中证实在感应到黄酮信号后，许多细菌蛋白发生了改变[7]。

来自于根瘤菌的信号同样会影响植物的蛋白质组，在 M. truncatula 的根瘤形成过程中，第一周时有 25 个蛋白发生了改变，在随后的二至五周内有 31 个蛋白改变，其中有豆根瘤蛋白和一个烯醇化酶同工型以及一些细菌来源的蛋白[8]。Wan 等研究了感染 B. japonicum 后 18 小时内大豆根中蛋白质的变化[9]，根瘤菌诱导产生 17 个蛋白，其中 11 个必须由根瘤菌合成的根瘤因子诱导产生，这些蛋白包括脂氧合酶、磷脂酶 D、维生素 C

过氧化物酶、葡萄糖磷酸变位酶、一个凝聚素、一个肌动蛋白同工型、一个囊胞融合蛋白，说明在根瘤菌对根的附着、识别和感染过程中，凝聚素和磷脂信号可能分别发挥着重要的作用。

在 M. truncatula 感染 S. meliloti 后 24 小时内，约 3700 个总蛋白中有 174 个差异蛋白，包括大量与能量、糖、氨基酸和黄酮代谢相关的酶，这些酶正是植物为适应根瘤形成而调节代谢的反映[10]；这些蛋白还包括 15 个 PR-10 病原相关蛋白，表明在感染早期，植物的机体防御功能发挥了作用[11]。PR-10 蛋白能结合多种配基，如脂肪酸、黄酮、甾族化合物、细胞激肽等，这种结合可修饰植物激素，从而调节植物的生理机能。

在对共生体的膜蛋白研究中，Panter 等确定了 8 种来源于大豆的蛋白，包括热激蛋白、蛋白酶和 2 个已知的结瘤素[12]。Saalbach G 等[13]用双向电泳鉴定了来自豌豆根瘤共生体的类菌体周膜（peribacteroid membrane, PMB）和类菌体周隙（peribacteroid space, PS）组分中的 46 个蛋白，大部分为内膜蛋白，说明宿主细胞的内膜系统在 PMB 形成中具有一定的作用。Wienkoop S[14]用蛋白质组技术分析豆科模式植物日本百脉根与根瘤共生体的 PMB 蛋白组，通过串联质谱分析鉴定了大约 94 个蛋白质，大多为转运体和膜蛋白，如糖和硫酸盐转运体、内膜有关蛋白（如 GTP 结合蛋白和囊泡受体）、参与信号转导蛋白（如受体激酶、钙调素、14-3-3 蛋白、病原体应答蛋白）。Natera S H 等[15]在中华根瘤菌与豆科植物白花根木樨（Melilotus alba）形成的根瘤蛋白的差异表达研究中发现，与未感染的根组织相比，在根瘤中有 250 多个差异蛋白，与根瘤菌相比，在根瘤中有 350 多个差异蛋白，这些蛋白包括参与碳和氮代谢的蛋白和参与氮获取的蛋白，如谷酰胺合成酶、脲酶、尿酰胺结合蛋白，说明类菌体参与氮高效固定的代谢。Djordjevic MA.等的研究鉴定了 810 个差异蛋白至少涉及 53 种代谢途径，其中与根瘤相关的包括固氮酶类、血红素合成酶、热激和压力相关蛋白以及去毒过程涉及的蛋白等，此外大量的转运蛋白表明在根瘤中存在频繁地营养物质的交换。

Mathesius U 等[16]用 2-D 电泳方法建立了一个苜蓿根蛋白组参照图，在 pH 4-7 胶图上显示 2500 多个蛋白点，用肽指纹图谱分析了其中 485 个蛋白点，并在目前的苜蓿 EST（expressed sequence tag）库进行检索，鉴定了 179 个蛋白，大多数鉴定蛋白为代谢途径酶和逆境响应蛋白，此外，在未接种的根组织中鉴定到 2 个结瘤素，这支持了结瘤素在正常根发育中具有一定作用的证据。

