农业资源研究中心小麦抗旱水分高效利用分子育种岗位应聘申请表

<table>
<tr><td>姓 名</td><td>刘洋</td><td>性 别</td><td>男</td><td>党 派</td><td></td><td rowspan="3">  </td></tr>
<tr><td>出生日期</td><td>1986.08</td><td colspan="2">参加工作时间</td><td colspan="2"></td></tr>
<tr><td rowspan="2">毕业院校</td><td rowspan="2">山东农业大学</td><td colspan="2">毕业时间</td><td colspan="2">2014 年 7 月</td></tr>
<tr><td colspan="2">出站时间</td><td colspan="2">年 月</td></tr>
<tr><td>学 历</td><td>研究生</td><td>学 位</td><td>博士</td><td>所学专业</td><td>植物学</td><td></td></tr>
<tr><td colspan="2">现工作/博士后单位</td><td colspan="5"></td></tr>
<tr><td colspan="2">现职务/职称</td><td></td><td>任职时间</td><td colspan="3"></td></tr>
<tr><td colspan="2">外语语种和水平</td><td colspan="2">英语六级</td><td colspan="2">与本所有无亲属关系</td><td>无</td></tr>
<tr><td rowspan="2">配偶情况</td><td>姓 名</td><td>孙庆娜</td><td>工作地点</td><td colspan="3">山东济南</td></tr>
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<tr><td colspan="3">非正式户口所在地（学生或博士后）</td><td colspan="3"></td></tr>
<tr><td>应聘岗位</td><td colspan="6">小麦抗旱水分高效利用分子育种</td></tr>
</table>

一、 学习进修经历（大学填起，研究生阶段注明指导教师

学历	学位	毕业院校及所学专业	学习起止年月	指导教师
本科	学士	山东农业大学生物科学专业	2005.08-2009.06	
研究生	博士	山东农业大学植物学专业硕博连读	2009.08-2014.07	李德全

二、工作经历（含工作时间、单位名称及任职情况等）

三、代表性研究工作或学位论文工作介绍（含参加/承担项目、研究基础、取得成果等）

以拟南芥胚胎发育晚期丰富蛋白（LEA proteins，Late embryogenesis abundant proteins）基因为模板进行同源比对，在玉米基因组中比对得到 29 个分属于 6 个不同家族的 *LEA* 蛋白基因。从中选取 2 族的 *ZmDHN13*，3 族的 *ZmLEA3* 和 5 族的 *ZmLEA5C* 进行研究,比较了他们在生理生化功能方面的异同。

研究结果：

1. *ZmDHN13* 和 *ZmLEA5C* 为组成型表达基因，但其转录也受各种非生物胁迫和信号分子的调节。*ZmLEA3* 是典型的诱导型表达 *LEA* 蛋白基因。
2. ZmDHN13 和 ZmLEA5C 可以被蛋白激酶 CKII 磷酸化。
3. ZmDHN13、ZmLEA3 和 ZmLEA5C 分别定位于细胞核、细胞质和细胞膜。
4. ZmDHN13、ZmLEA3 和 ZmLEA5C 都可以保护 LDH 的活性免受逆境胁迫的影响。
5. 过表达 *ZmDHN13*、*ZmLEA3* 或 *ZmLEA5C* 都可以提高转基因植株对渗透胁迫的抗性。
6. ZmDHN13 和 ZmLEA3 可以结合金属离子，并且提高转基因植株对氧化胁迫的抗性。ZmLEA5C 可以提高转基因植株对低温胁迫的抗性。
7. 对 ZmDHN13 及其缺失保守结构域的突变蛋白 ZmDHN13ΔK、ZmDHN13ΔS 和

ZmDHN13ΔNLS 的研究发现，NLS 结构域和 S 结构域可以影响 ZmDHN13 的核酸酶活性及磷酸化和核定位，K 结构域对 ZmDHN13 保护 LDH 的活性功能及其核酸酶活性具有重要作用。进一步研究表明，ZmDHN13 的三个保守结构域在植物体内可能具有协同作用。

