

樱桃MADS-box转录因子的生物信息学及其表达分析

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摘要: MADS-box转录因子在植物花和果实发育过程中发挥重要调控作用。本文从樱桃花芽转录组分析中, 获得18个具有全长开放阅读框的MADS-box转录因子(*PpcMADS*), 利用生物信息学方法对它们编码的氨基酸基本性质和结构进行了系统分析。结果表明, 除KP347550和KP347552以外, 均属于MIKC家族, 大部分为不稳定碱性亲水蛋白, 二级结构中同时含有α-螺旋、β-转角、扩展链和无规则卷曲结构, 其中α-螺旋所占比例最高。亚细胞定位分析显示, MADS-box蛋白主要定位在细胞核中, 而KP347549定位到细胞质、KP347545和KP347552定位到质膜的几率较高。序列主要含有4个保守基序, 其中基序1为该基因家族的保守基序, 含有MADS盒。*PpcMADS*转录因子可以分为AP3亚组、PI亚组、SHP亚组、AG亚组、AP1亚组、SEP亚组、SOC亚组、SVP亚组及4个未知亚组。KP347545、KP347546、KP347547、KP347549、KP347551、KP347552、KM243373、KM243375和KM243377只在花中表达, KP347548和KP347550在花和果实中均不表达, 其他7个基因在两个组织中都表达。

关键词: 樱桃; MADS-box; 转录因子; 生物信息分析; 表达分析

Bioinformatics Analysis of MADS-box Genes and Their Expression in Cherry

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Abstract: MADS-box gene family is a large group which plays important roles in regulation of plant growth and development. Totally, 18 MADS-box genes (*PpcMADS*) with full ORF were identified from transcriptome generated from flower bud of cherry. In order to reveal the function of *PpcMADS*, the property and structure of proteins were analyzed using bioinformatics methods. The results showed that 16 *PpcMADS* genes belonged to MIKC family, while KP347550 and KP347552 were the members of M-type. Most of them were unstable hydrophilic proteins. The secondary structure of *PpcMADS* protein included alpha helix, beta turn, extended strand and random coil, and alpha helix was major part. Most of *PpcMADS* proteins located in nucleus, while KP347549 may locate in cytoplasm, KP347545 and KP347552 were more likely to locate in plasma membrane. Four motifs were identified from *PpcMADS* protein, and the Motif 1 was the conserved structure of MADS-box family contained MADS domain. The result of phylogenetic analysis revealed that 18 *PpcMADS* genes could be divided into AP3 subclass, PI subclass, SHP subclass, AG subclass, AP1 subclass, SEP subclass, SOC subclass, SVP subclass and four unknown subclass. KP347545, KP347546, KP347547, KP347549, KP347551, KP347552, KM243373, KM243375 and KM243377 only expressed in flower, KP347548 and KP347550 did not express in flower and fruit, while the other 7 *PpcMADS* genes expressed in fruit and flower.

Key words: cherry; MADS-box; transcription factor; bioinformatics; expression analysis

MADS-box转录因子是真核生物中一类在进化上高度保守的基因家族, 其名称分别来自酿酒酵母*MCM1*基因、拟南芥*AGAMOUS*基因、金鱼草*DEFICIENS*基因和人血清应答因子*SRF4*基因的首字母, 在这些基因编码的蛋白质中均含有由56~58个氨基酸组成的高度保守区域, 被称为MADS盒(Messenguy和Dubois 2003)。现已先后在多种果树中分离出MADS-box转录因子, 包括葡萄(Poupin等

2007)、香蕉(张远森等2013; Hubert等2014)、桃(Li等2009; Yamane等2011)、梨(Saito等2013; Bai等2013)以及森林草莓(周厚成等2014)等。

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根据结构特征, 可将植物MADS-box转录因子分为两种类型: Type I和Type II。其中Type II主要由MADS (M)区、Intervening (I)区、Keratin-like (K)区和C-terminal (C)末端组成, 所以又被称为MIKC型(Kaufmann等2005), 且K区只存在于Type II中。植物MADS-box基因家族数量较多, 参与了植物根(Ku等2008)、茎(Ferrario等2006)、叶(Burko等2013)、花(Immink等2010)、果实的生长发育(Busi等2003)以及果实的成熟过程(Wang等2014; Xie等2014), 被认为是调节植物生长发育的关键基因家族。

