1. Zhang X, Jing Y, **Liu Z**, et al. Exogenous calcium alleviates heat stress in carnation via integrated physiological, anatomical and multi-omics modulations. Industrial Crops and Products, 2025, 232: 121241.(三作， SCI 一区， Industrial Crops and Products，已发表)

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Exogenous calcium alleviates heat stress in carnation via integrated physiological, anatomical and multi-omics modulations

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ARTICLE INFO

Keywords:
Carnation
Calcium
Heat stress
Photosynthesis
Multi-omics

ABSTRACT

Calcium (Ca^{2+}) is crucial for plant growth and helps regulate response to environmental stress. Heat stress (HS) adversely affects carnation (*Dianthus caryophyllus* L.), prompting this study to explore the potential of Ca^{2+} to alleviate HS. Initially, carnation seedlings were sprayed with varying concentrations of $CaCl_2$, with 15 mM proving to be the most effective treatment for promoting growth and physiological resilience to HS. Further analysis demonstrated that prolonged HS worsened seedlings damage, while Ca^{2+} ameliorated this damage. Under 12 d HS, carnation exhibited 48.35 %, 32.67 %, and 6.59 % reductions in aerial part fresh weight, dry weight, and relative water content, respectively. Notably, Ca^{2+} pretreatment restored these parameters by 23.96 %, 4.01 %, and 5.88 %. Ca^{2+} promoted stomatal opening and preserved chloroplast ultrastructure. HS caused reductions in stomatal length, width, aperture, and area by 33.36 %, 52.11 %, 28.29 %, and 37.53 %, respectively. In contrast, Ca^{2+} pretreatment improved these parameters by 33.41 %, 56.60 %, 17.55 %, and 40.88 % compared to the HS group. Transcriptomic analysis revealed Ca^{2+}-mediated upregulation of photosynthesis-related pathways, including PSII proteins (Psb) and light-harvesting chlorophyll protein complex (LHC) assembly. Integrated multi-omics indicated Ca^{2+} activated MAPK signaling (via genes like *MPK3*, *MKK9* and *WRKY33*), coordinated phenylpropanoid biosynthesis (e.g., PAL and CHS enzymes), and flavonoid metabolism (e.g., naringenin and hesperetin accumulation). Additionally, Ca^{2+} modulated hormone signaling cross-talk (ABA, JA, SA) to establish a multi-layered thermotolerance network. In conclusion, this study provides novel insights for using exogenous Ca^{2+} to alleviate heat damage in carnation and offers technical support for energy-efficient production of this flower.

1. Introduction

Under the global warming context, plants are suffering severe heat stress (HS) (Guihur et al., 2022). They attempt to cope with temperature fluctuations through self-regulatory mechanisms (Yang et al., 2019). However, when this stress exceeds their tolerance thresholds, it leads to irreparable damage. Abiotic stresses seriously affect plant growth and physiological status (Gharibiyan et al., 2023), among which HS exhibits particularly notable negative impacts on plant morphology, manifesting leaf yellowing, wilting, and suppressed growth and biomass accumulation (Liu et al., 2023). Moreover, HS disrupts the equilibrium between reactive oxygen species (ROS) production and scavenging in plants, resulting in elevated levels of hydrogen peroxide (H_2O_2) and superoxide anion ($O_2^{\cdot-}$) (X. Wang et al., 2022). To alleviate ROS-induced damage, plants activate enzymatic antioxidant systems [e.g., catalase (CAT), superoxide dismutase (SOD) and peroxidase (POD)] and non-enzymatic antioxidant systems [e.g., ascorbic acid (AsA) and glutathione (GSH)] to counteract the stress (X. Wang et al., 2022). Compounding these effects, HS impairs multiple aspects of plant photosynthesis and growth, including the synthesis of photosynthetic pigments, photosystem II (PS II) activity, stomatal function, and the structural integrity of chloroplasts and thylakoids (Mathur et al., 2014). The molecular response mechanism of plants to HS involve complex interactions among gene expression, metabolite alterations, and signaling transduction pathways (Haider et al., 2021). Specifically, plants adapt to HS by modulating the expression of photosynthesis-related genes, altering lipids and organic

