植物病程相关蛋白 PR10 研究进展

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摘 要:植物病程蛋白是植物受生物或非生物胁迫后诱导产生并积累的一类蛋白质总称,是植物防卫体系的重要组成部分。近年来,根据它们的结构、亲源关系和生物活性,PR 蛋白主要分为 17 个功能家族。PR10 蛋白是具有核酸酶相似结构,一般为分子量 15 ~ 19 kDa 的酸性蛋白。近年来相关研究表明,一些 PR10 蛋白具有核酸酶活性和体外抗菌功能,在植物防御反应中发挥重要作用,具有较为广泛的应用前景。为此,就 PR10 蛋白的基因结构、表达模式、核酸酶活性、抗病机制、在转基因方面应用等方面的最新研究进展并结合本实验室工作进行综述,为其在植物抗性育种方面的应用提供参考。

关键词:病程相关蛋白;PR10;研究进展

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Advances on Class 10 Pathogenesis-related Proteins

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Abstract: Pathogenesis-related(PR) proteins were originally discovered to accumulate in plants that were infected by pathogens, but were later found to accumulate in plants in response to a variety of biotic and abiotic stresses. PR proteins were the most crucial component of plant defense responses. Currently, PR proteins have been classified into 17 families on the basis of structural differences, serological relationships and biological activity. PR10 proteins are typically described as small, acidic, intracellular proteins of 15-19 kDa. Many PR10 proteins including CaPR10, LaPR10, SPE16, AhPR10, pea PR10.1, and maize ZmPR10 exhibit ribonuclease activity. The RNase activity of PR10 proteins suggests a potential role in defenses against pathogenic infections. Some studies showed PR10 proteins played important roles in plant defense system, having widespread applied prospect. The genetic structures of PR10s, expression patterns, ribonuclease activities, resistance mechanism and the application in transgenic plants were reviewed to provide a basis for disease resistant breeding.

Key words: Pathogenesis-related proteins; PR10; Advances

植物病程相关蛋白(pathogenesis related proteins, PRPs)是植物受生物或非生物胁迫后诱导产生并积累的一类蛋白质总称,是植物防卫体系的重要组成部分[1-2]。PR 蛋白是 van Loon 等于 1970 年在烟草花叶病毒侵染的烟草叶片中发现的,是受烟草花叶病毒侵染产生的蛋白[3]。根据其结构、亲源关系和生物活性,PR 蛋白主要分为 17 个亚类[1,3-4],广泛存在于单子叶和双子叶植物中。

1987 年,Legrand 等就检测到烟草病程相关蛋白 PR-2、PR-3 分别具有 β-1,3-葡聚糖酶的活性和几丁质酶活性。随后 PR-1、PR-4、PR-8 和 PR-11 也被检测到具有 β-1,3-葡聚糖酶的活性几丁质酶活性,PR-4 还具有几丁质结合蛋白的功能。PR-7、PR-8、PR-9 和 PR-10 分别具有蛋白水解酶、溶菌酶和核糖核酸酶活性。PR-6 是蛋白水解酶抑制蛋白。PR-12、PR-13 和 PR-14 分别具有防御素、巯基化合物和脂质转移蛋白的特性,这些病程相关蛋白以及渗调蛋白、类甜蛋白(PR-5)都具有膜透功能。PR-15、PR-16 分别具有萌发素和类萌发素蛋白的特性,具有多种酶活性和功能[5-6]。

其中具有核酸酶活性的第 10 类 PR 蛋白(简称 PR10, Pathogenesis-relatd protein 10)引起了研究者的兴趣。1988 年,Somssich 等[7]用激发子处理欧芹培养细胞首次发现 PR10 以来,在大麦[8]、蚕豆[9-10]、豌豆[11]、水稻[12-14]、苜蓿[15]、马铃薯[16]、玉米[17]、大豆[18]、棉花[19]、地瓜[20]、辣椒[5]、刺茄[21]、

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花生[22]、芦笋[23-24]、百合[25]、高粱[26]和芸苔[27]等植物中相继发现 PR10 家族成员。PR10 蛋白具有核酸酶相似结构,分子量为 16 ~ 19 kD,等电点偏酸性,大部分特异定位在细胞质中,具有体外核酸酶活性和抗菌活性[5,21,28-29]。

