

# 盐和干旱胁迫及光质对猕猴桃叶片维生素C含量与合成基因表达的影响

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**摘要:**【目的】探究盐和干旱胁迫及不同光质对猕猴桃维生素C(Vc)合成的影响,为解析猕猴桃维生素C响应以上胁迫的调控机制提供理论基础。【方法】以毛花猕猴桃为试材,测定其在盐、干旱和光照3种胁迫下叶片Vc含量及Vc代谢关键基因的变化。其中,盐胁迫包括了低盐、中盐、高盐和无盐对照4种溶液条件,干旱胁迫采用了PEG6000溶液模拟轻度干旱、中度干旱、重度干旱和清水对照条件,光质环境模拟了蓝光、红光、白光和红蓝1:1混合光4种不同光质条件。【结果】受到低浓度的盐环境( $3\text{ g}\cdot\text{L}^{-1}$  NaCl溶液)、干旱胁迫和红蓝混合光的影响,毛花猕猴桃叶片维生素C含量迅速积累;实时荧光定量PCR分析发现,维生素C合成途径相关基因AceGME、AceGMP和AceGGP受到胁迫,其表达模式的改变是促进了维生素C含量变化的潜在原因。【结论】发现利于提高猕猴桃维生素C含量的几种胁迫条件,发掘了不同胁迫所影响的Vc合成关键基因,为后续阐明猕猴桃维生素C响应不同环境条件的机制研究提供了数据支撑。

**关键词:**猕猴桃; 胁迫环境; 维生素C合成; 基因表达

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## Effects of salt and drought stresses and light quality on vitamin C content and expression of synthetic genes in kiwifruit leaves

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**Abstract:**【Objective】Ascorbic acid (Vitamin C) is an important agronomic trait of fruits and vegetables. Kiwifruit is rich in ascorbic acid. However, the effects of abiotic stresses on vitamin C synthesis remain largely unclear. Here, we investigated the changes in vitamin C content in the leaves of kiwifruit (*Actinidia eriantha*) under different abiotic stress environments and analyzed the relative expression levels of key synthetic genes in the pathway of vitamin C synthesis. The results of this research will clarify the regulatory mechanism of vitamin C accumulation under abiotic stresses in kiwifruit.【Methods】*Actinidia eriantha* ‘Huata’ was selected as the experimental cultivar because of its high vitamin C content in fruit ( $>600\text{ mg}\cdot100\text{ g}^{-1}$  fruit weight). Annual branches (about 1-2 cm thick and 50-100 cm long) with fresh leaves and tissue culture plantlets were incubated in a greenhouse for salt, drought and light treatments. Firstly, four salt treatments, including three salt concentrations (NaCl solutions at 3, 6 and  $9\text{ g}\cdot\text{L}^{-1}$ ) and clean water treatment (CK), were set to evaluate the effect of salt concentration on vitamin C synthesis in kiwifruit. Each treatment had 5 replicates. The leaf materials were sampled at 0 d, 2 d, 4 d and