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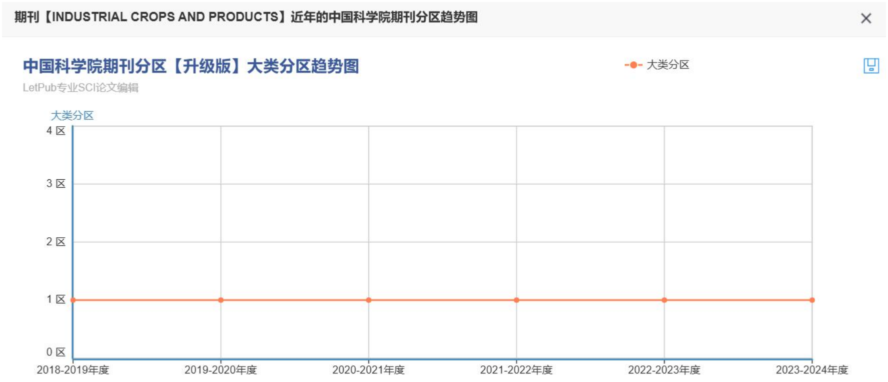
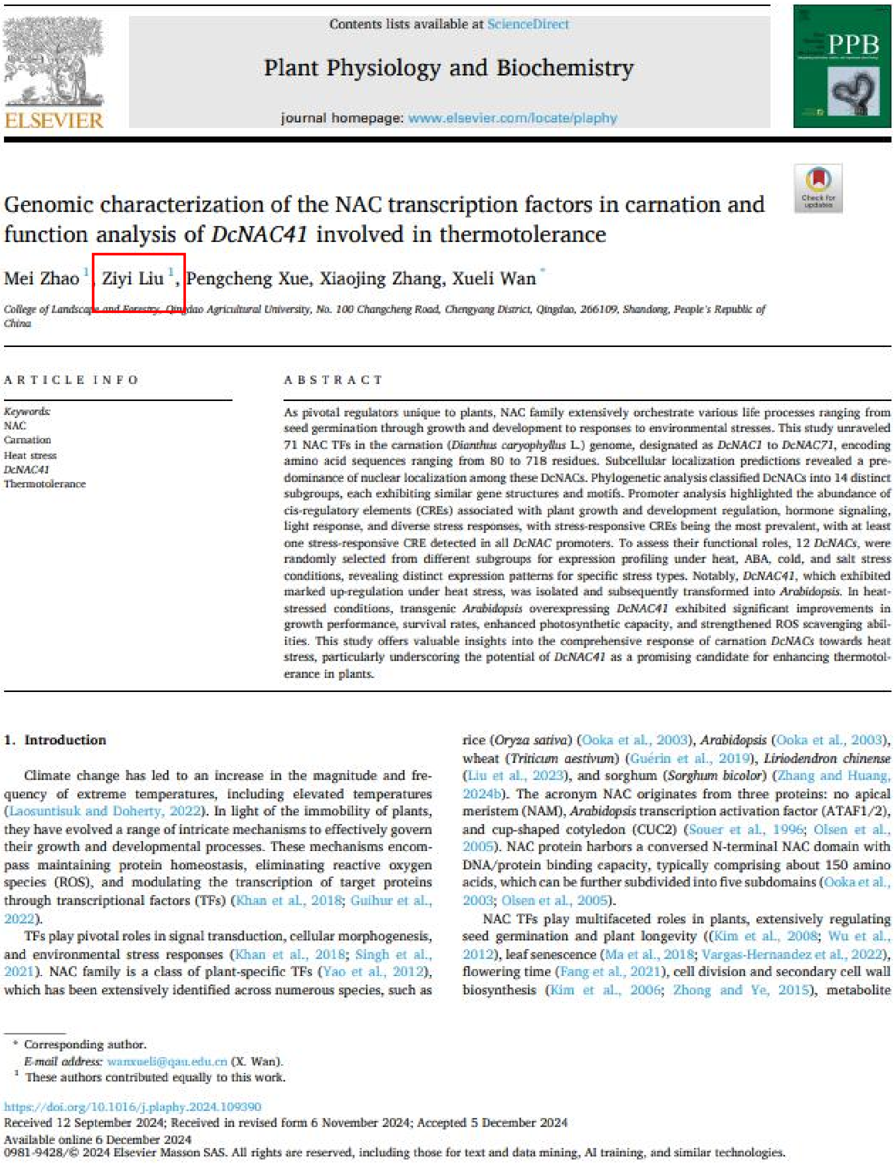


