

蔬菜作物中瓜氨酸代谢调控研究进展

杨东东,朱红菊,赵永,刘文革

(中国农业科学院郑州果树研究所 郑州 450009)

摘要:瓜氨酸为非编码蛋白质氨基酸,在蔬菜作物的氮代谢和抗逆反应中发挥重要作用,且对人体具有保健功能,有较高的药用价值。通过综述蔬菜作物特别是西瓜中瓜氨酸的研究现状,对蔬菜作物中瓜氨酸的含量分布、生理功能、合成代谢、转运调控和遗传机制等方面的研究进行了分析,并对蔬菜作物中瓜氨酸的生理生化与遗传机制相关研究进行了展望,对培育高瓜氨酸蔬菜作物具有重要意义。

关键词:蔬菜作物;西瓜;瓜氨酸;代谢调控

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Research progress on regulation of citrulline metabolism in vegetable crops

YANG Dongdong, ZHU Hongju, ZHAO Yong, LIU Wenge

(Zhengzhou Fruit Research Institute, Chinese Academy of Agricultural Sciences, Zhengzhou 450009, Henan, China)

Abstract: Citrulline is a non-coding protein amino acid, which plays an important role in nitrogen metabolism and stress resistance of vegetable crops. It also has health care function for human body and high medicinal value. This review covers the citrulline research status of vegetable crops, especially watermelon, citrulline content distribution, physiological function, regulation and control of synthetic metabolism, transport, and the genetic mechanism. Citrulline physiological, biochemical and genetic mechanism of related research is also discussed. It is of great significance to cultivate vegetable crop varieties with high citrulline content.

Key words: Vegetable crops; Watermelon; Citrulline; Metabolic regulation

瓜氨酸(Citrulline),又名氨基甲酰鸟氨酸,在植物中为精氨酸合成的前体物质^[1]。瓜氨酸在西瓜汁中首先被发现,分子构型为L型,故被称为L-瓜氨酸^[2],在葫芦科植物中广泛存在^[3-6]。一些其他植物如核桃^[7]、蘑菇、苋菜和羽衣甘蓝等^[8]中也含有少量瓜氨酸。

蔬菜作物中,瓜氨酸不仅作为氮代谢途径中重要物质,同时也作为重要的抗逆物质,在逆境胁迫条件下,维持作物的正常生长^[9-12],瓜氨酸下游物质精氨酸的代谢产物多胺(PA)和一氧化氮(NO)等在植物抗逆方面也具有重要作用^[13]。人体中,瓜氨酸能够清除体内的羟基,具有抗氧化、保护DNA、提高免疫力等作用^[14]。同时瓜氨酸在治疗男性功能障碍、精氨酸缺乏症以及促进人类肌肉运动和恢复等方面中也具有重要作用^[15-19]。

目前,瓜氨酸可进行商业化生产,主要是由特殊的微生物菌株发酵生产^[20]。虽然菌株发酵生产瓜氨酸产量高于植物生产,且更加经济,但蔬菜作物中除瓜氨酸以外还含有其他营养物质,相对于商业发酵生产的瓜氨酸,蔬菜中瓜氨酸更天然且更易摄取。因此,研究分析蔬菜作物中瓜氨酸的合成积累机制及发掘调控瓜氨酸合成关键酶和酶基因具有重要意义。笔者对西瓜等蔬菜作物中瓜氨酸的研究进展进行了综述,提出目前蔬菜作物中瓜氨酸研究存在的问题并进行了展望,旨在为蔬菜作物中瓜氨酸的深入研究提供参考。

1 瓜氨酸在蔬菜作物中的含量分布

瓜氨酸在蔬菜作物中广泛存在,如西瓜^[3]、栝蒌、南瓜、冬瓜、丝瓜、苦瓜^[4]、甜瓜^[5-6]、鹰嘴豆、洋葱、

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作者简介:杨东东,男,在读博士研究生,研究方向为代谢组学。E-mail:2625478799@qq.com

