

# 大白菜脱水素基因的鉴定和特征分析

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## 摘要

植物脱水素在非生物逆境响应过程中具有重要功能。但在我国重要蔬菜作物大白菜中缺乏研究。本文利用生物信息学的方法, 鉴定出12个大白菜脱水素基因, 对它们的结构特征、遗传进化和顺式调控元件进行了预测。结果显示, 大白菜的脱水素基因在基因组中非均衡分布, 大部分基因含有两个外显子, 所有的大白菜脱水素可划分为两个不同的类群, 其中*BrDhn4*单独为一个类群。顺式元件预测表明, 大白菜脱水素基因含有多个响应环境和激素信号的顺式元件, 可能在非生物逆境以及植物激素响应中具有一定功能。

## 关键词

大白菜, 脱水素, 结构, 进化, 顺式元件

# Identification and Characterization of Chinese Cabbage Dehydrin Genes

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## Abstract

Plant dehydrins play important roles in the process of abiotic stress responses. However, the dehydrin knowledge about the important vegetable—Chinese cabbage is scarce. In this paper, 12 dehydrin genes were identified in the Chinese cabbage genome through the bioinformatics method. Also, their structure, phylogeny and the cis-elements of them were analyzed. The results indicated that Chinese cabbage dehydrin genes are unevenly distributed in the genome, and most of them have 2 exons. They are divided into two phylogeny groups, and *BrDhn4* is singly as one group. What's more, Chinese cabbage dehydrin genes each have several different cis-elements responsive to different hormones and environmental stimuli, which suggests they may be involved in multiple abiotic stress and hormone responses.

## Keywords

Chinese Cabbage, Dehydrin, Structure, Phylogeny, Cis-Element

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## 1. 引言

脱水素是植物种子胚胎晚期丰富性蛋白(LEA)的一类,最初是在水稻和棉花种子中发现的。后来发现,脱水素在植物的营养器官和脱水组织中也普遍表达[1]。这类蛋白的一个共同特征是含有一个由富含赖氨酸的 15 个氨基酸残基组成的保守的结构域 EKKGIMDKIKEKLP,为脱水素的特征结构域,叫 K 结构域,一般位于碳末端附近[2]。它是脱水素行使其功能的结构基础,可以形成一个两亲  $\alpha$ -螺旋[3] [4],有助于与细胞膜的连接和在抗菌中发挥作用[5] [6]。另外,有的脱水素成员还含有一个富含丝氨酸残基的片段 S 片段,它被磷酸化后可将脱水素转运到向细胞核[7] [8];有的成员还有一个位于氮末端的 Y 片段 T/VDEYGNP,可与植物和细菌分子伴侣的核苷酸结合位点相匹配,发挥分子伴侣的功能[9] [10]。根据这三个保守区段的位置和数目的不同,将脱水素分为五个亚类: YnSKn、YnKn、SKn、Kn 和 KnS [11]。最近研究表明,苔藓脱水素 PpDHNA 中含有 D-segment: EG  $\phi$   $\phi$  D(R/K)AKDA  $\phi$ ,可能在减轻极端胁迫方面具有重要功能[12]。在一些脱水素中如拟南芥的 COR47 和杜鹃脱水素中含有 11 个氨基酸残基组成的 F-区段 DRGLDFDLGKK,具有乳酸脱氢酶保护的功能,可提高其冷胁迫的耐性[13] [14]。脱水素一般受 ABA 的诱导表达,在非生物逆境如干旱、盐、低温、重金属胁迫下大量累积[15] [16] [17]。它们可定位在细胞不同的部位,但主要定位在细胞质和细胞核中[18]。脱水素是植物细胞中的一类保护性物质,体外分析的结果显示 YSKn 类脱水素可以结合脂肪颗粒,KnS 可与金属离子结合,能够清楚羟自由基,防止脂膜过氧化,或者对冷敏感的酶具有保护作用[19] [20] [21]。越来越多的证据表明,脱水素在植物耐受非生物逆境过程中具有重要功能,不同类型的脱水素可能具有不同的功能[22] [23] [24]。

尽管脱水素的研究在拟南芥[25] [26]、大麦[27]、小麦[28]、水稻[29] [30]、短柄草[31]、玉米[32]、

大豆[33]、松树[34]、柑橘[35]、油菜[36]等植物上取得了很大进展,但是目前在我国重要蔬菜大白菜中只有一个脱水素基因报道[37]。大白菜基因组测序和数据库的建立,为解析大白菜功能基因提供了极大便利[38] [39]。本文利用比较基因组学和生物信息学的方法,从大白菜的基因组中鉴定出 12 个脱水素基因,并对这 12 个脱水素基因的遗传进化、编码蛋白的特征以及其顺式调控元件进行了分析,为下一步研究大白菜脱水素基因的功能和利用脱水素基因改良大白菜的抗逆性奠定基础。