8. 研究了模式植物烟草对 *Pst* DC3000（丁香假单胞杆菌）的响应情况，结果表明，烟草响应 *Pst* DC3000 主要依赖于 SA 信号途径，JA 对这一过程具有抑制作用。

四、获得的科技/荣誉奖励及研究成果情况（代表性研究论文、专利、获奖等，标注排名）

Liu, Y., Wang, L. Xing, X., Sun, L.P., Pan, J.W., Kong, X.P., Zhang, M.Y., Li.D.Q. ZmLEA3, a multifunctional group 3 LEA protein from maize (*Zea mays* L.), is involved in biotic and abiotic stresses. *Plant and cell Physiology*, 2013 (54): 944–959 (一作，IF=4.978)

Liu, Y., Wang, L. Cai, G.H., Jiang, S.S., Sun, L.P., Li, D.Q. Response of tobacco to the *Pseudomonas syringae pv. Tomato* DC3000 is mainly dependent on salicylic acid signaling pathway. *FEMS Microbiol. Lett.* 2013(344): 77–85(一作，IF=2.723)

Liu, Y., Wang, L. Jiang, S.S., Cai, G.H., Li, D.Q. Group 5 LEA protein, ZmLEA5C, enhanced transgenic tobacco and yeast tolerance to osmotic and low temperature stresses. Plant Physiology and Biochemistry, 2014 (84) 22–31 (一作，IF=2.352)

Wang, L., **Liu, Y.**, Cai, G.H., Jiang, S.S., Pan, J.W., Li, D.Q. Ectopic expression of *ZmSIMK1* leads to improved drought tolerance and activation of systematic acquired resistance in transgenic tobacco. *Journal of biotechnology*, 2014 (172): 18-29. （二作）

Sun, L.P., **Liu, Y.**, Kong, X.P., Zhang, D., Pan, J.W., Zhou, Y., Wang, L. et.al. ZmHSP16.9, a cytosolic class I small heat shock protein in maize (*Zea mays* L.), confers heat tolerance in transgenic tobacco. *Plant Cell Rep.*, 2012 (31):1473–1484 （二作）

刘洋，邢鑫，李德全。LEA 蛋白的分类与功能研究进展。生物技术通报.，2011(8): 36-43

2013 年博士研究生国家奖学金

五、提供两或三位同行具有高级职称推荐人的联系方式（姓名、职务、电话和邮箱地址）

李德全 教授　0538-8249137　dqli@sdau.edu.cn

孟庆伟 教授　0538-8249606　qwmeng@sdau.edu.cn

六、应聘岗位陈述（对岗位的认识、研究兴趣、应聘理由及优势、工作设想和其它说明）：

我在植物分子生物学及植物生理学方面有着较好的基础，利用我已经掌握的实验技术，再学习小麦育种的相关内容，就可以在小麦抗旱节水水分高效利用分子育种方面取得一定成果。

首先利用我在玉米方面的基础，在玉米抗旱水分高效利用方面申请国家自然科学基金，再同时兼干小麦分子育种，逐步发展。

七、附件：证明能力的：论文、证书影印件、其它材料等（PDF）

本人承诺以上情况真实无误，如有虚假，本人愿意承担一切后果。

申请人签名：　刘洋　　填表日期：　2014 年 12 月 18 日

博士研究生

毕业证书

研究生 刘洋 性别 男，一九八六 年 八 月 二十二 日生，于

二〇一一 年 九 月至二〇一四 年 六 月在 植物学

专业学习，学制 三 年，修完博士研究生培养计划规定的全部课程，成绩合格，

毕业论文答辩通过，准予毕业。

培养单位：山东农业大学 校(院、所)长：

证书编号：104341201401000030

二〇一四 年 七 月 一 日

博士学位证书

刘洋 ，男 ，1986 年 8 月 22日生。在 山东农业大学

植物学 学科（专业）已通过博士学位的课程

考试和论文答辩，成绩合格。根据《中华人民共和国学位条例》的规

定，授予 理学 博士学位。

校 长

山东农业大学 学位评定委员会主席

证书编号： 1043422014000029

二〇一四 年 六 月 十九 日

PCP
PLANT & CELL PHYSIOLOGY

ZmLEA3, a Multifunctional Group 3 LEA Protein from Maize (*Zea mays* L.), is Involved in Biotic and Abiotic Stresses