2.2 植物与菌根真菌的相互作用

与固氮菌有限的宿主相比，大多数植物可与菌根真菌形成互利互惠的共生体，真菌提供的最主要的物质是磷，而植物为真菌提供碳和磷酯类。在对 M. truncatula 感染菌根真菌 Glomus mosseae 后的时间动态蛋白质组研究中，早期阶段（附着胞形成期，感染后 4 天）有 14 个蛋白发生变化，感染 14 天和 3-4 周时分别有 23 和 24 个蛋白改变[8]，差异蛋白主要涉及氧化还原反应和压力应答相关蛋白（过氧化物酶和谷胱苷肽 -S- 转移酶）以及呼吸作用和细胞壁修饰蛋白等。为了研究植物和真菌膜蛋白的变化，Valot 等提取了感染 G. intraradices 的 M. truncatula 的膜蛋白，与野生型相比，36 个蛋白与真菌感染相关，其中有 2 个 ATP 酶、1 个凝聚素、1 个脂氧合酶、1 个硫氧还蛋白 H 及 1 个结瘤素来自植物[17]。

菌根真菌能促进植物生长，尤其在压力条件下。在研究菌根真菌感染的豌豆在镉压力下的蛋白质组时，1 个乙醇脱氢酶、1 个膜联蛋白、1 个 UTP-1- 磷酸尿苷转移酶、1 个岩藻糖苷酶以及抗性相关蛋白表现出差异，一些蛋白可能涉及压力和对镉的解毒反应[18]。

2.3 其它有益的相互作用

Azoarcus sp.是一类能够促进植物生长的固氮菌，但不能与植物形成稳定的根瘤，对感染 Azoarcus sp.的水稻蛋白质组的研究表明，47 种蛋白与感染相关，包括盐压力和病原抗性相关蛋白和一个受体激酶，这些蛋白可能限制内生真菌的感染，因为它们也受茉莉酸的诱导，而茉莉酸可抑制感染过程[19]。

Trichoderma sp. 属真菌同样是已知的对植物有益的真菌，可增强植物对土壤致病菌的抗性 [20]，T. asperellum 感染黄瓜后诱导宿主的蛋白质组发生改变，在差异表达的 51 个蛋白点中确定了 28 个，它们涉及抗性反应、类异戊二烯和乙炔生物合成、能量代谢、蛋白折叠等[21]。

植物根 - 菌共生体相互作用的蛋白质组研究结果列于表2。

3 总结与展望

模式豆科植物与根瘤菌和菌根真菌形成的共生体是研究植物与微生物相互作用较好的模型，对其相互作用的蛋白质组研究已取得了很大的进展，基因组和转录子研究与蛋白质组研究相辅相成，支持了蛋白质组的研究结果。但是由于缺乏有效的分离方法，感染了真菌的纯植物组织和纯真菌组织不易获得，由于植物蛋白质组数据库和基因数据库的不完善，许多蛋白质不能有效确定，限制了植物蛋白质研究的发展。目前，出现了多种用于大规模蛋白质分离和鉴定的新方法，如多维蛋白鉴定技术（multidimensional protein identification technology，MudPIT）、表面增强激光解吸电离飞行时间质谱（Surface Enhanced Laser Desorption Ionization-Time of Flight-Mass Spectrography, SELDI-TOF-MS）等，有效地推动了植物蛋白质组的发展。

以往的报道中表现出一种现象，即不同类型共生体的蛋白质组中可能出现相同或相似的蛋白质，如 PR-10 蛋白、致病相关蛋白、氧化还原相关蛋白、防御压力相关蛋白（过氧化物酶、谷胱苷肽 -S- 转移酶、氧化还原酶等），它们可能是在微生物作用下植物应对感染、信号、发育等改变的的应激反应所必需的蛋白；另外还可见到一些蛋白的同工型，它们可能是植物应对不同的相互作用的微调蛋白。2005 年 HUPO（human proteome organization）大会提出了蛋白组学研究应从蛋白表达转向蛋白功能研究的思路，进一步证实蛋白质功能将是今后植物蛋白质组学研究的方向。