期刊【INDUSTRIAL CROPS AND PRODUCTS】近年的中国科学院期刊分区趋势图

2.Zhao M, **Liu Z**, Xue P, et al. Genomic characterization of the NAC transcription factors in carnation and function analysis of DcNAC41 involved in thermotolerance. Plant Physiology and Biochemistry, 2025, 219: 109390.(共同一作， SCI 二区， Plant Physiology and Biochemistry， 已发表)



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journal homepage: www.elsevier.com/locate/plaphy

Genomic characterization of the NAC transcription factors in carnation and function analysis of *DcNAC41* involved in thermotolerance

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ARTICLE INFO

Keywords:
NAC
Carnation
Heat stress
DcNAC41
Thermotolerance

ABSTRACT

As pivotal regulators unique to plants, NAC family extensively orchestrate various life processes ranging from seed germination through growth and development to responses to environmental stresses. This study unraveled 71 NAC TFs in the carnation (*Dianthus caryophyllus* L.) genome, designated as *DcNAC1* to *DcNAC71*, encoding amino acid sequences ranging from 80 to 718 residues. Subcellular localization predictions revealed a predominance of nuclear localization among these DcNACs. Phylogenetic analysis classified DcNACs into 14 distinct subgroups, each exhibiting similar gene structures and motifs. Promoter analysis highlighted the abundance of cis-regulatory elements (CREs) associated with plant growth and development regulation, hormone signaling, light response, and diverse stress responses, with stress-responsive CREs being the most prevalent, with at least one stress-responsive CRE detected in all *DcNAC* promoters. To assess their functional roles, 12 *DcNACs*, were randomly selected from different subgroups for expression profiling under heat, ABA, cold, and salt stress conditions, revealing distinct expression patterns for specific stress types. Notably, *DcNAC41*, which exhibited marked up-regulation under heat stress, was isolated and subsequently transformed into *Arabidopsis*. In heat-stressed conditions, transgenic *Arabidopsis* overexpressing *DcNAC41* exhibited significant improvements in growth performance, survival rates, enhanced photosynthetic capacity, and strengthened ROS scavenging abilities. This study offers valuable insights into the comprehensive response of carnation *DcNACs* towards heat stress, particularly underscoring the potential of *DcNAC41* as a promising candidate for enhancing thermotolerance in plants.

1. Introduction

Climate change has led to an increase in the magnitude and frequency of extreme temperatures, including elevated temperatures (Laosuntisuk and Doherty, 2022). In light of the immobility of plants, they have evolved a range of intricate mechanisms to effectively govern their growth and developmental processes. These mechanisms encompass maintaining protein homeostasis, eliminating reactive oxygen species (ROS), and modulating the transcription of target proteins through transcriptional factors (TFs) (Khan et al., 2018; Guihur et al., 2022).

TFs play pivotal roles in signal transduction, cellular morphogenesis, and environmental stress responses (Khan et al., 2018; Singh et al., 2021). NAC family is a class of plant-specific TFs (Yao et al., 2012), which has been extensively identified across numerous species, such as rice (*Oryza sativa*) (Ooka et al., 2003), *Arabidopsis* (Ooka et al., 2003), wheat (*Triticum aestivum*) (Guérin et al., 2019), *Liriodendron chinense* (Liu et al., 2023), and sorghum (*Sorghum bicolor*) (Zhang and Huang, 2024b). The acronym NAC originates from three proteins: no apical meristem (NAM), *Arabidopsis* transcription activation factor (ATAF1/2), and cup-shaped cotyledon (CUC2) (Souer et al., 1996; Olsen et al., 2005). NAC protein harbors a conversed N-terminal NAC domain with DNA/protein binding capacity, typically comprising about 150 amino acids, which can be further subdivided into five subdomains (Ooka et al., 2003; Olsen et al., 2005).

NAC TFs play multifaceted roles in plants, extensively regulating seed germination and plant longevity ((Kim et al., 2008; Wu et al., 2012), leaf senescence (Ma et al., 2018; Vargas-Hernandez et al., 2022), flowering time (Fang et al., 2021), cell division and secondary cell wall biosynthesis (Kim et al., 2006; Zhong and Ye, 2015), metabolite