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6 d for Vc content determination and gene expression analysis. The leaf samples were freeze-dried and pretreated in liquid nitrogen, the RNA was extracted and reverse transcribed into cDNA for gene expression analysis. Secondly, the *A. eriantha* ‘Huata’ samples were treated with different osmotic conditions, namely, the control (treated with clean water, CK), mild (with 5% PEG6000 solution), moderate (10% PEG6000 solution) and severe (20% PEG6000 solution) osmotic stress. The sampling time and strategy were consistent with those of the salt treatments. Thirdly, four different light treatments, including white light, red light, blue light and red & blue light (red light:blue light =1:1), were designed in an artificial climate chamber. The wavelength of white, red and blue light were 450–465 nm, 650–700 nm and 465–480 nm, respectively. The light intensity was  $(200\pm5)$   $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ; the ambient temperature was  $(24\pm1)$  °C. The materials were treated in darkness for 48 h in advance, and then treated in different light for 12 h. The leaves were sampled in darkness, 1 h, 2 h, 6 h and 12 h under light treatment. The content of vitamin C in *A. eriantha* ‘Huata’ was determined with high performance liquid chromatography (Shimadzu liquid chromatograph). The expression levels of key metabolic genes of vitamin C pathway under different treatments were analyzed by real-time fluorescence quantitative PCR. Excel 2016 software was used for statistical analysis of the data, SPSS 21.0 software was employed for one-way analysis of variance, LSD, Tukey and Duncan’s multiple range tests, and Photoshop was used for plotting. Different lowercase letters indicate significant differences ( $p < 0.05$ ). **【Results】** Salt treatment experiments confirmed that low salt concentration ( $3 \text{ g}\cdot\text{L}^{-1}$  NaCl solution) significantly promoted vitamin C synthesis in *A. eriantha* ‘Huata’ leaves, while moderate and high salt concentrations caused damage on the experimental materials, resulting in no significant change in vitamin C content in their leaves. The vitamin C was significantly increased under osmotic stress treatments with the increase in stress time. In the light experiment, the concentration of vitamin C in *A. eriantha* leaves decreased under dark condition, whereas vitamin C increased sharply by more than five times within two hours of exposure to light. Of that, the mixed blue and red light treatment had the highest vitamin C accumulation, while the monochromatic blue light or red light had the least effect on vitamin C accumulation, even less than that in white light. Real-time fluorescence quantitative PCR results showed that the relative expression level of *AceGGP* in salt stress treatment was higher than that in the control group, indicating that the increased accumulation of vitamin C content under salt stresses might be related to the up-regulated expression of *AceGGP* gene. The expression levels of *AceGME*, *AceGGP* and *AceGPP* were increased by osmotic stress, which might be related to the increase in vitamin C accumulated in kiwifruit leaves. Compared with white light, the expression levels of *AceGME*, *AceGMP* and *AceGGP* genes were significantly increased under blue light ( $p < 0.05$ ), but there was no significant difference in *AceGPP* expression, which inferred that blue light may be an important factor affecting vitamin C synthesis. **【Conclusion】** The abiotic stress conditions, conducive to elevation of vitamin C content in kiwifruit were identified, and the key genes of vitamin C synthesis affected by different abiotic stresses were explored, providing data support for the subsequent study on the mechanism of vitamin C biosynthesis in response to different environmental conditions in kiwifruit. In addition, our results suggest that maintaining appropriate environmental conditions in commercial production will facilitate the production of kiwifruit with high vitamin C content.

**Key words:** Kiwifruit; Stress environment; Vitamin C synthesis; Gene expression

猕猴桃原产中国,属于猕猴桃科(*Actinidiaceae*)猕猴桃属(*Actinidia*)的重要果树<sup>[1]</sup>,因其富含维生素C(Vc,抗坏血酸)被称为水果中的“维C之王”<sup>[2]</sup>。Vc是不仅是一种重要的商品性状,而且作为一种功能性的代谢物质,在植物的生长发育、光合作用和延缓衰老方面有着十分重要的作用<sup>[3]</sup>。植物通过合成维生素C直接清除植株体内的活性氧<sup>[4]</sup>,增强植物的抗逆性。已有研究表明,施用外源Vc可以提高小麦<sup>[5]</sup>、玉米<sup>[6]</sup>、甜瓜<sup>[7]</sup>、黄瓜<sup>[8-9]</sup>、水稻<sup>[10]</sup>、大白菜<sup>[11]</sup>、紫花苜蓿<sup>[12]</sup>等植物的抗盐性及干旱胁迫下玉米<sup>[13]</sup>的抗氧化酶活性,不同光质处理可显著影响草莓果实维生素C的含量<sup>[14-15]</sup>。对于高维生素C含量的猕猴桃来说,探究猕猴桃通过调控Vc合成响应胁迫(如干旱、高盐、光质)具有重要科学意义。

维生素C生物合成途径包括D-半乳糖醛酸途径<sup>[16]</sup>、L-半乳糖途径<sup>[17]</sup>、L-古洛糖途径<sup>[18]</sup>和肌醇途径<sup>[19]</sup>,其中L-半乳糖途径是植物中Vc合成的主要途径<sup>[17]</sup>。相关研究发现不同物种控制维生素C的关键基因不同,在番茄中,*GMP*和*GME*基因的表达量影响着维生素C的含量<sup>[20]</sup>,且过表达*GME*基因明显增强非生物胁迫的耐受性<sup>[21]</sup>。在苹果和番茄叶片中,*GPP*基因对维生素C积累起主要的调控作用<sup>[22]</sup>。在猕猴桃中,L-半乳糖途径中的4个基因*GME*、*GMP*、*GGP*和*GPP*具有较高的转录水平,是猕猴桃维生素C合成的主要限速因子<sup>[23]</sup>。在高维生素C含量的毛花猕猴桃中,*GGP*基因的表达量明显高于低维生素C含量的山梨猕猴桃<sup>[24]</sup>,被认为是猕猴桃维生素C代谢的关键基因。但是,目前胁迫如何影响猕猴桃维生素C合成的关键基因的表达进而调控Vc的合成机制仍不清楚。