樱桃属于蔷薇科李属的多年生落叶果树, 在中国具有悠久的栽培历史, 其果实成熟期早, 素有“早春第一果”的美誉, 备受消费者喜爱。随着现代农业的快速发展, 因樱桃具有观赏性和早熟性(2~3月开花、4~5月成熟)等特点而被高度重视。因此开展樱桃花与果实分子生物学研究具有重要意义。为了更加全面研究樱桃花和果实生长发育调控机制, 本研究通过分析樱桃花芽转录组文库(GenBank登录号SRX695147), 发现了45个Unigene序列被注释为MADS-box转录因子(*PpcMADS*), 其中18个序列具有完整的ORF, 但其生物信息学和表达特性仍不清楚。为此, 本文对18个*PpcMADS*基因的结构和表达进行了系统分析, 为探明樱桃MADS-box转录因子功能提供了理论依据。

材料与方法

1 植物材料及序列来源

选用6年生樱桃(*Prunus pseudocerasus* Lindl.)‘短柄(Duanbing)’品种为植物材料。取需冷量完全满足的带花芽枝条, 长度约20 cm, 插在含有适量清水的烧杯中, 于光照培养箱中培养花芽萌发, 昼/夜温度为(25±1) °C/(20±1) °C, 湿度为70%, 光照强度为320 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 选取花和幼嫩果实作为MADS-box转录因子表达分析材料。所有样品液氮速冻后-80 °C保存用于总RNA提取。

MADS-box转录因子基因序列来自中国樱桃花芽转录组数据(GenBank登录号SRX695147)(Zhu等2015)。使用NCBI在线分析程序ORF Finder(Open Reading Frame Finder, <http://www.ncbi.nlm.nih.gov/projects/gorf/>)查找开放阅读框, 45个Uni-

gene序列被注释为MADS-box转录因子, 但只有18个序列含有完整的ORF, 以此作为后期分析的主要对象, GenBank登录号见表1。

2 MADS-box转录因子序列分析

氨基酸序列预测在植物转录因子数据库(Plant Transcription Factor Database, <http://planttfdb.cbi.pku.edu.cn/>)进行, 并在数据中筛选与*PpcMADS*相似性最高的桃(*Prunus persica*)和拟南芥(*Arabidopsis thaliana*)MADS-box转录因子序列用于进化树构建。进化树构建使用MEGA5.1软件neighbor-joining法则的P-距离(P-distance)模型Bootstrap method值为1 000。二级结构预测使用SOPMA程序完成(https://npsa-prabi.ibcp.fr/cgi-bin/npsa_automat.pl?page=npsa_sopma.html); 亚细胞定位预测由在线软件PSORT Prediction完成(<http://psort.hgc.jp/form.html>); 分子量、等电点、不稳定性等参数分析采用ProtParam在线工具(<http://www.expsy.org/tools/protparam>)。氨基酸序列保守基序(motif)分析利用在线软件MEME (Multiple Expectation Maximization for Motif Elicitation)工具(Motif-based sequence analysis tools, <http://meme.nbcr.net/meme/cgi-bin/meme.cgi>)进行, 参数设置为: 同一基序在1条序列中出现0或1次, 基序最大发现值为4, 长度范围为60个氨基酸残基, 其他参数为默认值。基序序列特征分析采用SMART (Simple Modular Architecture Research Tool, <http://smart.embl-heidelberg.de/>)在线软件分析。

3 樱桃MADS-box的表达分析

总RNA提取采用改良CTAB法, RNA质量检测采用分光光度法(Nanodrop), RNA浓度测定采用Agilent 2100 Bioanalyzer。cDNA的第一链合成采用PrimeScript™ 1st Strand cDNA Synthesis Kit (TaKaRa), cDNA保存于-20 °C。根据反转录PCR(reverse transcription PCR, RT-PCR)引物设计原则, 利用Primer Premier 5.0软件, 分别设计PCR引物, 内参基因选用肌动蛋白基因 $ACTB$ (β -actin), 所用引物由上海英骏生物技术有限公司合成, 序列见表1。RT-PCR反应体系为20 μL , 扩增程序为: 95 °C预变性30 s; 95 °C变性5 s, 60 °C退火30 s, 72 °C延伸30 s, 35个循环; 扩增产物使用3.0%琼脂糖凝胶检测。