Yang Liu[1], Li Wang[1], Xin Xing[1], Liping Sun[1,2], Jiaowen Pan[1], Xiangpei Kong[1], Maoying Zhang[1] and Dequan Li[1,*]

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Regular Paper

Late embryogenesis abundant (LEA) proteins accumulate to high levels during the late stage of seed maturation and in response to water deficit, and are involved in protecting higher plants from damage caused by environmental stresses, especially drought. In the present study, a novel maize (*Zea mays* L.) group 3 LEA gene, *ZmLEA3*, was identified and later characterized using transgenic tobacco plants to investigate its functions in abiotic and biotic stresses. Transcript accumulation demonstrated that *ZmLEA3* was induced in leaves by high salinity, low temperature, osmotic and oxidative stress as well as by signaling molecules such as ABA, salicylic acid (SA) and methyl jasmonate (MeJA). The transcript of *ZmLEA3* could also be induced by pathogens [*Pseudomonas syringae* pv. tomato DC3000 (*pst dc3000*)]. ZmLEA3 is located in the cytosol and the nucles. Further study indicated that the ZmLEA3 protein could bind Mn^{2+}, Fe^{3+}, Cu^{2+} and Zn^{2+}. Overexpression of *ZmLEA3* in transgenic tobacco (*Nicotiana tabacum*) and yeast (GS115) conferred tolerance to osmotic and oxidative stresses. Interestingly, we also found that overexpression of *ZmLEA3* in transgenic tobacco increased the hypersensitive cell death triggered by *pst dc3000* and enhanced the expression of *PR1a*, *PR2* and *PR4* when compared with the wild type. Thus, we proposed that the ZmLEA3 protein plays a role in protecting plants from damage by protecting protein structure and binding metals under osmotic and oxidative stresses. In addition, ZmLEA3 may also enhance transgenic plant tolerance to biotic stress.

Keywords: Hypersensitive response • Metal binding • Osmotic stress • Oxidative stress • Plant pathogens • ZmLEA3.

Abbreviations: APX, ascorbate peroxidase; BMGY, buffered glycerol-complex medium; BMMY, buffered methanol-complex medium; CaMV, *Caulifower mosaic virus*; CAT, catalase; CS4, citrate synthase 4; GFP, green fluorescent protein; HR, hypersensitive response; IMAC, immobilized metal ion affinity chromatography; JA, jasmonate; LEA, late embryogenesis abundant; LDH, lactate dehydrogenase; MDA, malondialdehyde; MeJA, methyl jasmonate; MS, Murashige and Skoog; PEG, polyethylene glycol; POD, peroxidase; PR, pathogenesis related; *pst dc3000*, *Pseudomonas syringae* pv. tomato DC3000; qRT–PCR, quantitative real-time reverse transcription–PCR; ROS, reactive oxygen species; SA, salicylic acid; TBA, thiobarbituric acid; TCA, trichloroacetic acid; SOD, superoxide dismutase; WT, wild type; YNB, yeast nitrogen base.

Introduction

Environmental stresses such as drought, high salinity and disease induce changes in enzyme activities and gene expression in crop plants, leading to considerable reduction in their growth and productivity. In response to various stresses, plants produce a series of proteins to protect cell metabolism. The synthesis of hydrophilic proteins is a major part of the plant response to stress conditions. Late embryogenesis abundant (LEA) proteins are major hydrophilic proteins, which can reduce the damage caused by adverse conditions.