通信作者:刘文革,男,研究员,主要从事西瓜遗传育种工作。E-mail:liuwenge@caas.cn

蘑菇等^[8]中均含有瓜氨酸。相较于其他蔬菜作物,在葫芦科作物如西瓜^[3]、甜瓜、南瓜、丝瓜、苦瓜等^[4-6]的果实中被认为含有大量的瓜氨酸,它们的其他器官如叶、根、茎、种子等^[6]中也含有瓜氨酸,且瓜氨酸的含量具有组织特异性,不同组织含量存在显著差异^[6,21-22],这表明瓜类种或亚种形成及驯化过程中可能存在一些进化保守的调控因子。不同葫芦科植物果实中瓜氨酸含量存在显著差异^[6]。Davis 等^[23]研究表明,西瓜果实鲜样中瓜氨酸含量可达 $7.21 \text{ g}\cdot\text{kg}^{-1}$,而部分葫芦科植物果实中瓜氨酸含量水平较低甚至不含有瓜氨酸,如黄瓜中瓜氨酸含量约为西瓜中的 $1/10$ ^[6],直颈黄南瓜中没有检测到瓜氨酸^[24]。

相比较于其他葫芦科作物,西瓜中的瓜氨酸含量最高^[5,25-27]。不同品种的西瓜果实中瓜氨酸含量存在差异,且均受生态环境影响,受环境影响的程度也有差异^[3,23,28]。西瓜中瓜氨酸含量与西瓜倍性和瓤色的关系一直被关注,Rimando 等^[29]研究发现,三倍体西瓜果实中瓜氨酸含量高于二倍体,黄、橙色瓜瓤的西瓜瓜氨酸含量高于红瓤;李蒙蒙等^[30]研究表明,西瓜瓜氨酸含量与果肉颜色有关;万学闪等^[27]研究表明,二倍体西瓜果实瓜氨酸含量为白瓤>黄瓤>红瓤;刘文革等^[31]研究发现,不同倍性西瓜果实中瓜氨酸含量为三倍体>四倍体>二倍体。而 Davis 等^[32]研究表明,瓜氨酸含量与西瓜倍性不相关,因为同源三倍体与二倍体和其诱导的同源四倍体亲本的瓜氨酸含量没有显著差异。但研究者均未进一步针对不同倍性西瓜中瓜氨酸含量差异的深层机制进行深入研究。综上可以看出瓜氨酸含量与西瓜品种、倍性、瓤色、环境等存在着相关关系。

2 瓜氨酸在蔬菜作物中的运输及分配机制

2.1 韧皮部与瓜氨酸转运

植物韧皮部运输是水分、营养物质和其他光合产物长距离分配的关键途径,在植物发育过程中和恶劣环境下从源组织到库组织的物质运输中发挥作用^[33]。许多研究结果表明,瓜氨酸可能参与韧皮部长距离运输,如桦木^[34]、核桃^[35]、南瓜属^[36]和褐藻^[37]等已被证明在韧皮分泌物中运输大量瓜氨酸。甜瓜叶片的韧皮部汁液中在光周期的光照早期会积累大量瓜氨酸,在暗期瓜氨酸水平显著下降^[38],表明瓜氨酸可能通过韧皮部从源运输到库;

Joshi 等^[39]也发现,瓜氨酸可能在西瓜其他器官合成并通过维管系统长距离运输到果实。一些参与瓜氨酸代谢的基因表达的研究也表明,瓜氨酸可能参与蔬菜作物韧皮部长距离运输。如西瓜韧皮液中乙酰鸟氨酸脱乙酰基酶基因(*Cl016179*)的表达量比维管组织中高约 35 倍,且乙酰鸟氨酸去乙酰化酶基因(*Cl016181*)在伴胞中也有表达^[40],瓜氨酸合成酶 OTC(鸟氨酸氨甲酰转移酶)和(氨甲酰磷酸合成酶)CPS(大亚基:*Cl005591* 和小亚基:*Cl022915*)基因在果实维管、果肉和果皮组织发育中均有表达,且在果皮和果肉的整个发育过程中,OTC 基因表达稳定,而精氨酸琥珀酸酶基因(*Cl022154*)和精氨酸琥珀酸合酶基因(*Cl019267*,*Cl002609*)的表达下调,瓜氨酸水平升高,且分解代谢酶基因的下调主要发生在果肉组织中^[40];其他研究表明,果实发育过程中,果肉中参与瓜氨酸分解代谢的精氨酸琥珀酸裂解酶基因(*Cl022154*)和精氨酸琥珀酸合酶基因(*Cl002609*,*Cl019267*)下调,相应果皮中瓜氨酸含量增高,而参与瓜氨酸合成的 N-乙酰鸟氨酸转氨酶基因(*Cl015337*)和 N-乙酰谷氨酸合成酶基因(*Cl014036*)在果实发育过程中仅在果皮组织中逐步上调^[41-42]。综上表明,西瓜等蔬菜作物果实中瓜氨酸含量的积累可能是瓜氨酸在叶片、果皮等部位合成并在果实成熟过程中由韧皮部维管转入果肉中,在多种参与瓜氨酸合成和分解酶的协同调节下维持一定的浓度。