表1 引物序列

Table 1 Sequences of primer for RT-PCR

GenBank登录号	引物名称	引物序列(5'→3')	扩增产物长度/bp
KM243368	Unigene16199 RP1	CGATTAGTTGAGAATGGAGGGAGAGGA	152
	Unigene16199 RP2	CAAGGCATAGTGGCGGTGA	
KM243369	Unigene14775 RP1	TGAAAATGAAAGGGCACACAGC	115
	Unigene14775 RP2	GGCCTCCAAGATTACAGGGAGG	
KM243370	Unigene12685 RP1	GTTCTGTAGCGCGAGAGTTAGG	159
	Unigene12685 RP2	ATTGTTTCAGTGACCGGTTAGGG	
KM243371	Unigene12679 RP	ATGCTAAATGAAGCAAATAAGACCCTGA	165
	Unigene12679 RP2	AATCTGTAACGTCGGCTCGCA	
KM243372	CL3592.Contig1 RP1	GTGATGGCTGGAGGGGGAAAG	108
	CL3592.Contig1 RP2	GCGTGAATTGTTACTGATGATTGGGT	
KM243373	Unigene4589 RP1	GCTGCACAAACAGGAGATGAAAATT	117
	Unigene4589RP2	ATAGGCTGAACACGAAAGGCAAAC	
KM243374	Unigene13475 RP1	CAGGAAAGAACAGGAAATCTGCTACATG	139
	Unigene13475 RP2	GGTGGATAGTGAACAAGTTGGACG	
KM243375	Unigene9506 RP1	AAGTTCCGTACATCATCTCTCTAG	147
	Unigene9506 RP2	TCAATTGCTCACATATTCTTCCAC	
KM243376	Unigene11986 RP1	AACAAGGAACAAATGCTAGTTGAAGCTAA	155
	Unigene11986 RP2	TGTGAGTGAGGATGATGAGGAAGG	
KM243377	Unigene11472 RP1	GGAACCATTATATTGATGCAACCTCG	167
	Unigene11472 RP2	GATGGGATTGCGACCACATACCT	
KP347545	Unigene17998 RP1	CCAACAACAAATCCGTTTCCACTG	128
	Unigene17998 RP2	CATGATCCTAGACCCCTCTCCAAAGA	
KP347546	CL5469 RP1	GCCCACAACTCATCCACCC	128
	CL5469 RP2	TCACCATCTTCATCCCTCC	
KP347547	CL1634 RP1	TGGGAAGGATGACACTTGTAGCA	239
	CL1634 RP2	TCCCGTAGCTTAGCATTTGTTCA	
KP347548	Unigene11917 RP1	GCGTGTAGAGATGCAAAGGGTG	217
	Unigene11917 RP2	GAAGTGCCAGAGCTGTCGTGG	
KP347549	Unigene15348 RP1	CAAAAGGAAAACGATCTGGAGAGA	186
	Unigene15348 RP2	TTCTGGGAACTGGTTGGT	
KP347551	Unigene6650 RP1	AGCTGGAAAACGAAAATGTGTGTC	174
	Unigene6650 RP2	TCTCTTGCTTGCTGTGGTAGG	
KP347550	Unigene23051 RP1	GAAACAAGTCCAATGGAACCAAC	138
	Unigene23051 RP2	ACCTCAGGCCACAGCACCAA	
KP347552	Unigene23321 RP1	ATTGGTGTCAATTGTTCTCCCT	151
	Unigene23321 RP2	GCCTCTCCACTGTTCATCATTCTT	
ACTB	Unigene353 RP1	CATTCTCGTCTGGACCTTGCTG	118
	Unigene353 RP2	TATCACGGACAATTCCCCGCTC	

实验结果

1 樱桃MADS-box序列的生物信息学分析

在樱桃花芽转录组中发现45个Unigene序列被注释为MADS-box转录因子, 18个序列含有完整的ORF。将18个MADS-box氨基酸序列在PlantTFDB数据库中进行预测, 结果表明KP347550和KP347552属于M-type家族, 不含有K盒结构, 其他

均为MIKC家族, 同时获得了每个序列相似性最高的桃和拟南芥同源基因序列(表2)。

采用ProtParam在线分析工具获得了中国樱桃MADS-box氨基酸序列的分子量、等电点、不稳定性等基本信息(表3)。除KP347552(187个氨基酸)以外, 其他MADS-box氨基酸序列均在200~270个残基之间。对应分子量在18 554.0~30 702.8 Da之间, 等电点分析发现, 除KP347548的等电点为