笔者在本研究中通过设置不同的盐、干旱和光质条件,采用高效液相色谱法测定毛花猕猴叶片维生素C含量的变化。现有研究表明,在遗传背景相同的猕猴桃后代中,可以用成熟叶片的维生素C含量预测成熟果实中的维生素C含量<sup>[25]</sup>。通过研究上述胁迫下猕猴桃叶片的维生素C含量,同时通过实时荧光定量PCR方法测定不同处理后维生素C合成相关基因的表达情况,探究盐和干旱胁迫及光质对猕猴桃维生素C合成的影响。

## 1 材料和方法

### 1.1 材料

供试品种为毛花猕猴桃华特(*Actinidia eriantha* Benth.),由浙江省农科院园艺所选育,试验材料取自中国科学院武汉植物园国家猕猴桃种质资源圃,盐和干旱胁迫试验组取1年生枝条(粗1~2 cm,长50~100 cm)水培萌发出叶片后进行试验,光质试验以新鲜的毛花猕猴桃叶片为外植体,经过植物组织培养诱导分化形成植株,置于不同光质下,25 °C环境下进行培养。

### 1.2 方法

1.2.1 盐胁迫试验 试验于2020—2021年春夏季在中国科学院武汉植物园进行,从毛花猕猴桃枝条经过水培抽芽发出若干片嫩叶开始,进行不同程度盐胁迫试验,育苗室内盐胁迫组设置清水水培处理(CK)、轻度盐胁迫处理(3 g·L<sup>-1</sup> NaCl溶液)、中度盐胁迫处理(6 g·L<sup>-1</sup> NaCl溶液)和重度盐胁迫处理(9 g·L<sup>-1</sup> NaCl溶液),每组处理设置5个重复,水培溶液体积均为1 L,水培溶液每2 d进行1次更换。盐胁迫组在处理前(0 d)和处理后2、4、6 d各取1次样品,每根水培枝条分别取3枚叶片装入茶包,浸入液氮后放入-80 °C冰箱保存样品,测定和比较不同盐处理下猕猴桃叶片的Vc含量。

1.2.2 干旱胁迫试验 育苗室内干旱胁迫组设置清水水培处理(CK)、轻度干旱胁迫处理(5% PEG6000溶液)、中度干旱胁迫处理(10% PEG6000溶液)和重度干旱胁迫处理(20% PEG6000溶液),每组处理设置5个重复,水培溶液体积均为1 L,水培溶液每2 d进行1次更换。从毛花猕猴桃枝条经过水培抽芽发出若干片嫩叶开始,进行不同程度干旱胁迫,盐胁迫处理后0、2、4、6 d,分别收集样品并测定和比较不同程度干旱胁迫处理下猕猴桃叶片的Vc含量,其他样品处理方法及Vc含量测定方法与盐胁迫组保持一致。

1.2.3 光质试验 组培室内设置白光、红光、蓝光和红蓝光(红光:蓝光=1:1)4种不同光质(图1),白光波长450~465 nm、红光波长650~700 nm、蓝光波长465~480 nm,光照度为(200±5) μmol·m<sup>-2</sup>·s<sup>-1</sup>,环境温度为(24±1) °C,每组设置5个重复。为测定不同光质对猕猴桃叶片Vc合成的影响,保持试验材料一致性,首先将通过外植体诱导分化的组培幼苗材料放置在黑暗条件下进行暗培养,暗培养处理48 h后分别放入白光、红光、蓝光和红蓝混合光4种不同光质条件下进行光照培养,取样时间点是暗培养处理0 h、



依次为白光、红光:蓝光=1:1、蓝光、红光。

The order is white light, red light:blue light = 1:1, blue light, red light.