近年来，不同条件下植物蛋白表达谱的研究日益增多，发现了许多与基因突变、发育、逆境、植物与微生物互作的新蛋白（或基因），但是进一步证明这些新蛋白（或新基因）的功能研究的报道很少。蛋白质翻译后修饰（posttranslated modifications, PTMs）在植物体中起着十分重要的作用，主要参与植物生长发育、病理、非生物逆境应答等细胞信号转导过程。常见的蛋白质

表 2 根 - 共生体相互作用的蛋白质组研究

Table2 The study of the proteome on the interaction of root- commensal vegetable

种类(genus)	研究目标(Objective)	发现(Found)	方法(Method)
宿主研究(Study on host)			
Cucumis sativus (cucumber)	Proteomic research of cucumber infected by Trichoderma asperellum	28 protein were determined	2DE, MALDI-TOF/TOF
Glycine max	Proteomic research of root tip infected by Bradyrhizobium japonicum	23 differentially expressed protein and 17 protein in response to Rhizobium infection in root tip were determined	2DE, MALDI-TOF, QqTOF-MS/MS
G. max	Proteomic research on Peribacteroid membrane protein	17 proteins were determined	2DE, N-terminal sequencing
G. max	Proteomic research on Root mitochondrial protein and nodule protein	50 differentially expressed protein in nodule and 20 protein in mitochondria were determined	2DE, MALDI-TOF, LC/MS/MS, N-terminal sequencing
Lotus japonicus (Lotus)	Proteomic research on peribacteroid membrane protein	94 membrane protein were determined	Total digest nano- LC/ MS/MS
Medicago truncatula (Medicago)	Proteomic research of M. truncatula root infected by S. melilot and G. mosseae	Specific protein in commensal was found, 23 of which were determined	2DE, MALDI-TOF, Q-TOF-MS/MS
M. truncatula	Proteomic research on nodules and bacteroid under the stress of drough	377 protein of nodules were determined	LC/MS/MS
M. truncatula	Proteomic research of wild type and mutant of root nodule induced by ethyne	Differentially expressed protein was found, 33 protein in response of ethyne were determined	2DE, MALDI-TOF /TOF
M. truncatula	Proteomic research of wild type and mutant of root nodule induced by hormone	Differentially expressed protein was found, 33 protein in response of hormone were determined	2DE DIGE,MALDI- TOF/TOF
M. truncatula	Proteomic research of wild type and mutant of root nodule infected by G. intraradices	Differentially expressed protein was found,11 protein related with cell attachment were determined	2DE, MALDI-TOF
M. truncatula	Proteomic research of root membrane protein infected by Glomus intraradices	Differentially expressed protein was found, 23 protein related with cell attachment were determined	2DE, MALDI-TOF, Q-TOF/MS/MS
M. truncatula	Proteomic research of root membrane protein infected by G. intraradices	78 Plasma membrane protein were determined	2D-LC-MS/MS and 2DE plus LC-MS/MS
M. truncatula	Proteomic research of commensal infected by S. meliloti and G. mosseae after dealt with mud	24 specific protein were determined	2DE, MALDI-TOF
M. truncatula	Proteomic research of root after dealt with quorum sensing signals (QSS) secreted by S. meliloti and Pseudomonas aeruginosa	Differentially expressed protein was found, 99 protein in response of QSS were determined	2DE, MALDI-TOF
Melilotus alba (melilotus)	Proteomic research of S. melilot cultured for the competitive research on nodule specific and bacteroid specific research	Differentially expressed protein were found, 100 of which was determined	2DE, N-terminal sequencing, MALDI-TOF
Oryza sativa	Coerced Proteomic research of Oryza sativa dealt with jasmonic acid JAand Azoarcus sp.	9 protein induced by JA, 7 protein induced by JA and Azoarcuswere determined	2DE, MALDI-TOF, LC/MS/MS