## 2. 材料与方法

利用拟南芥中的脱水素基因序列在 Genbank 中搜索比对大白菜的基因组序列和 EST 序列 (<http://blast.ncbi.nlm.nih.gov/Blast.cgi>),寻找大白菜的脱水素基因序列,并对鉴定出的大白菜脱水素基因进行进化分析和编码蛋白的结构分析,对它们在亚细胞组分中的定位进行预测,对脱水素基因启动子及上游序列(1500 bp)中的顺式调控元件进行分析。遗传进化分析利用 MEGA4.1 来进行进化树的构建,采用 Bootstrap Test-Neighbor Joining 方法,重复 500 次运算。蛋白结构分析通过 PlantsP Feature Scan ([http://plantsp.genomics.purdue.edu/html/feature\\_scan.html](http://plantsp.genomics.purdue.edu/html/feature_scan.html))来进行。顺式调控元件分析在 PlantCARE (<http://bioinformatics.psb.ugent.be/webtools/plantcare/html/>)中进行在线分析。

## 3. 结果与分析

### 3.1. 大白菜脱水素基因的鉴定和特征分析

本文通过生物信息学分析从白菜基因组中鉴定出 12 个脱水素基因,按照它们在染色体上的分布顺序分别命名为 *BrDhn1* 到 *BrDhn12*,其中一个已被报道的基因 *COR25* 在本文中命名为 *BrDhn6* (见表 1)。脱水素基因的编码蛋白序列分析表明, *BrDhn1* 编码的脱水素除含有一个 K 结构域外,其它特征不明显, *BrDhn4* 编码 KS 类型, *BrDhn3*、*BrDhn10*、*BrDhn11* 和 *BrDhn12* 编码  $Y_nSK_n$  类型的脱水素,其余脱水素基因编码  $SK_n$  类型的脱水素。这些脱水素基因编码区大小从 288 bp 到 816 bp 不等, *BrDhn4* 只有一个外显子,而 *BrDhn3* 有 3 个外显子,其余脱水素基因都含有 2 个外显子(见图 1)。染色体分布分析显示, *BrDhn1*、*BrDhn4*、*BrDhn5* 和 *BrDhn9* 分别位于 1 号、3 号、6 号和 8 号染色体, *BrDhn2* 和 *BrDhn3* 位于 2 号染色体, *BrDhn6*、*BrDhn7* 和 *BrDhn8* 三个基因位于 7 号染色体, *BrDhn10*、*BrDhn11* 和 *BrDhn12* 位于 9 号染色体。亚细胞定位预测结果表明, *BrDhn1*、*BrDhn2* 和 *BrDhn7* 编码蛋白定位在细胞核或者细胞质中, *BrDhn4* 和 *BrDhn5* 编码蛋白定位在细胞质或者细胞核中,其余脱水素只定位到细胞核中。

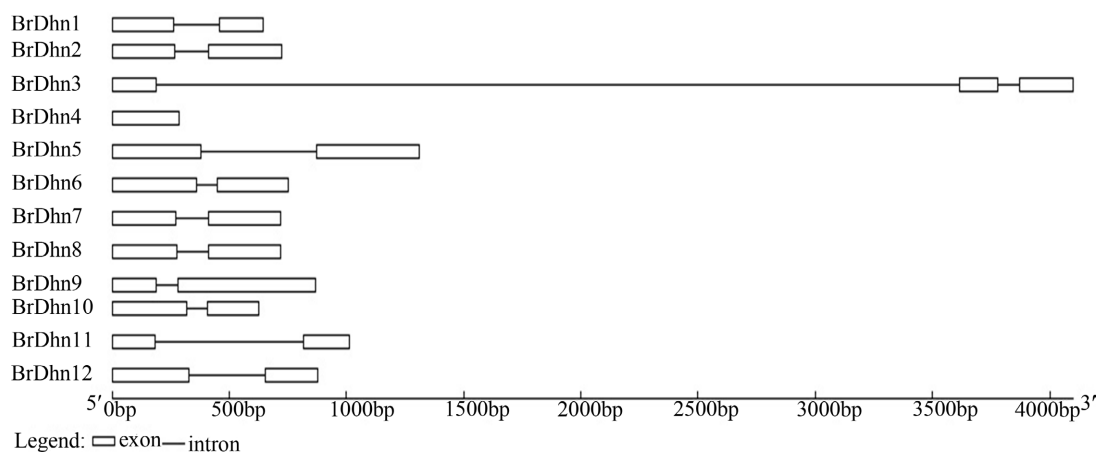
**Table 1.** Chinese cabbage dehydrin genes and their characters