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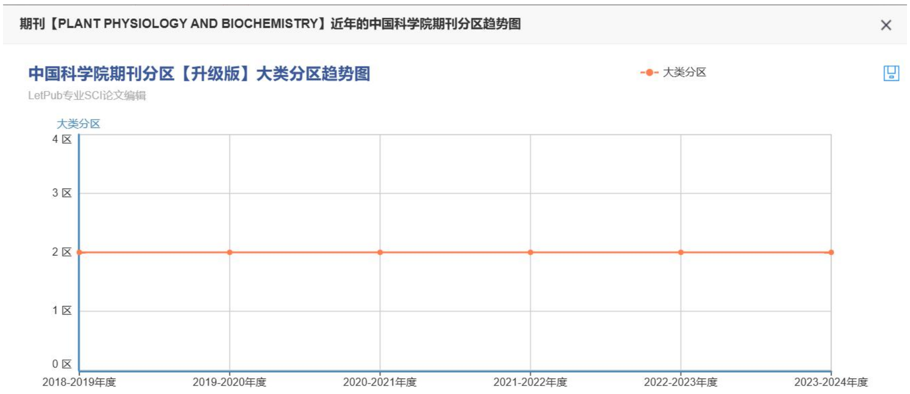

期刊【PLANT PHYSIOLOGY AND BIOCHEMISTRY】近年的中国科学院期刊分区趋势图

中国科学院期刊分区【升级版】大类分区趋势图

LetPub专业SCI论文编辑

3.主持青岛农业大学研究生创新创业项目（QNYCX24071)。

附件：

青岛农业大学 2024 年立项研究生创新计划项目一览表

序号	项目编号	项目名称	负责人	所在学院	指导教师	推荐类型
1	QNYCX24001	齐鲁农耕文化视觉形象数字传播研究	田心茹	动漫与传媒学院	孟庆波	资助
2	QNYCX24002	复方中草药添加剂对大肠杆菌感染肉鸡的保护作用及机理	唐凡迪	动物科技学院	刘华伟	资助
3	QNYCX24003	PLGF 对多胎湖羊子宫内膜微血管发育及容受性的调控	胡鑫恒	动物科技学院	高霄霄	资助
4	QNYCX24004	多肽铁螯合物对蛋鸡生产性能、蛋品质影响及在蛋鸡体内代谢和蛋黄中沉积机制研究	苗军红	动物科技学院	张凯	资助
5	QNYCX24005	高地隙山地液压拖拉机底盘的研究设计	姜成林	机电工程学院	王东伟	资助
6	QNYCX24006	翻秧式花生挖掘铺放机设计与试验研究	毛鹏辉	机电工程学院	王东伟	资助
7	QNYCX24007	粉状有机肥轻简化精准撒施智能装备研制	韩睿	机电工程学院	何晓宁	资助
8	QNYCX24008	数字化转型对畜牧企业碳绩效的影响研究	吴辰	经济管理学院（合作社学院）	张怡	资助
66	QNYCX24066	芝麻油体界面特性研究及在巧克力中的应用	李威	食品科学与工程学院	董绪燕	自筹
67	QNYCX24067	生牛乳中食源性致病菌的群落分析及耐药基因转移机制	徐乙萍	食品科学与工程学院	吴薇	自筹
68	QNYCX24068	海藻酸钙涂层 RS1 抗性淀粉对肠道菌群调控机制的研究	张康宁	食品科学与工程学院	姬娜	自筹
69	QNYCX24069	大肠杆菌噬菌体的分离鉴定及抑菌效果的研究	田幸幸	食品科学与工程学院	王军	自筹
70	QNYCX24070	基于荧光 CRISPR 快速检测乳中蓿实假单胞菌的方法研究	王玉景	食品科学与工程学院	杨永新	自筹
71	QNYCX24071	DcNAC41-DcHsfA2 调控香石竹高温胁迫响应的分子机制	刘子怡	园林与林学院	万雪丽	自筹
72	QNYCX24072	樟子松的体胚发生技术与机理研究	高丽娟	园林与林学院	孟鹏	自筹
73	QNYCX24073	茶树根尖感知氮素长距离运输信号单细胞级调控网络	段夏爽	园艺学院	柴国华	自筹
74	QNYCX24074	手性三唑类杀菌剂己唑醇的生物活性及其在苹果种植体系中选择性降解与残留消除技术研究	王毅然	园艺学院	韩令喜	自筹
75	QNYCX24075	植物激素调控顶芽生长的作用机理	胡清山	园艺学院	徐子健	自筹
76	QNYCX24076	去甲基化酶 ALKBH10B 介导转录因子 NAC90 的 m6A 甲基化调控大豆对大豆包囊线虫的抗性机制	郝光洋	植物医学学院	宋雯雯	自筹
77	QNYCX24077	降解菌 MZ-1 降解咪唑乙烟酸机理及影响因素	范晴晴	植物医学学院	张清明	自筹