大多数 PR-10 可受病原体(包括真菌、细菌、病毒)侵染所诱导表达[5,16,26,30-32]。另外,PR-10 也受各种生物胁迫的诱导,如盐处理、热处理、冷处理[31]、紫外照射[33]等。与此同时,一些植物激素及抗病信号分子也可使 PR-10 上调表达,如茉莉酸[31-33]、脱落酸[32]、水杨酸[31]和乙烯[34]。

近年来,随着 PR10 蛋白研究的迅速发展,其蛋白基因结构、表达模式以及抗病作用机制被不断发现,预示其在提高植物抗性中具有很高的应用价值。为此对近年来 PR10 的研究进展进行综述。

1 PR-10 的结构特征

在多种植物中发现的 PR-10 分子量为 16 ~ 19 kDa,等电点偏酸性,Liu 等[21]从刺茄中分离的 *SsPR*-10 基因开放阅编码 160 个氨基酸,分子量为 17.6 kDa,等电点为 5.29;Park 等[5]研究证实辣椒 *CaPR*-10 含 159 个氨基酸,分子量为 17.3 kDa,等电点为 5.2;Chen 等[17]研究表明玉米 *ZmPR*-10 编码蛋白分子量为 16.9 kDa,等电点为 5.38;Jwa 等[12]证实水稻 *JIOsPR*-10 的分子量为 17.7 kDa,等电点为 5.84;谢纯政等[35]克隆的花生抗黄曲霉相关基因 *ARAhPR*-10,其分子量为 16.9 kDa,等电点 5.03。上述研究表明 PR-10 是小分子量的酸性蛋白。

从 NCBI 中可以获得 100 多条与 PR10 相关的氨基酸序列。对 PR10 基因结构分析表明,PR10 基因开放读码框编码的氨基酸中都具有一个高度保守的 GXGGXG(X 是任意氨基酸)序列模型,被称为“P-LOOP”结构域。“P-LOOP”是一类广泛存在于磷酸化激酶和核酸结合蛋白的结构域[36],该区域的磷酸化可能与其核酸酶活性相关[37-38]。

2 PR10 在植物中的表达模式

虽然很多 PR10 蛋白都是在病原体侵染和激发子诱导的条件下表达,但研究表明 PR10 在组织、器官及发育时期也可表达,存在组成型表达。如刺茄 *SsPR*10 存在组成性表达,在根和幼茎中表达量较高,当幼叶接种 TMV 后,*SsPR*10 在老黄叶中表达量最高,其次是幼叶和根,茎的表达量最低[21]。玉米 *ZmPR*-10 和 *ZmPR*-10.1 也存在组成型表达,它们都在根中高水平表达,但 *ZmPR*-10 在各个组织的表达量明显高于 *ZmPR*-10.1[39]。

作为植物防御系统中的可诱导组分,PR10 受多种病原菌的诱导表达。在过敏反应特异途径中,辣椒 *CaPR*-10 的转录产物在接种 TMV-P_0 48 后开始大量积累,表明 *CaPR*-10 基因在受 TMV 侵染的超敏反应中特异性表达[5]。刺茄 *SsPR*-10 基因受病原 TMV 诱导上调表达[21]。Chadha 和 Das[22]发现花生 *AhPR*-10 基因受病原诱导,同时表现出对病原的选择性,其融合蛋白在体外能显著地抑制 *F. oxysporum*(尖镰孢菌)和 *R. solani*(纹枯病菌)的生长。

一些植物激素和植物抗病信号分子对 PR10 基因的表达模式有影响。许多物质,如茉莉酸(jasmonic acid,JA)、水杨酸(salicylic acid,SA)、脱落酸(abscicis acid, ABA)、赤霉素(gibberellic acid, GA_3)、茉莉酸甲酯(Methyl jasmonate,MeJA)、乙烯等均在植物抗病反应中起作用[40]。ABA 主要在冷害、盐害和干旱中起作用,而 JA 是植物受外伤及病原侵染后的主要防御物质。在水稻中,PR-10 mRNA 受 JA、SA 和 H_2O_2 诱导,但不受乙烯和 ABA 的诱导[12]。水稻中另一 PR10 基因(*RSOsPR*10)则受 JA 诱导,不受 SA 和 ABA 诱导[13]。Park 等[5]研究表明用 SA、乙烯、MeJA 处理辣椒叶片可显著提高 *CaPR*-10 的表达量。刺茄 *SsPR*10 的表达受 SA、ABA、MeJA、GA_3 等的诱导上调表达[21]。Wang 等[41]研究百合花药 PR-10 基因时发现,PR-10 基因的诱导表达存在两条途径,一条是 ABA 通过 MeJA 诱导 PR-10 基因表达,另一条是独立于 MeJA 的 ABA 诱导 PR-10 基因表达。