**表 1.** 大白菜脱水素基因及其特征

Gene	Chromo-some	Locus	Exons	Cds (bp)	Type	Subcellular localization
<i>BrDhn1</i>	A01	130221-130836	2	450	Unidentified	Nuclear, cytosol
<i>BrDhn2</i>	A02	14031452-14032176	2	585	SK <sub>2</sub>	Nuclear, cytosol
<i>BrDhn3</i>	A02	27801269-27805365	3	579	Y <sub>2</sub> SK <sub>2</sub>	Nuclear
<i>BrDhn4</i>	A03	19885050-19885337	1	288	KS	Cytosol, nuclear
<i>BrDhn5</i>	A06	8221432-8222743	2	816	SK <sub>3</sub>	Cytosol, nuclear
<i>BrDhn6</i>	A07	9172941-9173693	2	663	SK <sub>2</sub>	Nuclear
<i>BrDhn7</i>	A07	14744193-14744913	2	585	SK <sub>2</sub>	Nuclear, cytosol
<i>BrDhn8</i>	A07	20893371-20894088	2	588	SK <sub>2</sub>	Nuclear

Continued

<i>BrDhn9</i>	A08	4847473-4848338	2	774	SK <sub>6</sub>	Nuclear
<i>BrDhn10</i>	A09	4131765-4132388	2	435	Y <sub>2</sub> SK <sub>2</sub>	Nuclear
<i>BrDhn11</i>	A09	25451005-25452016	2	405	YSK <sub>2</sub>	Nuclear
<i>BrDhn12</i>	A09	32069086-32069961	2	552	Y <sub>3</sub> SK <sub>2</sub>	Nuclear



**Figure 1.** Intron-exon structure of Chinese cabbage dehydrin genes

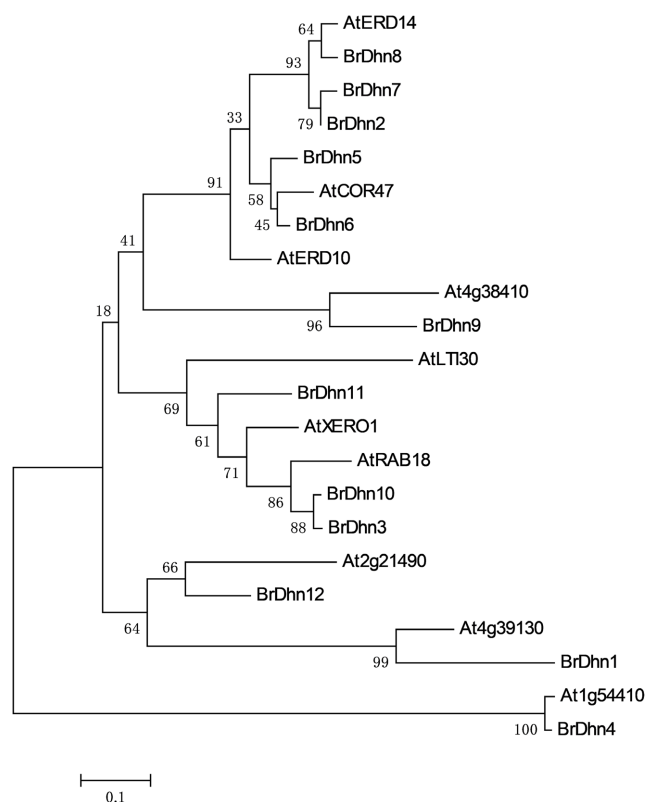
**图 1.** 大白菜脱水素基因的内含子 - 外显子结构

### 3.2. 大白菜脱水素基因的进化分析

为了寻找大白菜脱水素基因的功能线索,在得到大白菜的脱水素序列后,本文对它们的遗传进化进行了分析(见图 2)。结果表明,大白菜的脱水素基因可划分为两类,其中大白菜的 *BrDhn4* 比较特殊,单独划为一类,其余脱水素为一大类。序列比对分析显示, *BrDhn1* 和 *At4g39130* 同源,编码蛋白的序列一致性为 70.20%; *BrDhn2*、*BrDhn7* 和 *BrDhn8* 与 *AtERD14* 同源,其编码蛋白的序列一致性分别为 77.40% (*BrDhn2* Vs *AtERD14*)、75.98% (*BrDhn7* Vs *AtERD14*)和 78.92% (*BrDhn7* Vs *AtERD14*),而 *BrDhn2* 和 *BrDhn7* 编码蛋白的序列一致性为 78.43%; *BrDhn3* 和 *BrDhn10* 与 *AtRAB18* 同源,其编码蛋白的序列一致性分别为 80.10%和 77.37%; *BrDhn4* 和 *At1g54410* 直系同源,其编码蛋白的序列一致性为 88.78%; *BrDhn5* 和 *BrDhn6* 与 *AtCOR47* 同源,其编码蛋白的序列一致性分别为 62.72%和 54.58%; *BrDhn9* 与 *At4g38410* 同源,序列一致性为 66.67%, *BrDhn11* 与 *AtXERO1* 同源,其编码蛋白的序列一致性为 69.92%; *BrDhn12* 与 *At2g21490* 同源,其编码蛋白的序列一致性为 69.79%。已知拟南芥的脱水素基因大多受 ABA 的诱导表达,并且在冷胁迫和水分胁迫响应过程中具有重要功能[22]。作者认为大白菜的脱水素基因也具有类似的表达模式和功能。