表2 樱桃MADS-box转录因子在PlantTFDB数据库预测信息

Table 2 Prediction of cherry MADS-box in PlantTFDB

GenBank登录号	家族	同源性最高的桃氨基酸ID及E值	同源性最高的拟南芥氨基酸ID及E值	描述
KM243368	MIKC	ppa026083m (1e-129)	AT3G54340.1 (2e-82)	K-box region and MADS-box
KM243369	MIKC	ppa010578m (1e-149)	AT3G58780.1 (1e-114)	K-box region and MADS-box
KM243370	MIKC	ppa015338m (5e-41)	AT1G26310.1 (3e-44)	K-box region and MADS-box
KM243371	MIKC	ppa010679m (0)	AT1G24260.1 (1e-130)	K-box region and MADS-box
KM243372	MIKC	ppa010595m (0)	AT4G18960.1 (1e-126)	K-box region and MADS-box
KM243373	MIKC	ppa012927m (1e-100)	AT5G20240.1 (2e-88)	K-box region and MADS-box
KM243374	MIKC	ppa010807m (1e-150)	AT3G54340.1 (2e-73)	K-box region and MADS-box
KM243375	MIKC	ppa019932m (9e-48)	AT5G62165.3 (1e-82)	AGAMOUS-like 42
KM243376	MIKC	ppa010391m (0)	AT5G15800.1 (1e-106)	K-box region and MADS-box
KM243377	MIKC	ppa010723m (1e-144)	AT1G69120.1 (1e-118)	K-box region and MADS-box
KP347545	MIKC	ppa010578m (7e-47)	AT2G45660.1 (4e-98)	AGAMOUS-like 20
KP347546	MIKC	ppa010249m (1e-131)	AT5G60910.1 (2e-90)	AGAMOUS-like 8
KP347547	MIKC	ppb018415m (3e-56)	AT4G22950.1 (9e-82)	AGAMOUS-like 19
KP347548	MIKC	ppa011063m (1e-70)	AT2G22540.1 (2e-73)	K-box region and MADS-box
KP347549	MIKC	ppa022942m (1e-96)	AT2G45650.1 (6e-69)	AGAMOUS-like 6
KP347551	MIKC	ppa011140m (1e-164)	AT4G09960.1 (1e-118)	K-box region and MADS-box
KP347550	M-type	ppa018168m (1e-147)	AT5G48670.1 (2e-66)	AGAMOUS-like 80
KP347552	M-type	ppa024816m (1e-119)	AT2G34440.1 (1e-48)	AGAMOUS-like 29

表3 樱桃MADS-box转录因子氨基酸基本信息

Table 3 The basic information of cherry MADS-box

GenBank登录号	阅读框长度/bp	氨基酸数量/aa	分子量/Da	等电点	不稳定系数	脂肪系数
KM243368	615	204	23 564.9	9.87	40.98	70.74
KM243369	741	246	18 554.0	9.55	65.93	73.78
KM243370	648	215	24 329.7	8.82	51.69	84.37
KM243371	723	240	27 570.3	8.79	39.72	80.50
KM243372	732	243	27 978.6	9.44	60.93	73.91
KM243373	633	210	24 324.6	8.40	47.41	82.62
KM243374	708	235	27 152.8	9.42	46.70	82.55
KM243375	642	213	24 430.8	8.36	60.16	82.86
KM243376	756	251	28 613.4	8.82	38.44	80.44
KM243377	717	238	27 889.9	8.66	50.45	86.89
KP347545	648	215	24 782.1	9.24	63.12	75.72
KP347546	810	269	30 702.8	8.45	59.15	77.62
KP347547	660	219	24 988.6	9.04	47.68	75.25
KP347548	660	219	24 585.0	6.93	49.26	92.65
KP347549	723	240	27 638.3	8.23	41.93	84.04
KP347550	681	226	26 142.2	9.36	52.14	71.19
KP347551	669	222	25 640.3	9.41	51.91	85.27
KP347552	570	187	20 772.7	9.37	49.85	75.67

6.93显酸性以外, 其他均大于8.2, 显碱性。从不稳定系数来看, KM243371和KM243376小于40, 为稳定蛋白, 其他均大于40, 为不稳定蛋白。由脂肪系数可知, 18个MADS-box蛋白均小于100, 为亲水性蛋白。SOPMA程序分析(表4)发现, 樱桃MADS-

box蛋白二级结构均含有 α -螺旋(alpha helix)、 β -转角(beta turn)、扩展链(extended strand)和无规则卷曲(random coil)结构。其中, α -螺旋所占比例最高, 其次是无规则卷曲(KP347551除外)。亚细胞定位分析发现, KP347549定位到细胞质的几率较高,