批准立项编号：QNYCX24071

青岛农业大学研究生创新计划
项目中期检查报告书

项目名称：DcNAC41-DcHSFA2 调控香石竹高温胁迫响应的分子机制

申请单位：园林与林学院

项目类别：自然科学 ☑ 人文社会科学 □

项目负责人：刘子怡

所在单位：（盖章）

指导教师：万雪丽 单位 园林与林学院

填报日期：2025 年 6 月 11 日

下一步工作计划：

1. 完成 *DcNAC41* 在香石竹幼苗中的功能鉴定；
2. 完成 *DcHSFA2* 在香石竹幼苗中的功能鉴定；
3. 完成论文的撰写并发表。

项目负责人意见：

项目正在按计划推进，完成了香石竹 *DcNAC41* 的生物学功能的初步验证，并探究了 *DcNAC41* 与 *DcHSFA2* 的调控关系。目前正在进行 *DcNAC41* 与 *DcHSFA2* 在香石竹幼苗中的功能鉴定，将进一步完善项目内容并完成论文撰写与发表。

项目负责人（签字）：

年　　月　　日

指导教师意见：

项目按计划开展，完成了 *DcNAC41* 的热胁迫功能验证，并探究了 *DcNAC41* 与 *DcHSFA2* 的调控关系，取得了阶段性成果。该生在项目执行过程中表现出严谨的研究态度，分析解决问题的能力得到了提升，能够按预期目标完成项目内容。

指导教师（签字）：

年　　月　　日

所在单位审核意见：（是否按照任务书中的考核指标，完成相关工作，包括项目进展情况，成果产出情况，经费使用情况等。）

已完成.

青岛农业大学

分管院长（签字）：　　　单位（公章）

2023 年 6 月13日

4. 参加国家级会议： 2025 年中国园艺学会观赏园艺学术研讨会，并汇报研究主要进展。

12:00-14:00 午餐					
作重一楼报告厅：学术报告（十） 主持人：杨凤玺					
1	14:00-14:10	产祝龙	教授	郁金香发育及衰老调控机理	华中农业大学
2	14:10-14:20	丁宝清	教授	猴面花花瓣外卷的分子调控机理	南京农业大学
3	14:20-14:30	祝朋芳	教授	羽衣甘蓝花青素积累机制	沈阳农业大学
4	14:30-14:40	刘换换	讲师	96 种铁线莲花香分析	江苏农林职业技术学院
5	14:40-14:50	金亮	副研究员	探寻空气凤梨从陆地向“空中”跃迁的进化与遗传印记	浙江省园林植物与花卉研究所
6	14:50-15:00	冯磊	助理研究员	中国引进观赏植物的生态风险与入侵潜力研究	浙江省亚热带作物研究所
7	15:00-15:10	路兆庚	讲师	银杏 GbNAC75 响应高温胁迫调控叶片衰老的分子机制	扬州大学
8	15:10-15:20	冯珊	博士后	表观遗传学调控康乃馨鲜切花衰老	华中农业大学
9	15:20-15:30	姜赟	博士后	国产郁金香新品种‘幸运之星’品种特性研究	辽宁省农业科学院花卉所
15:30-15:50 茶歇					
作重一楼报告厅：学术报告（十二） 主持人：产祝龙					
10	15:50-16:00	秦贺兰	教授级高工	低维护、长花期花卉新品种选育、光合生理及花叶形成的分子机制初探	北京市园林绿化科学研究院
11	16:00-16:10	刘颖竹	教授	基于碳量子点纳米材料调控园艺植物非生物胁迫的生理与机制研究	安徽农业大学
12	16:10-16:20	张佩华	副研究员	花卉废弃物炭化产物特性及其栽培应用研究	云南省农业科学院花卉研究所
13	16:20-16:30	余惠文	讲师	姜荷花新品种选育及产业化	闽南师范大学
14	16:30-16:40	杜学林	初级研发员	三角梅种质资源收集、评价与创新利用	广州市林业和园林科学研究院
15	16:40-16:50	刘子怡	硕士研究生	DcmiR172c 靶向 DcNAC41 介导 HSF-HSP70 级联通路调控香石竹耐热性	青岛农业大学
17:00-17:30 闭幕式：作重一楼报告厅					


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观赏园艺学术研讨会
Conference on Ornamental Horticulture of CSHS, 2025