一些环境因素也可诱导 *PR*-10 基因的表达,如黑暗处理、冷处理、盐胁迫、Cu^{2+} 和 H_2O_2 等。Xie 等[39]研究玉米 *ZmPR*10 和 *ZmPR*10.1 基因表达模式时发现,H_2O_2、$CuCl_2$ 均能诱导 *ZmPR*10 和 *ZmPR*10.1 基因的过量表达;在高盐处理后表达量在 0.5 h 迅速增加,3 h 内恢复正常水平;冷处理下基因表达量在 2 h 内逐渐减少,16 h 明显增加;黑暗条件则是基因过量表达[39]。Park 等[5]研究辣椒 *CaPR*-10 基因时发现,其在高盐处理后 30 min 开始积累,6 h 后表达最强。刺茄 *SsPR*10 的表达受 $CuCl_2$ 诱导上调表达,暗处理没有明显影响,而冷胁迫则引起其表达下调[21]。在辣椒中,*PR*10 基因的转录水平受冷处理和盐胁迫的诱导明显增加[42]。这些结果都进一步说明,植物中 PR10 表达受病原体、植物激素和植物抗病信号分子及各种环境因素的诱导,可能是植物适应生物或非生物胁迫的表现。

3 PR10 蛋白的抑菌活性

目前大部分的研究认为 PR10 蛋白具有抗菌特

性[43],Chadha 和 Das[22]从花生中克隆花生 *AhPR*10 基因,其原核表达的融合蛋白具有抗 *F. oxysporum*(尖镰孢菌)和 *R. solani*(纹枯病菌)菌活性。Park 等[5]研究表明辣椒 CaPR10 蛋白对辣椒疫霉菌的菌丝生长有明显的抑制作用。Liu 等[21]研究表明刺茄 SsPR10 蛋白也具有体外抑制稻瘟病菌活性的作用。Luo 等[44]筛选花生抗黄曲霉相关基因时发现花生 *AhPR*10 基因明显上调表达,推测具有抗黄曲霉活性。玉米 ZmPR10 和 ZmPR10.1 蛋白对黄曲霉菌的菌丝生长有明显的抑制作用[39]。葡萄 *VrPR*10.2 基因可明显抑制葡萄霜霉菌的生长[45]。本实验室克隆的抗大豆疫霉菌相关 PR10(GmPR10)原核表达融合蛋白,具有核酸酶活性,且在体外可以抑制大豆疫霉菌丝的生长(未发表)。

4　病程相关蛋白 PR10 的抑菌机制

研究表明,PR10 在病原菌入侵,生物、非生物胁迫中起重要作用,而且 PR10 蛋白具有体外抑菌功能,但对其抗病机理的报道尚少。大多数病程相关蛋白 PR10 的抑菌机制都被认为与它的核酸酶活性有关。PR10 基因开放读码框编码的氨基酸中都具有一个高度保守的 GXGGXG(X 是任意氨基酸)序列模型,被称为"P-LOOP"结构域。"P-LOOP"是一类广泛存在于磷酸化激酶和核酸酶结合蛋白的结构域[36],该区域的磷酸化可能与其核酸酶活性相关[37-38]。Gajhede 等[46]研究桦树花粉过敏原 Betv 1 的 X-ray 和 NMR 结构发现,在 Betv 1 的 47 ~ 52 位氨基酸中存在一个 GXGGXG 的序列(P-LOOP 结构域),与核酸酶活性有关[36]。在 Betv1 中存在与核酸酶活性有关的 3 个保守氨基酸,即 Glu-96、Glu-148 和 Tyr-150[28]。Zhou 等[19]发现棉花 PR10 蛋白(GaPR10)的核酸酶活性结构域中的氨基酸 Glu-148 和 Tyr-150 被替换后,其蛋白的核酸酶活性几乎丧失。甘薯 PR10 蛋白(SPE16)的保守序列 Glu95A、Glu147A 和 Tyr149A 突变后,核酸酶活性明显丧失[20]。花生 PR10 蛋白(AhPR10)具有 Betv1 结构域,具有核酸酶活性,但结构域中的 Lys55、Phe148 和 His150 突变后,AhPR10 蛋白也明显地丧失核酸酶活性[22]。这些研究表明,Lys54、Glu96、Tyr148 和 Glu150 等保守氨基酸在形成核酸酶活性结构域中具有重要作用。但是在刺茄 PR10 基因(*SsPR*10)中,Glu97、Glu149 和 His151 突变并未失去活性,分析认为该蛋白中 Asp76、Gly111 和 Gly112 可能替代形成了这一结构域[21]。