表4 樱桃MADS-box转录因子蛋白质二级结构与亚细胞定位

Table 4 The secondary structure and subcellular localization of cherry MADS-box

GenBank登录号	α -螺旋/个	β -转角/个	扩展链/个	无规则卷曲/个	亚细胞定位
KM243368	106	26	35	37	细胞核
KM243369	131	18	30	67	细胞核
KM243370	105	7	36	67	细胞核
KM243371	137	13	29	61	细胞核
KM243372	125	14	45	59	细胞核
KM243373	97	24	44	45	细胞核
KM243374	107	26	50	52	细胞核
KM243375	133	15	24	41	细胞核
KM243376	134	16	35	66	细胞核
KM243377	141	18	34	45	细胞核
KP347545	130	9	22	54	质膜
KP347546	128	20	39	82	细胞核
KP347547	123	15	29	52	细胞核
KP347548	118	16	40	45	细胞核
KP347549	127	17	36	60	细胞质
KP347551	135	21	36	30	细胞核
KP347550	122	11	25	68	细胞核
KP347552	101	15	20	51	质膜

KP347545和KP347552定位到质膜的几率较高, 其他蛋白定位到细胞核的几率较高。

2 樱桃MADS-box氨基酸序列保守基序分析

利用MEME软件分析了中国樱桃MADS-box氨基酸序列的保守基序, 结果发现4种类型基序(图1), 其中基序1含57个氨基酸, 在所有MADS-box序列中均含有, 最佳匹配序列为MGRGKIEIKRIENTTNRQVTFCKRRNGLFKKAYELSVLCDAE-VALIIFSPRGKLYEY, SMART软件分析表明该基序为MADS盒, 是MADS-box转录因子的典型结构, 属于SRF-TF结构域(Pfam reference登录号PF00319)。在MADS盒之后的是I (Intervening)区, 包含基序3, 最佳匹配序列为SSSSMQKTIERYQKCCYD, 但在KM243368、KM243374和KP347550序列中不包含基序3。I区之后是K (Keratin)区, 包含基序2, 除KP347552以外, 所有序列均含有基序2, 最佳匹配序列为KAQIEVLQRSQRHLLGEDLDPCTHKELQNLEHQLETGLNRIRSRKTQFM。最后是基序4, 除KM243373、KP347550和KP347552外, 其他序列均含有, 最佳匹配序列为DQIEYLQWK-EKMLQEENNCLRHKIAE (图2)。

3 樱桃MADS-box转录因子保守结构域系统进化分析

采用邻接法对樱桃、桃和拟南芥MADS-box

保守结构域进行系统进化分析, 结果如图3所示。樱桃MADS-box转录因子被分为12个亚组。其中KM243368和KM243374属于AP3亚组, KM243373属于PI亚组, KM243369和KM243372属于SHP亚组, KP347551属于AG亚组, KM243377和KP347546属于AP1亚组, KM243371、KM243376和KP347549属于SEP亚组, KM243375、KP347545和KP347547属于SOC亚组, KP347548属于SVP亚组; 其他序列分别属于4个未知亚组。

4 樱桃MADS-box转录因子表达特性分析

采用RT-PCR技术对PpcMADS进行表达分析发现(图4), 尽管18个樱桃MADS-box转录因子克隆均来自花芽组织, 但在花和果实中表达模式不同。KP347548和KP347550在花和果实中均不表达, KP347545、KP347546、KP347547、KP347549、KP347551、KP347552、KM243373、KM243375和KM243377只在花中表达, 其他基因在两个组织中都表达。

讨 论

随着高通量测序技术的发展, 越来越多果树的MADS-box转录因子家族基因被系统研究, 主要有葡萄(*Vitis vinifera*) 38个(Diaz-Riquelme等2009)、