LEA proteins were first identified in cotton seeds 31 years ago (Dure and Galau 1981); they are accumulated during the late stages of seed development and are associated with the acquisition of desiccation tolerance in maturing seeds. LEA proteins have high hydrophilicity, a lack or low proportion of cysteine and tryptophan residues, and a preponderance of certain amino acid residues such as glycine, glutamate, lysine and threonine. According to amino acid sequences and conserved motifs, LEA proteins are categorized into seven distinctive groups (Battaglia et al. 2008). Three major groups (numbered 1, 2 and 3) of LEA proteins have been described in a range of different plants and plant tissues. Group 3 LEA protein functions have been extensively studied in transgenic plants, and are characterized by a repeating motif of 11 amino acids TAQAAKEKAGE (Dure 1993). Circular dichroism (CD) analysis

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FEMS MICROBIOLOGY LETTERS

RESEARCH LETTER

Response of tobacco to the *Pseudomonas syringae* pv. *Tomato* DC3000 is mainly dependent on salicylic acid signaling pathway

Yang Liu[1], Li Wang[1], Guohua Cai[1], Shanshan Jiang[1], Liping Sun[1,2] & Dequan Li[1]

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DOI: 10.1111/1574-6968.12157

Editor: Bernard Glick

Keywords
Pseudomonas syringae pv. Tomato DC3000; salicylic acid; jasmonic acid; defense response; tobacco.

Abstract

Pseudomonas syringae pv. Tomato DC3000 (*Pst* DC3000) was the first pathogen to be demonstrated to infect *Arabidopsis* and to cause disease symptoms in the laboratory setting. However, the defense response to *Pst* DC3000 was unclear in tobacco. In this report, the expression profiles of twelve defense response–related genes were analyzed after treatment with salicylic acid (SA), jasmonic acid (JA), and pathogen *Pst* DC3000 by qRT-PCR. According to our results, it could be presented that the genes primarily induced by SA were also induced to higher levels after *Pst* DC3000 infection. SA accumulation could be induced to a higher level than that of JA after *Pst* DC3000 infection. In addition, SA could result in hypersensitive response (HR), which did not completely depend on accumulation of reactive oxygen species. These results indicated that tobacco mainly depended on SA signaling pathway rather than on JA signaling pathway in response to *Pst* DC3000. Further study demonstrated that JA could significantly inhibit the accumulation of SA and the generation of the HR induced by *Pst* DC3000.

Introduction

Plants are sessile organisms, and thus, they have evolved efficient mechanisms to combat attacks from pathogens, including the basal immune systems and highly specific resistance (Jones & Dangl, 2006). One of the most effective defense mechanisms to against pathogens is the hypersensitive response (HR; Hammond-Kosack & Jones, 1996). The HR prevents pathogens from extracting nutrients from the host plant's healthy tissue. It is initiated as the plant develops necrotic lesions in the locally infected tissue, and is accompanied by the accumulation of salicylic acid (SA) and jasmonic acid (JA; Malamy *et al.*, 1990; Metraux *et al.*, 1990). Finally, some pathogenesis-related (PR) proteins become activated and participate in the HR (Bol *et al.*, 1990; Ohshima *et al.*, 1990; Seo *et al.*, 1997).

The plant hormones SA and JA are thought to be involved in the regulation of signaling networks, including pathogen-associated molecular patterns (PAMP) responses and effector-triggered immunity (Bent & Mackey, 2007; Zipfel, 2009). Following the early signaling that occurs after a pathogen attack, plant-generated SA and JA usually act as secondary signaling molecules. So the accumulation of SA and JA has been widely used as a reliable marker of defense responses and is closely associated with redox homeostasis, hypersensitive cell death, and systemic acquired resistance (Dong, 2004; Song *et al.*, 2004).