图 1 不同光质试验

Fig. 1 Different light quality test

24 h、48 h 和光照培养后 1 h、2 h、6 h、12 h, 在这 7 个时间点分别取猕猴桃叶片后测定其 Vc 含量, 比较不同光质条件下猕猴桃叶片的 Vc 含量的变化, 其他样品处理方法及 Vc 含量测定方法与盐胁迫组保持一致。

**1.2.4 维生素 C 含量的测定** 依照李国秀等<sup>[26]</sup>的高效液相色谱法测定猕猴桃中 Vc 含量的方法并加以改进, 色谱柱: Shim-pack GIST C18 柱 (4.6 mm × 250 mm, 5 μm); 流动相:  $V_{0.1\% \text{ 偏磷酸溶液}} : V_{\text{甲醇}} = 98:2$ ; 流速: 1.0 mL · min<sup>-1</sup>; 检测波长: 243 nm; 柱温: 40 °C; 进样量: 10 μL。

**1.2.5 猕猴桃维生素 C 合成相关基因表达分析** 利用实时荧光定量 PCR 技术, 分析盐胁迫处理后 2 d、

干旱胁迫处理后 2 d 和光质试验中光照 2 h 维生素 C 合成途径相关基因表达水平。使用植物 RNA 提取试剂盒(天根生化科技有限公司)分别提取不同处理叶片的总 RNA, 反转录成 cDNA。以猕猴桃中 *Actin* 为内参基因进行 qPCR 分析, 实时荧光定量 PCR 检测系统型号为 7500FAS, 由 Applied Biosystems 公司提供; 反应体系中 qPCR Mix 加 5 μL, cDNA 加 1 μL, 正反向引物各加 0.2 μL, 加无菌水补齐到 10 μL; 反应步骤为 94 °C 预变性 30 s, 然后进行 45 个循环的 94 °C 变性 5 s、60 °C 退火 30 s。每个基因 3 个技术重复, 基因相对表达量的计算公式为:  $2^{(-\Delta\Delta CT)}$ 。所用引物见表 1。

表 1 实时荧光定量 PCR 分析所用引物

Table 1 Primers for real-time PCR analysis

基因名称 Gene name	正向引物 Forward prime	反向引物 Reverse prime
<i>Actin</i>	TGAGAGATTCCGTTGCCAGAAGT	TTCCTTACTCATGCGGCTGCGAT
<i>AceGME</i>	ATGGTCAGCATGAATGAGATGGCCG	GCTTCTCCTTAATCAGGGTGTGTC
<i>AceGMP</i>	GCTCTGGCTAGGGACAAACTGAT	TGGAATTGATCATCTCTTTG
<i>AceGGP</i>	GAGAGCTTCTTGCTTGC	GCACCCAAGCTGTTGTAACC
<i>AceGPP</i>	ATCAGAGAAGGGCGAAGGAGACAAT	ACGAACCAGGTCAACGGCGTCTTA

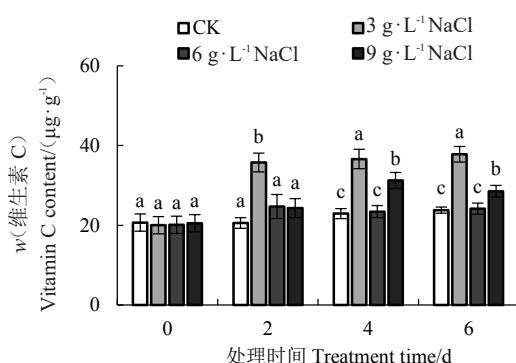
### 1.3 数据处理

试验数据采用 Excel 2016 软件进行常规统计分析, 用 SPSS 21.0 软件对数据进行单因素方差分析, 多重比较采用 LSD 法、Tukey 法、Duncan 法, 不同小写字母表示差异显著( $p < 0.05$ ), 使用 Photoshop 软件进行绘图。

## 2 结果与分析

### 2.1 不同程度盐胁迫对猕猴桃叶片维生素 C 合成的影响

由图 2 可知, 相对于对照处理的猕猴桃叶片随着盐胁迫处理时间增加, 轻度盐胁迫均显著促进猕猴桃叶片的 Vc 合成( $p < 0.05$ ), 中度盐胁迫对 Vc 的积累没有明显的作用, 而重度胁迫对猕猴桃叶片 Vc 的积累在胁迫 4 d 时有所增加, 在 6 d 时下降。上述结果表明, 轻度盐胁迫( $3 \text{ g} \cdot \text{L}^{-1}$  NaCl 溶液)显著促进



不同小写字母表示差异显著( $p < 0.05$ )。下同。

Different lowercase letters indicate significant differences ( $p < 0.05$ ). The same below.

