



唐丽华,杨丽涛,李杨瑞.植物冷驯化转录调控的影响因素初探[J].黑龙江农业科学,2019(4):134-138.

# 植物冷驯化转录调控的影响因素

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**摘要:**植物在冷驯化过程中通过转录调控发生大量生理生化上的变化,遗传物质、光照、温度等是影响转录调控的关键因素。本文从遗传物质及环境因子方面对植物冷驯化转录调控的影响进行了概述,希望人们在设计实验时能对其重要性予以重视。

**关键词:**冷驯化;转录调控;遗传物质;环境因子

很多植物,例如:拟南芥、冬小麦,都能进行冷驯化,即经历一段非冰冻低温能够增加植物抗冻性<sup>[1]</sup>。冷驯化过程中发生一系列生理生化变化,如糖、保护蛋白的合成,这些变化大部分是由转录水平调控<sup>[2]</sup>。转录组分析是一项强有力的技术,在各植物物种中进行了大量的冷驯化差异表达基因(Differentially Expressed Genes, *DEGs*)鉴定,其中10%~15%的拟南芥、玉米及水稻利用microarray及RNA-Seq技术完成<sup>[3-5]</sup>,RNA-Seq技术已经成为研究冷驯化转录调控的主要方法,使研究者们能够对冷驯化转录调控过程进行全局分析<sup>[6]</sup>。光照、温度等试验参数是冷驯化转录调控重要影响因素,然而一些转录组分析文章中并没有对光周期、光强、开始冷驯化时间点、降温方式等试验参数进行详细陈述,鉴于此本文初步概述了影响植物冷驯化转录调控的因素,旨在引起研究人员在试验设计时予以更多的关注,为相关研究提供参考。

## 1 遗传物质与冷驯化转录调控

冷驯化及抗冻性是植物的一种复杂的遗传特

性<sup>[7]</sup>。相近物种及同一物种不同基因型/生态型之间的抗冻性可存在显著差异,这可能是由遗传因素造成的<sup>[8]</sup>。

运用转录组分析方法鉴定 *DEGs* 的同时,它也为相近物种间由遗传物质造成的转录调控差异的分析鉴定提供了一种手段<sup>[9]</sup>。

大量的转录组测序对植物不同基因型/生态型在同一胁迫条件下的转录调控进行了比较分析,结果表明GO(Gene Ontology)及KEGG(Kyoto Encyclopedia of Genes and Genomes)富集分析存在差异。Chen等<sup>[10]</sup>对番茄不同抗性基因型(*Solanum lycopersicum*, *S. habrochaites*)进行低温胁迫,结果表明抗性强的基因型在苯丙素代谢过程、氨基酸衍生物生物合成过程及类黄酮代谢过程响应快于冷敏感基因型;番茄另外两种基因型(*S. acaule*, *S. tuberosum*)的转录组分析表明,只有在抗性基因型中出现腐胺及精氨酸脱羧酶基因 *ADC1* 富集<sup>[11]</sup>;黑麦草中只在温暖地区适应型中出现昼夜节律及苯丙素生物合成富集,且主成分分析表明不同基因型占比66%<sup>[12]</sup>;一些研究表明在一定冷驯化时间内只在冷敏感基因型中出现叶绿体或光合作用相关项富集<sup>[10,13-14]</sup>。这些差异是否在转录调控及物种间的抗性差异中具有重要作用,可结合蛋白组、代谢组分析进行进一步的鉴定。

同时在一些研究中为遗传物质对转录调控影响的研究,提供了可能的方法,Torres-Oliva等<sup>[9]</sup>

收稿日期:2018-11-18

基金项目:广西自然科学基金项目(2013NXNSFAA019073)。

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使用同一个参考基因集及基因注释接口,结果显示不同基因型间基因集的可比性显著提高;Davidson 等<sup>[15]</sup>利用聚类分析方法表明位于相同位点的同源基因更有可能出现相似的转录调控模式;Zhang<sup>[16]</sup>通过比较玉米两亚种间的重复基因进而对高粱-玉米、玉米亚种 1-亚种 2 的同源基因转录调控差异进行鉴定,高粱与玉米亲缘关系相近<sup>[17]</sup>,具有相同的起源地区及相似的抗冻性<sup>[18-20]</sup>,且胁迫响应基因启动子具有高度保守性<sup>[21]</sup>,然而分析结果表明玉米-高粱、玉米亚种 1-亚种 2 冷驯化转录调控均具有显著差异,此外 Waters 等<sup>[5]</sup>的研究同样证明了两基因型中低温胁迫响应存在显著差异。