2.2 转运蛋白与瓜氨酸转运

氨基酸通过韧皮部和木质部的长距离运输由膜结合转运蛋白的装载和卸载活动介导^[43]。氨基酸转运蛋白(AAT)在高等植物中介导氨基酸跨细胞膜的转运、长距离转运以及植物对生物和非生物胁迫的反应^[44]。拟南芥中转运蛋白 AAP3 和 AAP5 在碱性氨基酸如精氨酸的高效转运中发挥作用^[45],其中 AAP5 的调控基因(*At1g44100*)在许多组织中表达,介导根中碱性氨基酸的吸收^[39,43],而 AAP3 的调控基因(*At1g77380*)主要在根和韧皮部中表达,可能促进韧皮部的装载^[46]。瓜氨酸也属于碱性氨基酸^[47],可能由这些转运蛋白转运到植物体各个部位。目前还没有针对蔬菜作物中 AAP3 和 AAP5 基因开展研究工作。

拟南芥 L-鸟氨酸跨膜转运蛋白/线粒体载体家族蛋白 BAC1(*AT2G33820*)和 BAC2(*AT1G79900*)可转运碱性和中性氨基酸,其中 BAC2 显示出 L-瓜

氨酸转运的特异性^[48],且 *BAC1* 和 *BAC2* 在大多数器官中组成型表达,在花朵和果实中也有较高的表达^[49]。在与拟南芥 *BAC2* 基因具有高度同源性的两个西瓜基因中,*BAC2-like* 基因 *Cla012675* 在韧皮部特异性表达,其转录仅在果皮组织,而 *Cla015439* 的表达相对较低,仅存在果肉和果皮组织^[39],这些基因的差异表达表明,它们可能在西瓜中参与瓜氨酸转运,这与拟南芥 *BAC2* 基因在胁迫和衰老过程中被诱导的结果一致^[50]。在药西瓜干旱胁迫的叶片^[51]和栽培西瓜的根^[52]中的研究表明,*Cla012675* 基因对瓜氨酸具有高度特异性,可能在非生物胁迫或衰老期间的蔬菜作物根部或叶子中转运瓜氨酸。目前尚无西瓜中 *BAC1* 和 *BAC2* 直系同源物亚细胞水平的研究。但有研究表明,瓜氨酸在质体中合成,预测质体膜上的蛋白质具有输出瓜氨酸的能力^[39]。综上表明,对瓜氨酸的转运蛋白进行研究非常重要,目前蔬菜中转运蛋白在瓜氨酸转运中的作用、底物特异性、组织特异性和发育调节以及亚细胞定位尚不清楚。但对瓜氨酸生物合成和分解代谢相关的转录产物进行研究可能是寻找蔬菜作物候选瓜氨酸转运蛋白的一种有效方式。