许多的 PR10 蛋白都具有核酸酶活性[5,19,47-49]。Kim 等[47]研究发现水稻 JIOsPR10 蛋白具有核酸酶活性。Park 等[5]研究发现证实的辣椒 PR10 蛋白(CaPR10)比非磷酸化的 CaPR10 具有更高的 RNase 活性。玉米 ZmPR10 和 ZmPR10.1 蛋白和刺茄 SsPR10 蛋白也具有核酸酶活性[21,39]。He 等[45]研究证实葡萄 PR10(VpPR10.2)蛋白同时具有 RNase 和 DNase 活性。

5　PR10 基因在转基因作物中的应用

研究表明,PR10 基因可有效提高植物的抗病功能。Xie 等[39]将克隆的玉米 *ZmPR*10 和 *ZmPR*10.1 基因转入到拟南芥植物中,对离体的植物叶片接种丁香假单胞菌番茄变种 DC3000 后发现,非转基因作物出现更加严重的病害,*ZmPR*10 和 *ZmPR*10.1 基因有效提高了植物的抗病性。转葡萄 *VrPR*10.2 基因的葡萄叶片对葡萄霜霉菌的抗病性明显增强[45]。

但是,并不是所有的 PR10 基因都能提高植物的抗病性。Ypr10 家族中 *STH*-2 基因的过量表达,并没有增强马铃薯对马铃薯晚疫病和马铃薯病毒 X 的抗病性[50]。Wang 等[41]对豌豆 *PR*10.1 基因研究时发现了同样的情况。这些可能是由于 PR10 蛋白具有选择性抑制的功能[22]。本实验室将克隆的抗大豆疫霉菌相关基因 PR10(*GmPR*10)转入到大豆中发现,转基因大豆对大豆疫霉菌的抗性明显提高(未发表)。

6　展　望

PR10 蛋白是具有核酸酶相似结构,一般为分子量 16 ~ 19 kDa 的酸性蛋白,具有核酸酶活性和体外抑菌作用,同时可以提高转基因作物的抗病性,在病原体入侵,生物和非生物胁迫下诱导表达,是植物防御系统中重要的组成成分。虽然关于 PR10 的报道已有不少,但仍有很多问题亟待解决。许多的 PR10 都具有 RNase 活性,并且 RNase 活性在抑菌方面起到重要作用,He 等[45]研究发现 VpPR10.2 蛋白同时具有 RNase 和 DNase 活性,DNase 活性可能在植物过敏反应中也起到重要作用。Colditz 等[51]利用 RNAi 技术将苜蓿的 PR10 基因沉默后,发现 PR10 蛋白的表达量下降,其他 PR 蛋白表达量升高,植株对 *Aeuteiches* 抗性增强,PR10 蛋白在苜蓿抵抗病原菌的过程中不是重要的,因此 PR10 在抗病抗逆过程中可能还有其他病程相关蛋白协同发挥作用。与此同时,PR10 受多种生物和非生物胁迫诱导,它是如何参与这些信号途径? 过量表达的 PR10 基因并不是都能提高植物的抗病性,PR10 是

如何进行选择性抑制？PR10 主要定位于细胞壁和细胞质，它又是怎样进入细胞发挥作用？这些问题还需进一步深入研究。对 PR10 基因结构、表达模式、核酸酶活性、抑菌机制等研究，可为 PR10 和其他 PR 转基因植物提供理论依据，为培育抗病性品种，拓宽种质资源奠定基础。

参考文献

[1] van Loon L C, van Strien E A. The families of pathogenesis-related proteins, their activities, and comparative analysis of PR-1 type proteins[J]. Physiological and Molecular Plant Pathology, 1999, 55:85 - 97.