### 4. 大白菜脱水素基因的顺式元件分析

顺式调控元件在基因的表达调控中具有重要作用。为了探讨大白菜的脱水素基因可能受哪些因子调控,本文对 12 个脱水素基因的启动子部分及上游序列进行了顺式元件分析(见表 2)。结果显示, *BrDhn1-3,5-8,11,12* 可应答 ABA 信号, *BrDhn1-4,7,9,10,12* 可应答茉莉酸甲酯, *BrDhn1,2,5,9-12* 可应答乙烯信号, *BrDhn3,5-9,11,12* 可应答赤霉素信号, *BrDhn3-6,8,9* 可响应热胁迫, *BrDhn5-9,11,12* 可响应冷胁迫, *BrDhn4-8,10,12* 可响应干旱胁迫, *BrDhn1,2,4-8* 可进行防卫应答, *BrDhn-8,11* 可应答水杨酸信号。综上,推测大白菜的脱水素基因可能在发育及生物逆境响应过程中具有重要功能。目前,有关脱水素在大白菜发育和生物逆境响应中的功能研究还未见报道,值得深入探讨。



**Figure 2.** Phylogeny of Chinese cabbage dehydrins  
**图 2.** 大白菜脱水素的遗传进化分析

**Table 2.** Cis-elements of Chinese cabbage dehydrin genes  
**表 2.** 大白菜脱水素基因的顺式元件

Gene	ABRE/C E3	CGTCA- motif	ERE/EIR E	GARE-m otif/P-box	HSE	LTR	MBS/DRE	TC-rich repeats	TCA-ele ment
<i>BrDhn1</i>	2	4	/1					1	3
<i>BrDhn2</i>	5/1	1	1					2	1
<i>BrDhn3</i>	6/1	1		2	1				1
<i>BrDhn4</i>		1			2		1	1	1
<i>BrDhn5</i>	6/1		/1	1	2	1	2	1	1
<i>BrDhn6</i>	3			2	2	1	1/1	2	1
<i>BrDhn7</i>	4/1	2		2		1	1	2	2
<i>BrDhn8</i>	7/			1	2	1	1	2	1
<i>BrDhn9</i>		1	2	/1	8	2			
<i>BrDhn10</i>		2	1				/1		
<i>BrDhn11</i>	5		1	/1		1			4
<i>BrDhn12</i>	2	1	/1	1		2	1		

注: ABRE, ABA 应答顺式元件; AuxRR-core 为生长素应答元件; Box-W1 为真菌激发子应答元件; CGTCA-motif, 茉莉酸甲酯应答元件; HSE, 热胁迫应答元件; MBS, 为干旱胁迫应答元件; TC-rich repeats 为防卫和逆境应答元件; TCA-element, 水杨酸应答元件; W box 为防卫应答元件; 空白代表没有。

## 5. 结论

笔者利用生物信息学的方法从大白菜基因组中解析出 12 个脱水素基因, 分析发现它们非均匀分布在大白菜不同的染色体上, 而且结构类型也不一样。外显子 - 内含子结构分析显示, 大白菜的脱水素基因多数含有 2 个外显子。亚细胞定位预测显示, 它们编码的蛋白均定位于细胞质或者细胞核中, 这与前人在其它物种中的研究结果一致。遗传进化分析表明, 大白菜的脱水素基因可分为两个类群, *BrDhn4* 比较特殊(KS 类型), 单独划为一类, 其余的脱水素基因分为另一个类群。大白菜的大部分脱水素基因都能在拟南芥中找到相应的直系同源基因, 相应的序列一致性大都在 60% 以上。启动子上游序列顺式元件分析表明, 大白菜的脱水素基因大都含有多个激素和逆境应答顺式元件, 而且各不相同。这说明大白菜的脱水素基因在功能上存在分化。目前研究表明: 植物脱水素基因不仅在非生物逆境胁迫中具有重要功能, 在生物胁迫应答中也发挥一定作用。植物脱水素不仅受激素和转录因子调控表达[40] [41], 而且还可被蛋白激酶的磷酸化调控[8], 和在渗透胁迫下激活谷胱甘肽转移酶基因的表达[42]。至于大白菜脱水素基因的具体功能以及它们表达调控的机制, 需要进一步研究。本文为深入挖掘大白菜脱水素基因的功能和表达调控机理提供了重要线索。

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