Plants defend themselves against a pathogen attack using two principally different mechanisms: (1) their existing defense faculties, such as physical barriers; and (2) inducible defense responses. When a pathogen breaks through a plant's physical barriers, the plant cells send signals alerting of the breach and then activate the inducible defense mechanisms. The inducible defense response often requires a large number of defense genes to be expressed, which produce many different types of proteins, such as cell wall proteins, hydrolytic enzymes (chitinases and β-1, 3-glucanases), and other PR proteins, WRKY transcriptional factors, protease inhibitors (PIs),

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Research article

Group 5 LEA protein, *ZmLEA5C*, enhance tolerance to osmotic and low temperature stresses in transgenic tobacco and yeast

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ABSTRACT

Group 5 LEA (Late Embryogenesis Abundant) proteins contain a significantly higher proportion of hydrophobic residues but lack significant signature motifs or consensus sequences. This group is considered as an atypical group of LEA proteins. Up to now, there is little known about group 5C LEA proteins in maize. Here, we identified a novel group 5C LEA protein from maize. The accumulation of transcripts demonstrated that *ZmLEA5C* displayed similar induced characteristics in leaves and roots. Transcription of *ZmLEA5C* could be induced by low temperature, osmotic and oxidative stress and some signaling molecules, such as abscisic acid (ABA), salicylic acid (SA) and methyl jasmonate (MeJA). However, transcription of *ZmLEA5C* was significantly inhibited by high salinity. Further study indicated that the *ZmLEA5C* protein could be phosphorylated by the protein kinase CKII. *ZmLEA5C* could protect the activity of LDH under water deficit and low temperature stresses. Overexpression of *ZmLEA5C* conferred to transgenic tobacco (*Nicotiana benthamiana*) and yeast (GS115) tolerance to osmotic and low temperature stresses.

1. Introduction

In response to adverse conditions, plants have developed multiple pathways for adaptation or adjustment to survive under these conditions. Late-Embryogenesis Abundant (LEA) proteins accumulate during the late stages of seed development. These proteins have a low molecular weight and highly hydrophilic characteristics and are ubiquitous in plants (Dure et al., 1989). Many studies have demonstrated that LEA proteins are associated with desiccation tolerance in maturing seeds and plants. Some LEA proteins could act as a kind of oxygen scavengers (Hara et al., 2013; Kim et al., 2013).

The nomenclature of LEA proteins is different according to different classification methods (Dure et al., 1989; Wise and Tunnacliffe, 2004; Battaglia et al., 2008). According to the amino acid sequence homology and the conserved motifs, LEA proteins are categorized into seven distinctive groups. The classified methods define the structural, functional, and evolutionary relationships of different group LEA proteins (Battaglia et al., 2008). Groups 1 (Em), 2 (dehydrin), 3, 4, 6, and 7, which have specific motifs within each respective group, are considered as typical LEA protein. While group 5 lacks a significant signature motif or a consensus sequence, it is considered an atypical LEA protein. According to the nomenclature (Cuming, 1999; Battaglia et al., 2008), the LEA proteins were also annotated as the first proteins described for this group: group 1 (D-19), group 2 (D-11), group 3 (D-7/D-29), and group 4 (D-113), group 6 (LEA18) and group 7 (ASR1). Group 5 LEA proteins are nonhomologous proteins, which were assigned to three subgroups 5A, 5B, and 5C. The three subgroups are also annotated as D-34, D-73 and D-95 by Cumming (1999), which were the first described proteins for this group. Group 5 LEA proteins contain a significantly higher proportion of hydrophobic residues than typical LEA proteins. Unlike typical LEA proteins, group 5 LEA proteins have a globular conformation, which is not soluble after boiling (Cuming, 1999; Baker et al., 1988; Galau et al., 1993).

Although significant similarity has not been detected among the different LEA protein families, recent studies have provided experimental evidence demonstrating the roles of LEA proteins under a broad range of stresses (Battaglia et al., 2008; Sun et al.,

Abbreviations: ABA, abscisic acid; GFP, green fluorescent protein; LEA, late embryogenesis abundant; ORF, open reading frame; qRT-PCR, quantitative real-time reverse transcription-PCR; JA, jasmonate; SA, salicylic acid; LDH, lactate dehydrogenase; ROS, reactive oxygen species; MD, minimal dextrose medium; BMGY, buffered glycerol-complex medium; BMMY, buffered methanol-complex medium; YNB, yeast nitrogen base; YPD, yeast extract peptone dextrose medium; RWC, relative water content.