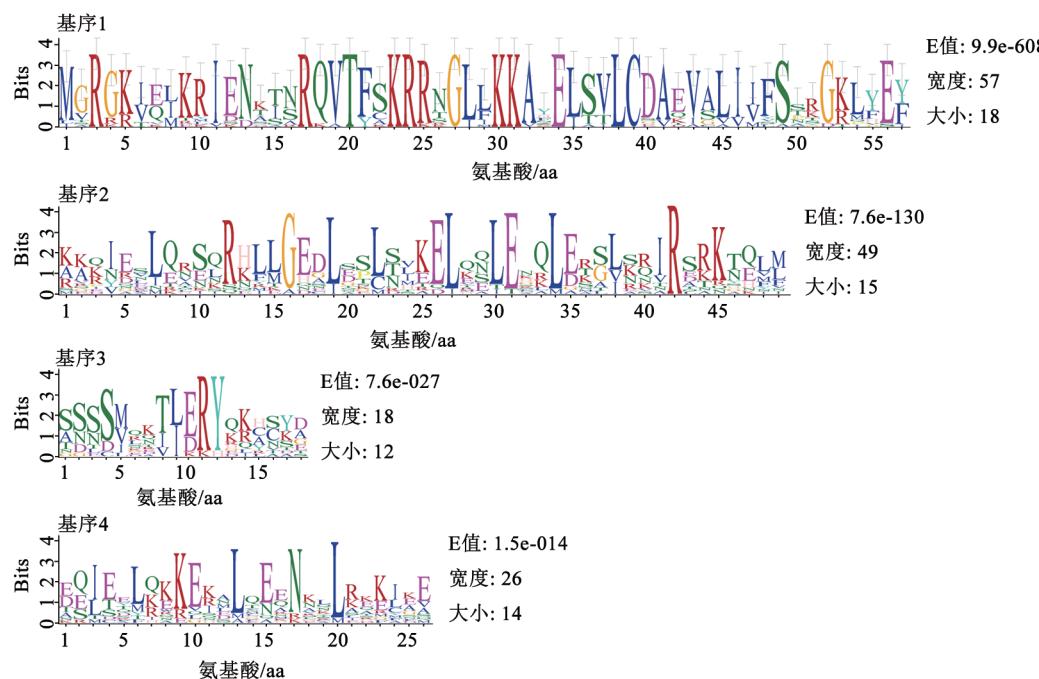


图1 樱桃MADS-box保守基序

Fig.1 Conserved motifs identified from MADS-box of cherry using MEME

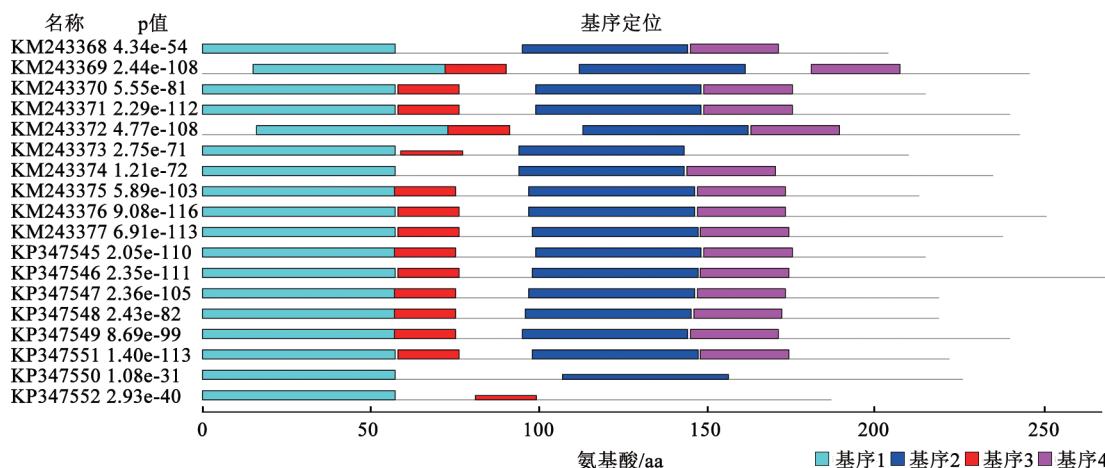


图2 樱桃MADS-box转录因子推导氨基酸序列保守基序及分布图

Fig.2 Distribution of Motifs in deduced amino acid of cherry MADS-box

香蕉(*Musa acuminata*) 71个(张远森等2013)、森林草莓(*Fragaria vesca*) 85个(周厚成等2014)、梅(*Prunus mume*) 80个(Xu等2014)以及苹果(*Malus domestica*) 146个(Tian等2015)。在植物转录因子数据库(PlantTFDB)中共有5 842个MADS-box转录因子, 其中M-type 2 978个和MIKC型2 864个, 分布在83个物种中, 其中桃(*Prunus persica*)含有80个。本研究在缺少樱桃基因组信息的情况下, 首次通

过分析花芽转录组数据获得了18个具有完整ORF的MADS-box转录因子, 丰富了植物MADS-box基因家族信息, 也为樱桃生长发育调控研究奠定了基础。关于樱桃MADS-box转录因子的报道较少, 林苗苗等(2011a, b)先后在甜樱桃(*Prunus avium*)克隆了*PaMADS2*和*PaMADS3*, 分析发现*PaMADS2*与B类*PI*基因关系较近, 在雄蕊和花瓣中表达, 而*PaMADS3*则与*SEP*高度同源, 在花瓣、雄蕊、心皮中