[2] van Loon L C, Rep M, Pieterse C M J. Significance of inducible defense-related proteins in infected plants[J]. Annual Review of Phytopathology, 2006, 44:135-162.

[3] van Loon L C, Pierpoint W S, Boller T, et al. Recommendation for naming plant pathogenesis-related proteins[J]. Plant Molecular Biology Reporter, 1994, 12:245-264.

[4] Sels J, Mathys J, de Coninck B M, et al. Plant pathogenesis-related (PR) proteins: a focus on PR peptides[J]. Plant Physiology and Biochemistry, 2008, 46:941-950.

[5] Park C J, Kim K J, Shin R, et al. Pathogenesis-related protein 10 isolated from hot pepper functions as a ribonuclease in an antiviral pathway[J]. The Plant Journal, 2004, 37(2):186-198.

[6] Park C J, An J, Shin Y C, et al. Molecular characterization of pepper germin-like protein as the novel PR-16 family of pathogenesis-related proteins isolated during the resistance response to viral and bacterial infection[J]. Planta, 2004, 219(5):97-806.

[7] Somssich I E, Schmelzer E, Kawalleck P, et al. Gene structure and in situ transcript localization of pathogenesis-related protein 1 in parsley[J]. Molecular and General Genetics, 1988, 213(1): 93-98.

[8] Meier I, Hahlbrock K, Somssich I E. Elicitor-inducible and constitutive in vivo DNA footprints indicate novel cis-acting elements in the promoter of a parsley gene encoding pathogenesis-related protein 1[J]. The Plant Cell, 1991, 3:309-315.

[9] Walter M H, Liu J W, Grand C, et al. Bean pathogenesis-related (PR) proteins deduced from elicitor-induced transcripts are members of a ubiquitous new class of conserved PR proteins including pollen allergens[J]. Molecular and General Genetics, 1990, 222: 353-360.

[10] Walter M H, Liu J W, Wunn J, et al. Bean ribonuclease like pathogenesis-related protein genes (Ypr10) display complex patterns of developmental, dark-induced and exogenous-stimulus dependent expression[J]. European Journal of Biochemistry, 1996, 239: 281-293.

[11] Fristensky B, Horovitz D, Hadwiger L A. cDNA sequences for pea disease response genes[J]. Plant Molecular Biology, 1988, 11: 713-715.

[12] Jwa N S, Kumar Agrawal G, Rakwal R, et al. Molecular cloning and characterization of a novel Jasmonate inducible pathogenesis-related class 10 protein gene, JIOsPR10, from rice (*Oryza sativa* L.) seedling leaves[J]. Biochemical and Biophysical Research Communications, 2001, 286(5):973-983.

[13] Hashimoto M, Kisseleva L, Sawa S, et al. A novel rice PR10 protein, RSOsPR10, specifically induced in roots by biotic and abiotic stresses, possibly via the jasmonic acid signaling pathway[J]. Plant and Cell Physiology, 2004, 45(5):550-559.

[14] Midoh N, Iwata M. Cloning and characterization of a probenaole-inducible gene for an intracellular pathogenesis-related protein in rice[J]. Plant and Cell Physiology, 1996, 37:9-18.

[15] Breda C, Sallaud C, El-Turk J, et al. Defense reaction in *Medicago sativa*: a gene encoding a class 10 PR protein is expressed in vascular bundles[J]. Molecular Plant Microbe Interactions, 1996, 9(8):713-719.

[16] Matton D P, Brisson N. Cloning, expression and sequence conservation of pathogenesis related gene transcripts of potato[J]. Molecular Plant Microbe Interactions, 1989, 2(6):325-331.

[17] Chen Z Y, Brown R L, Rajasekaran K, et al. Identification of a maize kernel pathogensis-related protein and evidence for its involvement in resistance to *Aspergillus flavus* infection and aflatoxin production.[J]. Phytopathology, 2006, 96:87-95.