图2 不同程度盐胁迫处理猕猴桃叶片的维生素C含量

Fig. 2 Vitamin C content of kiwifruit leaves treated with different salt concentrations

猕猴桃叶片Vc的合成。

## 2.2 不同程度干旱胁迫对猕猴桃叶片维生素C合成的影响

由图3可知,相对于对照组猕猴桃叶片,不同程度的干旱胁迫均能显著促进叶片Vc的积累( $p < 0.05$ )。随着干旱胁迫时间的增加,轻度干旱胁迫对猕猴桃叶片Vc含量的影响相对稳定,而中度和重度干旱胁迫随着胁迫时间的增加,对Vc的积累有轻微的增加。上述结果表明,干旱环境下会增加猕猴桃叶片Vc的积累。

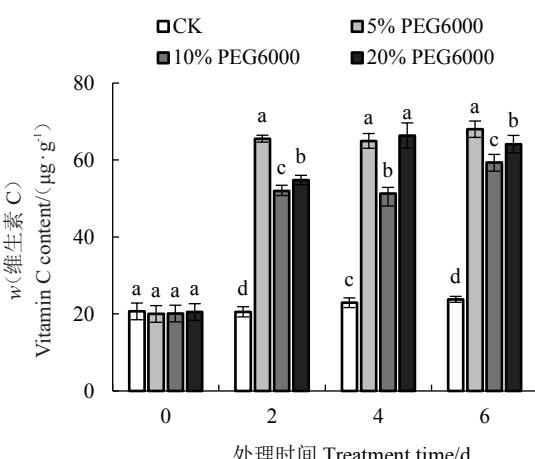


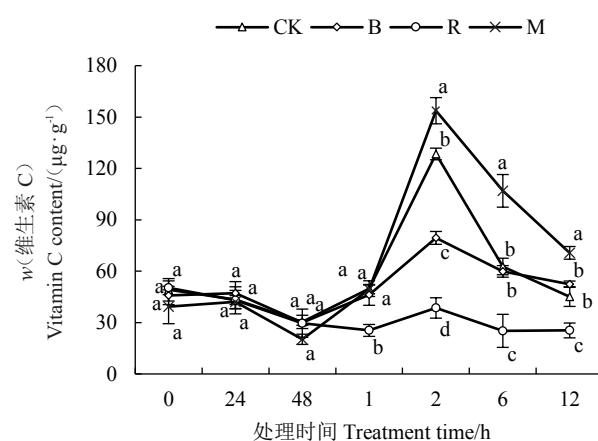
图3 不同程度干旱胁迫猕猴桃叶片的维生素C含量

Fig. 3 Vitamin C content of kiwifruit leaves treated with different drought levels

## 2.3 不同光质条件下猕猴桃叶片维生素C含量的变化

如图4所示,黑暗条件下,猕猴桃叶片Vc含量

显著低于光照条件,并且随着黑暗处理时间的增加,Vc的合成逐渐降低;当猕猴桃从黑暗转移到光照条件后,其Vc含量迅速积累,并且在光照后2 h达到峰值。在4种不同光照条件下,相对于黑暗条件,4种不同光质均能促进猕猴桃叶片Vc合成,其中红光的促进作用较弱。相对于白光,红蓝混合光对猕猴桃叶片Vc合成的促进作用最明显,而蓝光和红光2种单色光对Vc积累的促进作用不如白光。上述结果表明,黑暗条件抑制猕猴桃叶片Vc的积累,而光照条件促进Vc合成,其中红蓝混合光的促进作用比单色光强。



CK. 白光; B. 蓝光; R. 红光; M. 红蓝混合光。下同。

CK. White light; B. Blue light; R. Red light; M. Red and blue mixed light. The same below.