在同一试验参数处理下,不同基因型冷驯化转录调控可表现出显著差异性,说明遗传物质作为决定植物抗寒性内在因素的至关重要性,然而由于转录调控的复杂性及现有的分析工具十分有限,即使是亲缘关系十分相近的植株间的转录调控差异分析都具有难度。

## 2 环境因子与冷驯化转录调控

冷驯化过程影响因素除了遗传物质外,同时各种环境因素可相互结合对转录调控产生影响<sup>[16]</sup>。温度、光照(光强、光周期、光质)、昼夜节律、春化作用是影响基因表达变化的重要因素<sup>[22]</sup>。

### 2.1 温度与光照对冷驯化转录调控的影响

温度是冷驯化转录调控主要驱使因子,在低温处理数小时内大量的转录因子(Transcription Factors, TFs)激活以响应低温。在拟南芥中,快速降温及逐渐降温激活不同的信号通路, DREB1(Dehydration-Responsive Element Binding protein 1)是不同降温方式的主开关,其中一条信号通路: CAMTAs (Calmodulin Binding Transcription Activators) 诱导 DREB1B、DREB1C 表达只有在快速降温时被激活,另一条信号通路: CCA1/LHY (Circadian Clock Associated1/Late Elongated Hypocotyl) 参与信号转导,强烈诱导 DREB1A、DREB1C 表达,微弱诱导 DREB1B 表达,此通路在快速降温及逐渐降温中

均可被激活<sup>[23]</sup>;随着低温处理时间的推进,转录丰度发生变化,乌苏里梨冷驯化早期转录丰度明显高于后期<sup>[24]</sup>,然而,在橘子和番茄中,变化趋势相反<sup>[10,25]</sup>。

光是冷驯化转录调控的关键因素。光是植物进行光合作用获得养分的能量来源,低温胁迫下光合作用第一时间受到影响<sup>[26]</sup>。大量的研究表明光合作用相关基因在冷驯化中持续下调<sup>[12,27]</sup>。在光强、光周期、光质的共同作用下能引起信号转导<sup>[22]</sup>;在低温处理时间、光周期及温度的共同作用下可使转录调控发生改变<sup>[28]</sup>;拟南芥冷驯化中,在短周期及低红光/远红光率(R:FR)作用下能够增强 AtCBFs 表达,增强植株抗冻性<sup>[29]</sup>;大麦在常温下部分 HvCBFs 受远红光诱导<sup>[30]</sup>;此外,光响应基因受到光谱的影响<sup>[22]</sup>。

### 2.2 春化作用与光周期对冷驯化转录调控的影响

越冬植物(如:冬小麦、大麦)可在霜冻来临之前进行冷驯化,且只有经历一段时间低温才能由营养生长转变为生殖生长,即春化作用<sup>[31]</sup>。基因 VRN1 (Vernalization 1)、VRN2、VRN3/FT1 是春化作用的关键基因<sup>[32]</sup>,其中 VRN1 是主开关<sup>[33]</sup>,VRN2 的表达可抑制 VRN1<sup>[34]</sup>,VRN3 在开花调控网络中是整合春化作用及光周期的节点,多种调控信号集于此基因<sup>[35]</sup>。温度及光周期影响植物开花的时间,日长影响大量转录因子的表达<sup>[36]</sup>。大麦冷驯化及长日照下,VRN1 控制 COR14B 基因表达<sup>[37-39]</sup>;小麦冷驯化及长日照下,基因 VRN1 结合 CBFs 基因启动子,并下调 CBF1<sup>[40]</sup>;光周期敏感作物冷驯化及短日照下,VRN2 基因下调,可去除春化作用或降低春化作用要求<sup>[34,41]</sup>;在草甸羊茅中,延长冷驯化时间,使 CBF6、COR14B 下调,可使春化作用加速<sup>[42]</sup>。在春化作用开始时,植物抗冻性及相关 CORs 下调,进入生殖生长,植物逐渐失去抗冻性<sup>[43]</sup>,温度的波动性增加了越冬作物受冷害可能性。在越冬作物中,冷驯化、春化作用、光周期形成了一个复杂的调控网络,VRNs 与 CBFs 高度互作。