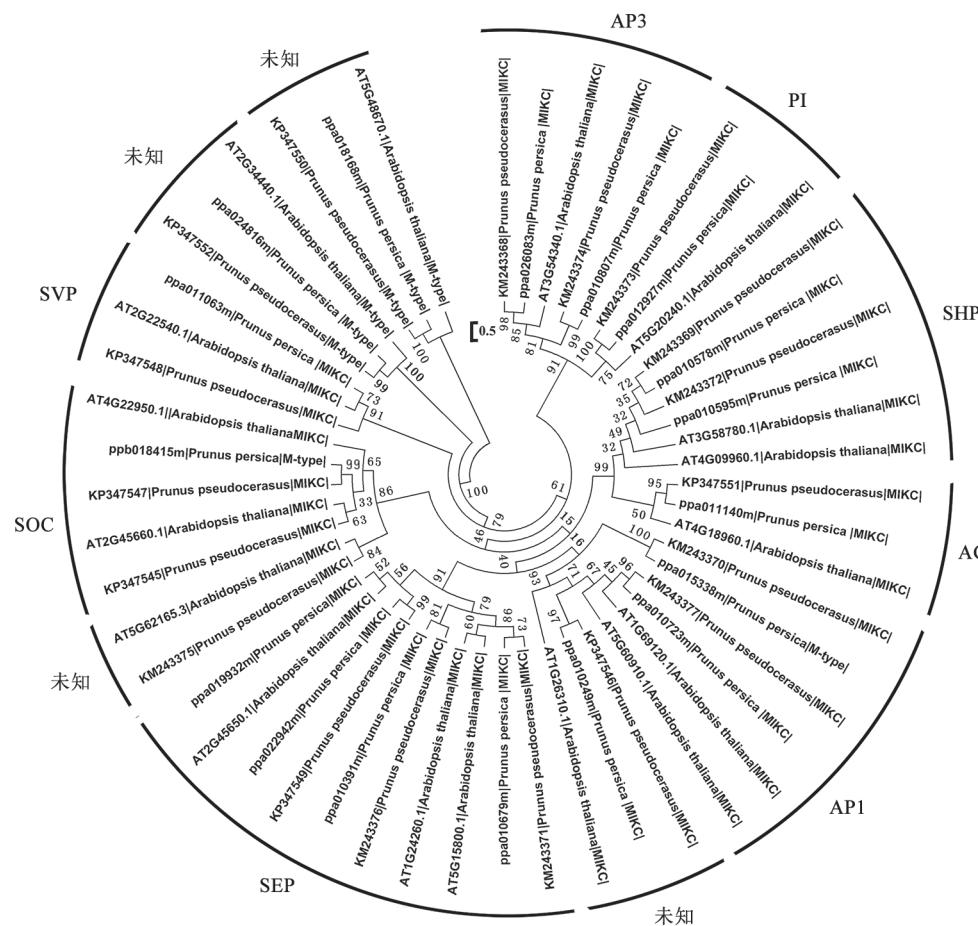


图3 樱桃、桃和拟南芥的MADS-box转录因子保守结构域系统进化树
Fig.3 Phylogenetic tree of MADS-box conserved domain from cherry, peach and *Arabidopsis*

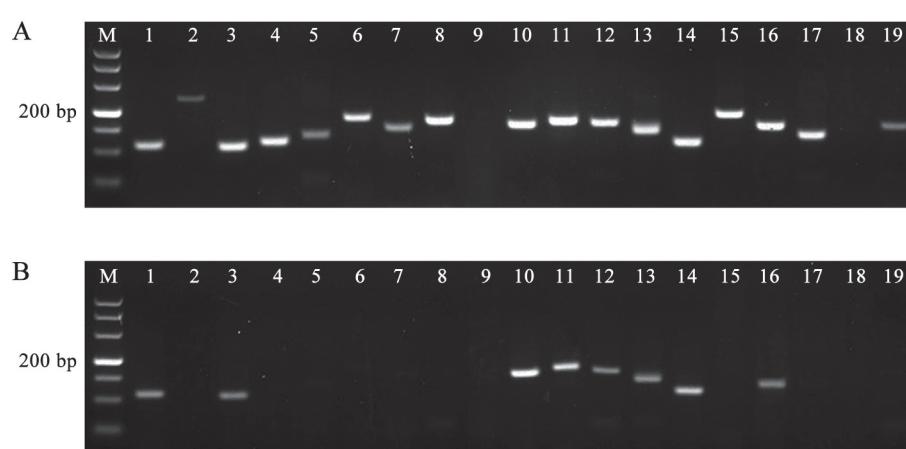


图4 樱桃MADS-box在花和果实中的表达分析
Fig.4 Expression analysis of Cherry MADS-box in flower and fruit using RT-PCR