图4 不同光质处理猕猴桃叶片的维生素C含量变化

Fig. 4 Vitamin C variation of kiwifruit leaves under different light conditions

## 2.4 盐、干旱胁迫和不同光质条件对猕猴桃维生素C合成相关基因表达的影响

如图5所示,L-半乳糖途径的AceGME、AceGMP、AceGGP和AceGPP基因在一定程度上呈现出与Vc相似的表达趋势。在盐胁迫处理中,AceGMP的相对表达量比对照组低,AceGME和AceGPP基因则无明显差异,而AceGGP的相对表达量在重度盐胁迫时高于对照组,表明盐胁迫促进猕猴桃叶片Vc含量的积累可能与AceGGP基因的上调表达有关。

在干旱胁迫处理中,相对于对照组,AceGMP基因随着干旱程度的增加,表达水平先降低后上升,AceGME、AceGGP和AceGPP在干旱胁迫后均呈现表达水平上升的趋势。干旱胁迫下AceGME、AceG-

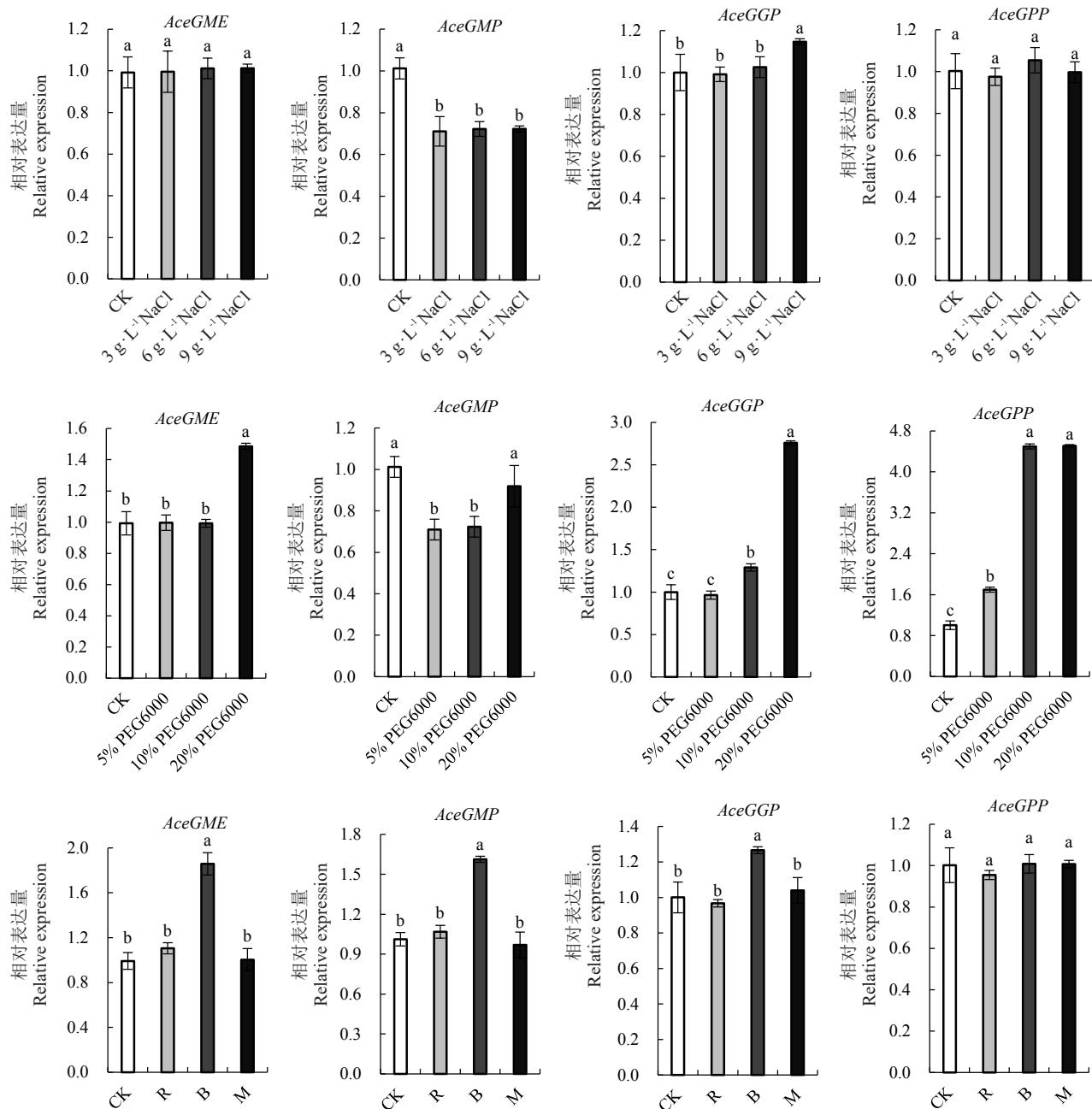


图 5 盐、干旱胁迫和不同光照条件下维生素 C 合成途径相关基因的表达情况

Fig. 5 The expression of Vitamin C synthesis pathway-related genes under abiotic stress and different light conditions

*GP* 和 *AceGPP* 基因表达上调能够较好地解释猕猴桃叶片 Vc 积累增加的现象。

通过分析不同光照条件下 *AceGME*、*AceGMP*、*AceGGP* 和 *AceGPP* 基因的表达水平, 相对于白光, 发现在蓝光条件下, *AceGME*、*AceGMP* 和 *AceGGP* 基因的表达水平显著上升( $p < 0.001$ ), *AceGPP* 基因则无明显差异; 红光和红蓝混合光对 Vc 合成相关基因表达的影响与对照组没有明显的差异, 蓝光可能是影响维生素 C 合成的一个重要因子。