### 2.3 昼夜节律对冷驯化转录调控的影响

在最近的一项冬小麦的研究中<sup>[44]</sup>,为昼夜节

律调控冬小麦抗冻性提供了证据,试验结果表明冬小麦抗冻性随昼夜节律呈现周期性的变化,在日中点/夜中点开始 $-3^{\circ}\text{C}$ 处理可获得较大的抗冻性,在日/夜起点开始处理获得抗冻性较低,同时观察到 *CBF14*、*CBF15* 随昼夜节律呈现周期性变化;Bieniawska 等<sup>[36]</sup>在拟南芥的研究中同样证明了这一点,很多冷诱导基因的转录调控受昼夜节律影响,日中点的转录丰度高于日起点;大麦中,常温及低 R/FR 下, HvCBFs (HvCBF2A, -4B, -9, 14) 受昼夜节律调控,在夜起点时开始表达<sup>[30]</sup>;Kenchanmane Raju 等<sup>[45]</sup>发现在日中点开始冷驯化的玉米植株表型损伤更重。

值得注意的是,大部分冷驯化过程在生长箱中进行,恒定的温度设计与自然中波动的温度存在差异,由此得出的试验结论如果运用到实践中可能出现偏差。土壤条件、大气湿度和二氧化碳含量等都有可能对冷驯化转录调控产生影响。

### 3 总结与展望

冷驯化过程是植物应对低温逆境形成的一种遗传特性,通过转录水平的调控引起各种生理生化变化<sup>[2]</sup>,近 20 年来由于测序方法的不断更新增强,利用 RNA-Seq、microarray 对植物冷驯化转录调控过程进行了大量的转录组分析<sup>[6]</sup>,DEGs 的 GO、KEGG 富集分析同时也验证了冷驯化过程中信号转导、TFs 及 CORs 的快速响应。遗传物质是影响物种间抗性的内在因素,即使是亲缘关系相近的物种间在冷驯化转录调控过程也存在显著差异<sup>[17]</sup>,转录组分析有利于挖掘物种间导致抗性差异的基因。值得引起注意的是,众多的环境因素及试验参数的设计都有可能影响转录调控,其中温度是主要的驱使因子,光是关键影响因素<sup>[22]</sup>,这些因素是通过哪些途径影响冷驯化转录调控仍然需要进一步的研究,然而在一些研究中并没有对光强、光周期、开始冷驯化时间点、降温方式等因素进行陈述,其重要性希望能引起人们更多的关注,为相关研究的试验设计提供参考。

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## Influence Factors of Transcriptional Regulation During Plants Cold Acclimation

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**Abstract:** In the process of plants cold acclimation, a lot of physiological and biochemical changes occurred through transcriptional regulation. Genetic material, light, temperature, etc. are the key factors influence transcriptional regulation. In this paper, we summarized the factors of transcriptional regulation during plants cold acclimatization from the genetic and environmental aspects, hoping the importance of factors attracts more attention when designing experiments.

**Keywords:** cold acclimation; transcriptional regulation; genetic material; environmental factors

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## Problems and Countermeasures of Soybean Planting in Kazakhstan

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**Abstract:** In order to carry out bilateral cooperation in agricultural production and soybean production in the ‘One Belt and One Way’ framework, and promote the development of soybean production in Kazakhstan, the depth and breadth of national food security will be extended to promote the development of Kazakhstan’s agricultural modernization and China’s overseas agricultural development. In this paper, the problems of soybean planting in Kazakhstan were analyzed, and the corresponding technical measures were put forward.

**Keywords:** soybean; Kazakhstan; planting problem; technical measures