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E-mail addresses: dqli@sdau.edu.cn, b00011@sdau.edu.cn (D. Li).

[1] These authors contributed equally to this work.

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ORIGINAL PAPER

ZmHSP16.9, a cytosolic class I small heat shock protein in maize (*Zea mays*), confers heat tolerance in transgenic tobacco

Liping Sun · Yang Liu · Xiangpei Kong · Dan Zhang · Jiaowen Pan · Yan Zhou · Li Wang · Dequan Li · Xinghong Yang

Received: 6 January 2012 / Revised: 15 February 2012 / Accepted: 2 April 2012 / Published online: 26 April 2012

Abstract Various organisms produce HSPs in response to high temperature and other stresses. The function of heat shock proteins, including small heat shock protein (sHSP), in stress tolerance is not fully explored. To improve our understanding of sHSPs, we isolated *ZmHSP16.9* from maize. Sequence alignments and phylogenetic analysis reveal this to be a cytosolic class I sHSP. *ZmHSP16.9* expressed in root, leaf and stem tissues under 40 °C treatment, and was up-regulated by heat stress and exogenous H_2O_2. Overexpression of *ZmHSP16.9* in transgenic tobacco conferred tolerance to heat and oxidative stresses by increased seed germination rate, root length, and antioxidant enzyme activities compared with WT plants. These results support the positive role of *ZmHSP16.9* in response to heat stress in plant.

Key message The overexpression of *ZmHSP16.9* enhanced tolerance to heat and oxidative stress in transgenic tobacco.

Keywords Heat stress · Small heat-shock protein · Maize · Heat tolerance

Communicated by K. Chong.

L. Sun · Y. Liu · X. Kong · D. Zhang · J. Pan · Y. Zhou · L. Wang · D. Li · X. Yang (✉)
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L. Sun
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Introduction

Plants as sessile organisms are exposed to persistently changing stress factors that limit the growth and yield of diverse crop plants. The environmental factors include drought, salinity, high and low temperatures and chemicals (Zhu 2002). It is generally accepted that the worldwide greenhouse effect produces a warmer world. The heat stress is even more damaged and can disturb cellular homeostasis and lead to severe retardation in growth and development, and even death (Kotak et al. 2007). However, plants deploy a variety of sophisticated mechanisms to rapidly sense a changing environment and protect themselves from these environmental stresses (Xiong et al. 2002; Zhu 2001, 2002).

The heat shock protein (HSP) superfamily is one of the proteins universally accumulated under heat stress condition (Schlesinger 1990). In plants, HSP genes are also induced in response to a large number of abiotic stresses, such as cold, salinity, drought, and some signaling molecules, such as abscisic acid (ABA), salicylic acid (SA), and H_2O_2, suggesting that HSPs play important roles in protecting plants against stress and in the reestablishment of cellular homeostasis (Charng et al. 2006; Guan et al. 2004; Ma et al. 2006; Malik et al. 1999; Rampino et al. 2009; Sun et al. 2001; Volkov et al. 2006). Molecular weight placed the plant HSPs into six groups: HSP100s; HSP90s; HSP70s; HSP60s; and small HSPs (sHSPs) (12–40 kDa) (Sanmiya et al. 2004), and co-chaperones HSP40 or DNAJ family (Qiu et al. 2006).