### 3 讨 论

笔者探究了不同盐浓度、干旱程度以及不同光质条件处理下猕猴桃维生素 C 含量的变化, 发现在低盐环境下, 猕猴桃维生素 C 含量上升, 随着盐浓度的增加, 维生素 C 含量逐渐降低。推测是因为在盐胁迫环境中, 体内活性氧产生速率增加, 自由基浓度上升, 而 Vc 被认为是活性氧的清除剂<sup>[27]</sup>, 在低盐环境下, 由于活性氧的增加, 刺激了 Vc 的合成, 但是随

着盐浓度不断上升,膜脂过氧化作用增强,破坏了细胞的结构和功能,导致Vc含量下降<sup>[28]</sup>。在干旱环境中,猕猴桃叶片Vc的积累增加,在其他的研究中也发现适度的干旱有利于辣椒果实中Vc含量的增加<sup>[29]</sup>。在光照条件下,红蓝混合光下Vc含量积累最高,这与彭鑫<sup>[30]</sup>的研究一致,不同光质处理可显著影响植株Vc含量。对遗传背景相同的猕猴桃果实与叶片维生素C的相关性分析研究中,叶片与果实维生素C含量的相关系数较高<sup>[25]</sup>,以上胁迫环境可以改变猕猴桃叶片中维生素C含量,也代表了猕猴桃果实的维生素C含量也可能会受到以上胁迫环境的影响。通过这些结果可以明显发现不同胁迫环境中猕猴桃维生素C含量的变化,推测维生素C也可以提高猕猴桃在胁迫环境中的抗性。

通过分析盐和干旱胁迫和不同光质条件猕猴桃维生素C合成相关基因的表达,发现猕猴桃中的AceGME、AceGMP、AceGGP和AceGPP基因表达水平与Vc合成水平相似。相关研究表明,在水淹胁迫下,不结球白菜中的GME基因表达量变化趋势与维生素C含量变化一致<sup>[31]</sup>。通过抑制GGP基因的表达,可以降低番茄抵抗低温胁迫的能力<sup>[32]</sup>。在本研究中,笔者发现盐胁迫中猕猴桃叶片中Vc含量的增加主要与AceGGP基因的表达上调有关,干旱胁迫下猕猴桃叶片Vc积累增加与AceGME、AceGGP和AceGPP基因的表达上调有关。这些结果表明,维生素C含量与Vc合成基因表达量的相关性会随着胁迫环境的变化而改变,但Vc合成基因受到非胁迫环境影响后的反馈机制还有待进一步研究。

## 4 结 论

通过设计盐和干旱胁迫及不同光质条件试验,首次发现盐、干旱和光质影响毛花猕猴桃Vc合成并改变其关键基因表达,这说明适合的环境条件能够促进猕猴桃Vc积累,为未来通过设施栽培生产高营养猕猴桃提供了可能。

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