Phaseolus Vulgaris(Phaseolus)	Proteomic research of P.Vulgaris after the combined action of Trichoderma and atroviride	Differentially expressed protein were found, which was determined	2DE, MALDI-TOF
Pisum sativum(pea)	Proteomic research on week gap protein and peripheral membrane protein of bacteroid	46 protein were determined, interference of bacteroid and inner membrance	2DE, nano-LC/MS/MS
P. sativum	Proteome analysis of root infected by Glomus mosseae response for cadmium	Cadmium responsive protein of pea belonged to different genotypes were determined, 17 of which were determined	2DE, LC-MS/MS
Trifolium subterraneum (Trifolium)	Proteomic research of root infected by P Rhizobium leguminosarum of wild type and mutant	16 differentially expressed protein were found, 10 of which was determined	2DE, N-terminal sequencing
共生体研究(Study on commensal)			
Bradyrhizobium japonicum (Bradyrhizobium)	Proteomic research of B. japonicum in soybean nodulation	180 protein of bacteroid were determined, which was classified according to metabolic pathway	2DE, MALDI-TOF
B. japonicum	Proteomic research of B. japonicum at the state of independent growth and symbiotic state	300 differentially expressed protein in independent growth fungi were determined	2DE, MALDI-TOF
Frankia aln (Frank genus)	Proteomic research of Frankia aln at the state of independent growth , N-insufficient and N- insufficient state	126 differentially expressed protein in N- insufficient state were determined	2DE, MALDI-TOF
Glomus intraradices	Proteomic research on peripheral protein of root	438 protein were determined	2DE ,MALDI-TOF/TOF
Rhizobium leguminosarum bv trifolii(Rhizobium)	Proteomic research on protein induced by flavone	2 protein indeuced by flavones and 10 constitutive protein were determined	2DE, N-terminal sequencing
Sinorhizobium meliloti	Competitive Proteomic research on protein at the state of independent growth and symbiotic state	1545 protein were determined, which was classified according to metabolic pathway	2DE, MALDI-TOF
S. meliloti	Competitive Proteomic research on protein at the state of independent growth and Nutritional stress	1180 protein were determined, including protein induced by symbiotic specificity and nutritional stress	2DE, MALDI-TOF
S. meliloti	Competitive Proteomic research on luteolin-inducible proteins of wild type and mutant	60 differentially expressed protein were found, 19 of which were determined, and protein induced by luteolin were assessment	2DE, N-terminal sequencing, MALDI-TOF
S. meliloti	Research on specific protein at the growth stage and protein induce by QSS	100 protein induced by QSS were found, 80 differentially expressed protein during growing period were determined	2DE, MALDI-TOF
S. meliloti	Research on induced protein by QSS in the mutant containing lactonase	60 differentially expressed protein in QSS mutant were found, 52 of which were determined	2DE, MALDI-TOF
Trichoderma harzianum (Trichoderma)	Research on secretory protein induced by the components of cell wall in fungal	New protease was determined	2DE, MALDI-TOF,

2DE- 2-Dimensional gel Electrophoresis; DIGE -Difference In-Gel Electrophoresis;ESI-QTOF-Electrospray Ionization Quadrupole-Time of Flight mass spectrometry; LC-MS/MS - Liquid Chromatography/tandem mass spectrometry; MALDI-TOF - Matrix-Assisted Laser Desorption/Ionization Time Of Flight mass spectrometry; QqTOF-MS/MS-Quadrupole-Quadrupole Time Of Flight tandem mass spectrometry.

翻译后修饰过程有磷酸化、泛素化、糖基化、脂基化、甲基化和乙酰化等,但是,目前缺少对翻译后修饰蛋白质的有效分离、纯化和检测技术。因此,在改进分离、纯化和检测技术的同时,完善植物蛋白质和基因数据库,并发展功能蛋白质组研究是今后植物蛋白质组研究的重要方向。

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