[18] Crowell D, John M E, Russell D, et al. Characterization of a stress-induced developmentally regulated gene family from soybean[J]. Plant Molecular Biology, 1992, 18:459-466.

[19] Zhou X J, Lu S, Xu Y H, et al. A cotton cDNA (GaPR-10) encoding a pathogenesis-related 10 protein with in vitro ribonuclease activity[J]. Plant Science, 2002, 162(4):629-636.

[20] Wu F, Yan M, Li Y, et al. cDNA cloning, expression, and mutagenesis of a PR-10 protein SPE-16 from the seeds of *Pachyrrhizus erosus*[J]. Biochemical and Biophysical Research Communications, 2003, 312:761-766.

[21] Liu X J, Huang B B, Lin J, et al. A novel pathogenesis-related protein (SsPR10) from Solanum surattense with ribonucleolytic and antimicrobial activity is stress and pathogen-inducible[J]. Journal Plant Physiology, 2006, 163(5):546-55.

[22] Chadha P, Das R. A pathogenesis related protein, AhPR10 from peanut: an insight of its mode of antifungal activity[J]. Planta, 2006, 225:213-222.

[23] Warner S A, Scott R, Draper J. Isolation of an asparagus intracellular PR gene (AoPR1) wound-responsive promoter by the inverse polymerase chain reaction and its characterization in transgenic tobacco[J]. The Plant Journal, 1993, 3(2):191-201.

[24] Warner S A J, Scott R, Draper J. Characterization of a wound-induced transcript from the monocot asparagus that shares similarity with a class of intracellular pathogenesis-related (PR) proteins[J]. Plant Molecular Biology, 1992, 19(4):555-561.

[25] Huang J C, Chang F C, Wang C S. Characterization of a lily tapetal transcript that shares similarity with a class of intracellular pathogenesis-related (IPR) proteins[J]. Plant Molecular Biology, 1997, 34:681-686.

[26] Lo S C C, Hipskind J D, Nicholson R L. cDNA cloning of a sorghum pathogenesis-related protein (PR-10) and difierential expression of defense-related genes following inoculation with *Cochliobolus heterostrophus* or *Colletotrichum sublineolum*[J]. Molecular Plant Microbe Interactions, 1999, 12:479-489.

[27] Srivastava S, Fristensky B, Kav N N V. Constitutive expression of a PR10 protein enhances the germination of *Brassica napus* under sa-

line conditions[J]. Plant and Cell Physiology,2004,45(9):1320-1324.

[28] Moiseyev G P,Fedoreyeva L I,Zhuravlev Y N,et al. Primary structures of two ribonucleases from ginseng calluses. New members of the PR-10 family of intracellular pathogenesis-related plant proteins[J]. FEBS Letters,1997,407:207-210.

[29] Linthorst H J M. Pathogenesis-related proteins of plants,952Crit. Rev[J]. Plant Science,1991,10:123-150.

[30] Robert N,Ferran J,Breda C,et al. Molecular characterization of the incompatible interaction of *Vitis vinifera leaves* with P*seudomonas syringae* pv *pisi*,expression of genes coding for stilbene synthase and class 10 PR protein[J]. The European Journal of Plant Pathology,2001,107:249-261.

[31] McGee J D,Hamer J E,Hodges T K. Characterization of a PR-10 pathogenesis-related gene family induced in rice during infection with *Magnaporthe grisea*[J]. Molecular Plant Microbe Interactions,2001,14:877-886.

[32] Borsics T,Lados M. Dodder infection induces the expression of a pathogenesis-related gene of the family PR-10 in alfalfa[J]. The Journal Experimental Botany,2002,53:1831-1832.

[33] Rakwal R,Agrawal G K,Yonekura M. Separation of proteins from stressed rice *Oryza sativa* L. leaf tissues by two dimensional polyacrylamide gel electrophoresis,induction of pathogenesis-related and cellular protectant proteins by jasmonic acid,UV irradiation and copper chloride[J]. Electrophoresis,1999,20:3472-3478.