Plant sHSPs are divided into six classes: three classes of (classes CI, CII and CIII) sHSPs are localized in the cytosole or in the nucleus and the other three in the plastids, endoplasmic reticulum and mitochondria (CIV, CV and CVI) (Sun et al. 2002; Wang et al. 2004). Completion

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Ectopic expression of *ZmSIMK1* leads to improved drought tolerance and activation of systematic acquired resistance in transgenic tobacco

Li Wang, Yang Liu, Guohua Cai, Shanshan Jiang, Jiaowen Pan, Dequan Li*

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SAR

ABSTRACT

The mitogen-activated protein kinase (MAPK) cascades play pivotal roles in diverse signaling pathways related to plant biotic and abiotic stress responses. In this study, a group B MAPK gene in *Zea mays*, *ZmSIMK1*, was functionally analyzed. Quantitative real-time PCR (qRT-PCR) analysis indicated that *ZmSIMK1* transcript could be induced by drought, salt, *Pseudomonas syringae* pv. *tomato* DC3000 (*Pst* DC3000) and certain exogenous signaling molecules. Analysis of the *ZmSIMK1* promoter revealed a group of putative *cis*-acting elements related to drought and defense responses. β-Glucuronidase (GUS) staining produced similar results as qRT-PCR. ZmSIMK1 was mainly localized in the nucleus, and further study indicated that the C-terminal domain (CD) was essential for targeting to the nucleus. Transgenic tobacco accumulated less reactive oxygen species (ROS), had higher levels of antioxidant enzyme activity and osmoregulatory substances and exhibited an increased germination rate compared with wild-type (WT) tobacco under drought stress. ROS-related and drought stress-responsive genes in transgenic tobacco were significantly upregulated compared with the same genes in WT lines under drought stress. Moreover, overexpression of *ZmSIMK1* promoted the hypersensitive response (HR) and pathogen-related gene (*PR*) transcription in addition to triggering systemic acquired resistance (SAR) in tobacco.

1. Introduction

Plants are exposed to diverse stress conditions, including drought, salt and pathogen infection, throughout their life cycles. To address various stresses, plants have evolved a variety of biochemical and physiological mechanisms. Among the stresses, drought and pathogens constitute major limits to crop productivity. MAPK cascades have been demonstrated to play roles in a myriad of cellular processes, including biotic and abiotic stresses, growth, differentiation and cell death (Nakagami et al., 2005; Rodriguez et al., 2010; Kosetsu et al., 2010). MAPK is activated by its upstream specific MAPKK via the phosphorylation of conserved threonine (T) and tyrosine (Y) residues in the catalytic subdomain. MAPKK itself is activated via the phosphorylation of two serine/threonine residues in a conserved S/T-X3-5-S/T motif by an upstream MAPKKK (Chang and Karin, 2001). After activation, the MAPK module is either translocated into the nucleus or maintained in the cytoplasm to initiate the cellular responses through the phosphorylation of downstream proteins (Qiu et al., 2008; Nadarajah and Sidek, 2010). Thus, MAPKs, as the last component of the MAPK cascade, play a major role in signal transduction from upstream components to the target. MAPKs are ubiquitous proteins in eukaryotes and exist as a gene family. For example, the *Arabidopsis thaliana* genome contains a total of 20 MAPK genes, and 17 MAPK genes have been identified in the rice genome (Rohila and Yang, 2007; Nadarajah and Sidek, 2010), indicating the complexity of the MAPK cascades in the plant kingdom.

Since the first report of a plant MAPK identified MsERK1 in alfalfa (Duerr et al., 1993) and D5 kinase in pea (Stafstrom et al., 1993), MAPK components have been isolated from many plant species (Mizoguchi et al., 1993; Wilson et al., 1993). Among these, specific MAPKs involved in drought and biotic stress signal transduction have been identified, including AtMPK4 and AtMPK6, which are activated by osmotic stress, and AtMEKK1-AtMKK1/AtMKK2-AtMPK4, which is involved in drought, cold and salt stress signal