2.3 渗透酶与瓜氨酸转运

部分氨基酸渗透酶在瓜氨酸转运中发挥重要作用,如来自蓖麻子的氨基酸渗透酶基因(*RcAAP3*)已被克隆^[53],其特异性介导酵母转运突变体中瓜氨酸的摄取,对瓜氨酸具有高亲和力;水稻 AAPs 家族中 *OsAAP1* 和 *OsAAP3* 运输中性和带正电形式的碱性氨基酸,包括精氨酸和瓜氨酸^[46],与精氨酸相比,*OsAAP1* 对瓜氨酸表现出更高的亲和力,可能在瓜氨酸的运输中发挥作用,亚细胞定位表明,洋葱和拟南芥中 *OsAAP1* 和 *OsAAP3* 定位于质膜,在洋葱表皮细胞或在拟南芥中稳定表达^[46];西瓜基因组中发现了 2 个拟南芥 *AAP3/5-like* 序列的直系同源物,西瓜氨基酸通透酶基因(*Cla023187* 和 *Cla013912*)与拟南芥氨基酸渗透酶具有 88% 的同源性,与蓖麻的 *AAP3* 具有 80% 的同源性,与水稻 *AAP1* 具有 60% 的同源性^[39],对瓜氨酸具有高亲和力;前人研究发现,在西瓜成熟期间,氨基酸通透酶基因 *Cla023187* 和 *Cla013912* 在果肉和果皮组织中显著持续下调,这 2 种酶基因还可能选择性地允许瓜氨酸在叶片和根部积累,因为它们在野生西瓜干旱胁迫的叶片^[51]和栽培西瓜干旱胁迫的根^[52]中显著上调。综上所述,蔬菜作物中瓜氨酸可能受到瓜氨酸特异性氨基酸渗透酶的调节。

3 瓜氨酸在蔬菜作物氮代谢过程中的作用

植物中有机氮的运输主要是通过氨基酸形式,富含氮的精氨酸和瓜氨酸可能是内源性氮储存和运输的重要部分^[54],可作为主要可溶性氮产物、木质部汁液中固氮含量的主要产物^[55-57],瓜氨酸能改变木质部汁液中的氮营养、根瘤活性和含氮化合物的转运水平^[58],在氮供应中断胁迫^[59]以及外界补充氮含量的条件下参与内部氮素贮存中发挥重要作用^[60-64]。在蔬菜作物如葫芦科物种中,瓜氨酸是有机氮含量的主要载体^[65],在黄瓜开花期间,叶片和子房中检测到约占总氨基酸含量 1/3 的瓜氨酸,并通过木质部移动^[66]。前人研究发现,爱尔兰苔藓内存在高浓度瓜氨酸-精氨酸二肽,以补充硝酸盐或氨,占氮储备的一半^[67],但在蔬菜作物中,瓜氨酸大多以游离形式单独存在,目前在蔬菜作物中还未发现瓜氨酸与其他氨基酸结合存在。综上所述,瓜氨酸在蔬菜作物氮代谢过程中发挥了重要的作用,但是具体作用机制尚不清楚。

4 瓜氨酸的代谢通路及重要酶基因

4.1 蔬菜作物中瓜氨酸代谢通路

瓜氨酸是鸟氨酸循环的重要组成部分、精氨酸合成的前体物质和一氧化氮循环的中间体。瓜氨酸的合成与精氨酸紧密联系。瓜氨酸合成途径在动物^[68]、真菌^[69]、原核生物^[70]以及模式植物拟南芥^[39,71]中研究较多,目前在一些特殊工程菌中瓜氨酸的代谢通路以及调控机制已经研究得非常清晰并且已经应用于生产^[72],而在植物中的研究还不够清晰。

植物中,瓜氨酸的合成途径主要分为两个过程,第一个过程是谷氨酸通过循环途径或线性途径生成鸟氨酸;第二个过程是鸟氨酸生成瓜氨酸以及鸟氨酸的再生(图 1),又叫“鸟氨酸循环”^[73]。其中谷氨酸到 N-乙酰鸟氨酸和乙酰基的生成被称为“鸟氨酸合成途径”,此合成途径在植物中高度保守^[74]。

4.2 蔬菜作物中瓜氨酸重要调控酶基因

瓜氨酸在植物中积累代谢调控酶以及酶相关基因的克隆和功能鉴定的研究主要集中在模式植物拟南芥上^[71,73,75]。除拟南芥外,对西瓜^[40]、番茄^[48]、水稻^[76]等作物的瓜氨酸合成途径相关基因也有一定的研究。一些植物中瓜氨酸合成途径中的部分调控基因目前也已被克隆,一些基因的功能也已经得