[34] Poupard P,Parisi L,Campion C,et al. A wound and ethephon-inducible PR-10 gene subclass from apple,is differentially expressed during infection with a compatible and an incompatible race of *Venturia inaequalis*[J]. Physiology and Molecular Plant Pathology,2003,62:3-12.

[35] 谢纯政,梁炫强,李玲,等. 花生抗黄曲霉相关 ARAhPR10 基因克隆及其原核表达[J]. 基因组学与应用生物学,2009,28(2):237-244. (Xie C Z,Liang X Q,Li L,et al. Cloning and prokaryotic expression of ARAhPR10 gene with resistance to *Aspergillus flavus* in peanut[J]. Genomics and Applied Biology,2009,28(2):237-244.)

[36] Saraste M,Sibbald P R,Wittinghofer A. The P-loop—a common motif in ATP-and GTP-binding proteins[J]. Trends in Biochemical Sciences,1990,15(11):430-434.

[37] Hoffmann-Sommergruber K,VanekKrebitz M,Radauer C,et al. Genomic characterization of members of the Bet v 1 family:genes coding for allergens and pathogenesis-related proteins share intron positions[J]. Gene,1997,197:91-100.

[38] Bantignies B,Seguin J,Muzac I,et al. Direct evidence for ribonucleolytic activity of a PR-10-like protein from white lupin roots [J]. Plant Molecular Biology,2000,42(6):871-881.

[39] Xie Y R,Chen Z Y,Brown R L,et al. Expression and functional characterization of two pathogenesis-related protein 10 genes from *Zea mays*[J]. Journal Plant Physiology,2010,167:121-130.

[40] Dong X. SA,JA,ethylene,and disease in plants[J]. Current Opinion in Plant Biology,1998,1:316-323.

[41] Wang C S,Huang J C,Hu J H. Characterization of two subclasses of PR-10 transcripts in lily anthers and induction of their genes through separate signal transduction pathway[J]. Plant Molecular Biology,1999,40:807-814.

[42] Hwang E W,Kim K A,Park S C,et al. Expression profiles of hot pepper (*Capsicum annuum*) genes under cold stress conditions [J]. J Biosci,2005,30:657-667.

[43] Edreva A. Pathogenesis-related proteins:research progress in the last 15 years[J]. General and Applied Plant Physiology,2005,31:105-124.

[44] Luo M,Liang X Q,Dang P,et al. Microarray-based screening of differentially expressed genes in peanut in response to *Aspergillus parasiticus* infection and drought stress[J]. Plant Science,2005,169(4):695-703.

[45] He M Y,Xu Y,Cao J L,et al. Subcellular localization and functional analyses of a PR10 protein gene from *Vitis pseudoreticulata* in response to *Plasmopara viticola* infection [J]. Protoplasma,2012,DOI 10.1007/s00709-012-0384-8.

[46] Gajhede M,Osmark P,Poulsen F M,et al. X-ray and NMR structure of Betv 1,the origin of birth pollen allergy[J]. Nature Structural Biology,1996,3,1040-1045.

[47] Kim S,Yu S,Kang Y,et al. The rice pathogen-related protein 10 (JIOsPR10) is induced by abiotic and biotic stresses and exhibits ribonuclease activity [J]. Plant Cell Reports,2008,27(3):593-603.

[48] Srivastava S,Emery R J N,Kurepin L V,et al. Pea PR 10.1 is a ribonuclease and its transgenic expression elevates cytokinin levels [J]. Plant Growth Regulation,2006,49(1):17-25.

[49] Yan Q,Qi X,Jiang Z,et al. Characterization of a pathogenesis-related class 10 protein(PR-10) from *Astragalus mongholicus* with ribonuclease activity[J]. Plant Physiology and Biochemistry,2008,46(1):93-99.

[50] Constabel C P,Bertrand C,Brisson N. Transgenic potato plants overexpressing the pathogenesis-related STH-2 gene show unaltered susceptibility to *Phytophthora infestans* and potato virus X[J]. Plant Molecular Biology,1993,22(5):775-782.

[51] Colditz F,Niehaus K,Krajinski F. Silencing of PR-10-like proteins in Medicago truncatula results in an antagonistic induction of other PR proteins and in an increased tolerance upon infection with the oomycete *Aphanomyces euteiches*[J]. Planta,2007,226:1-57.