A: 花; B: 果实。M: DM500 DNA marker; 1: *ACTB*; 2: KP347547; 3: KM243372; 4: KM243373; 5: KP347546; 6: KP347551; 7: KM243375; 8: KM243377; 9: KP347548; 10: KM243376; 11: KM243371; 12: KM243370; 13: KM243374; 14: KM243369; 15: KP347549; 16: KM243368; 17: KP347545; 18: KP347550; 19: KP347552。

表达。在拟南芥中超量表达甜樱桃*PaAPI*基因促进转基因拟南芥提前开花(Wang等2013)。

关于MADS-box转录因子在花发育中的功能研究较深入, 现已根据金鱼草和拟南芥的研究结果提出了ABC模型, 随后发展为ABCDE模型(Theissen 2001)。*APETALA1 (API)*属于A类基因、*PISTILATA (PI)*和*APETALA3 (AP3)*属于B类基因、*AGAMOUS (AG)*属于C类基因、*SEEDSTICK (STK)*和*SHATTERPROOF (SHP)*属于D类基因、*SEPALLATA (SEPI、SEP2、SEP3和SEP4)*属于E类基因(Kaufmann等2005)。萼片发育由A/E调控、花瓣发育由A/B/E调控、雄蕊发育由B/C/E调控、心皮发育由C/E调控、胚珠发育由D/E调控(Theissen 2001)。根据进化关系, 可推测KM243377和KP347546属于A类基因, 调控萼片和花瓣发育; KM243368、KM243373和KM243374属于B类基因, 调控花瓣和雄蕊发育; KP347551属于C类基因, 调控雄蕊和心皮发育; KM243369和KM243372属于D类基因, 调控胚珠发育; KM243371、KM243376和KP347549属于E类基因, 可先后调控萼片、花瓣、雄蕊、心皮和胚珠发育; KM243375、KP347545和KP347547属于*SUPPRESSOR OF OVEREXPRESSION OF CONSTANS (SOC1)*类(Zhu等2015), KP347548属于SVP类, 可能调控开花时间(Wu等2012)。

MADS-box转录因子也可以调控果实发育和成熟。*FRUITFULL (FUL-1)*属于AGL8类MADS-box转录因子, 在拟南芥果实发育过程中调控细胞分化(Gu等1998)。苹果*MdMADS4*与拟南芥*AGL2*和*AGL4*同源, 在果实形态分化期心皮维管束和种胚中表达(Sung等2000)。在番茄中, *FRUITFULL*同源基因*FUL1*和*FUL2*对LeMADS-RIN产生关键性调控(Fujisawa等2014), RIN进一步通过调控乙烯合成关键酶*ACS2*基因的表达而调控番茄的成熟(Vrebalov等2002), LeMADS-MC在萼片、花瓣和心皮中表达(Martel等2011; Shima等2013)。番茄*MADS1*在萼片和果实中表达, 该基因功能缺失后, 乙烯合成基因和响应基因均上调表达而加快成熟(Dong等2013)。超量表达MADS-box基因*SIFYFL*能够延缓衰老、脱落和果实成熟(Xie等2014)。在香蕉中, *MuMADS1*属于D类基因, 在雄蕊和果实不同发育阶段表达, 通过参与乙烯响应而与果实成熟密切相关(Liu等2009)。香蕉*MaMADS1*和*Ma-*

*MADS3*参与果皮发生, *MaMADS2*参与果肉中乙烯合成(Elitzur等2010)。在桃中, *PpPLENAZA*基因在果实成熟过程中表达增强, 在转基因番茄中超量表达后促进果实形成浆果, 而在转基因草莓中加速果实成熟(Zhang等2008)。*AGAMOUS-like*、*SEEDSTICK-like*和*SEPALLATA-like*被证实在桃果实发育和成熟过程中发挥作用(Tani等2009)。在草莓中, *FaMADS9*属于*SEPI/2 like*基因, 表达沉默后花瓣、种子和果实发育和成熟受阻(Vrebalov等2002; Seymour等2011)。在本研究中并未发现果实特异性表达的*PpcMADS*, 因此, 它们在果实发育中的作用还需要进一步研究。此外, 还有研究发现MADS-box基因参与落叶果树花芽休眠与休眠解除, 但其调控机制仍不清楚(Zhu等2015)。

由以上各方面可以看出, 植物MADS-box转录因子是一个庞大的基因家族, 在植物生长发育中发挥着不同功能。本研究利用转录组数据分析了18个中国樱桃MADS-box转录因子氨基酸基本信息、亚细胞定位、二级结构、保守结构域特征和系统进化关系以及在花和果实中的表达特性, 丰富了MADS-box转录因子家族信息, 为进一步研究它们在花和果实发育中的调控机制奠定了基础。

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