Abbreviations: MAPK, mitogen-activated protein kinase; qRT-PCR, quantitative real-time PCR; RT-PCR, reverse transcription PCR; *Pst* DC3000, *Pseudomonas syringae* pv. *tomato* DC3000; ROS, reactive oxygen species; *PR*, pathogen related genes; SAR, systemic acquired resistance; ABA, abscisic acid; SA, salicylic acid; MeJA, methyl jasmonate; GFP, green fluorescent protein; DAPI, 4′6-dianidino-2 phenylindole; CD, C-terminal domain; KD, kinase domain; REL, relative electrolyte leakage; MDA, malondialdehyde; NBT, nitroblue tetrazolium; DAB, 3,3′-diaminobenzidine; APX, ascorbate peroxidase; CAT, catalase; POD, peroxidase; SOD, superoxide dismutase; DMTU, dimethylthiourea; H_2O_2, hydrogen peroxide; HR, hypersensitive response; CaMV, cauliflower mosaic virus; CTAB, cetyl-trimethyl-ammonium bromide; GUS, β-glucuronidase.

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LEA 蛋白的分类与功能研究进展

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摘 要：胚胎发育晚期丰富蛋白（late embryogenesis abundant proteins，LEA 蛋白）具有广泛的生物学功能，低温、干旱、盐渍及 ABA 等均可以诱导 LEA 蛋白的表达，LEA 蛋白的显著特点是具有较高的亲水性与热稳定性。根据 LEA 蛋白结构特征可将其分为不同的家族，研究发现 LEA 蛋白具有清除活性氧自由基、稳定膜结构和保护酶活性等功能。介绍 LEA 蛋白的分类依据、功能和基因表达调控等方面研究的进展。

关键词：LEA 蛋白 分类 特征 表达调控 功能

Studies on the Classification and Function of LEA Proteins

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Abstract: LEA proteins (late embryogenesis abundant proteins) had important biological function. Low temperature, drought, salinity and ABA can induce the expression of LEA proteins. Significant physical and chemical properties of LEA proteins are high hydrophilic and thermal stability. According to the character, LEA proteins can be divided into different groups. LEA proteins can scavenge ROS and free radical, stabilize the structure of membrane, and protect enzyme against inactivation. The classification, function and expression regulation of LEA proteins were summarized in this paper.

Key words: LEA protein Classification Character Expression and regulation Function

在低温、干旱和盐渍等逆境条件下，植物会产生一系列具有保护功能的蛋白来维持其正常代谢活动，胚胎发育晚期丰富蛋白（late embryogenesis protein abundant，LEA 蛋白）就是其中的一种。目前研究已发现 LEA 蛋白具有稳定细胞膜，清除活性氧自由基，结合金属离子等功能。根据 LEA 蛋白的保守结构域可将其分成不同的家族[1-3]。LEA 蛋白共有的显著特点是具有较高的亲水性，高的热稳定性，含有高比例的甘氨酸、赖氨酸和组氨酸，缺少丙氨酸和丝氨酸，缺乏明显的二级结构[4]。虽然关于 LEA 蛋白行使功能的具体机制仍不十分清楚，但是在植物受到水分胁迫时通常都伴随着 LEA 蛋白的积累，异源表达发现某些 LEA 蛋白可以增强转基因植物和酵母菌对水分胁迫的抗性[5]。最近有研究发现，LEA 蛋白的积累与植物抗性存在一定的相关性[6]。Saavedra 等[7]将苔藓中脱水素基因 PpDHNA 敲除，去除逆境胁迫后，其突变体难以恢复到正常状态，这说明该脱水素在苔藓逆境恢复过程中起重要作用。Liu 等[8]研究发现，过表达沙冬青 LEA 蛋白 AmLEA 能增强大肠杆菌对低温和高温胁迫的抗性。

1 LEA 蛋白的分类及特征

通常根据氨基酸序列或亲水性对 LEA 蛋白进行分类，Dure[9]将 LEA 蛋白分为 6 个家族，Battaglia 等[5]根据 LEA 蛋白的保守结构域及亲水系数等将其分为 7 个家族，两种分类依据基本类似，以下将着重介绍各族 LEA 蛋白的分类依据及特征。

一族 LEA 蛋白一般由 83 -153 个氨基酸组成，在溶解条件下呈现高度无序的状态，其显著特点是由 20 个氨基酸组成的保守结构域（TRKEQ [L/M] G

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