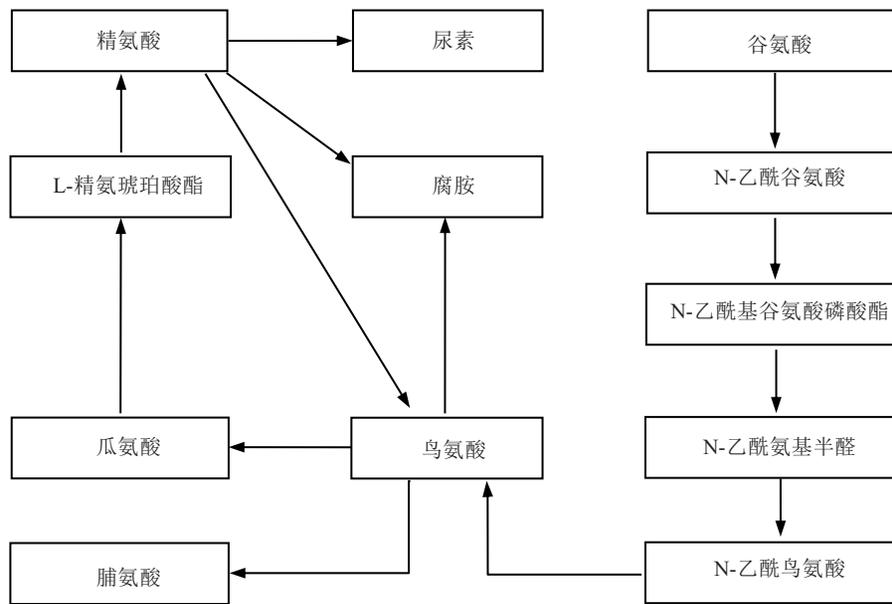


图1 植物中瓜氨酸合成代谢途径^[39]

到初步的认证(表1)。

N-乙酰谷氨酸合成酶(NAGS)受精氨酸反馈调节,活性被高浓度的精氨酸抑制而被低浓度精氨酸激活^[77-78],番茄中 *SINAGSI* 基因蛋白与拟南芥中两个猜测的NAGS蛋白NAGS1和NAGS2有较高的相似性,其表达具有组织特异性^[77],主要位于叶绿体

中,超表达 *SINAGSI*,拟南芥中瓜氨酸和野生型相比含量升高,对干旱和盐胁迫忍受能力也有提高^[79]; N-乙酰谷氨酸激酶(NAGK)是一种质体定位蛋白,位于拟南芥的叶绿体中^[80-81],是瓜氨酸合成途径的关键酶和限速酶,活性可被高浓度精氨酸抑制^[82],这个过程是通过调节PII蛋白与NAGK的相互作用

表1 拟南芥与蔬菜作物中部分已鉴定的瓜氨酸合成相关基因及其功能

基因	基因功能	植物	参考文献
<i>At2g22910, At4g37670</i>	调控 NAGS	番茄和拟南芥	Slocum[73]
<i>SINAGSI</i>	调控 NAGS, 主要位于叶绿体中, 参与耐盐和耐旱过程, 表达具有组织特异性, 为单拷贝基因。除根外, 在地上组织中均有表达	番茄	Kalamaki et al[77]
<i>AT3G57560</i>	调控 NAGK	拟南芥	Slocum[73]
<i>At2g19940</i>	编码 NAGPR, 拟南芥中 NAGPR 由单基因 <i>At2g19940</i> 编码	拟南芥	Levin et al[95]
<i>Atlg80600</i>	编码 NAOAT	拟南芥	Fremont et al[97]
<i>TUMOR PRONE</i>	编码 NAOAT, 主要位于叶绿体中, 和根系表型和逆性相关	拟南芥	Fremont et al[97]
<i>Atlg80600</i>	编码 GAT	拟南芥、西瓜	Xia et al[76]
<i>At4g17830</i>	编码 NAOD	拟南芥	Fremont et al[97]
<i>At1g75330</i>	编码 OTC	拟南芥	Schmid et al[85]
<i>AT4G24830</i>	编码 ASS	拟南芥	Anwar et al[108]
<i>At5G10920</i>	编码 ASL, <i>At5G10920</i> 为拟南芥中 <i>ASL</i> 基因	拟南芥	Anwar et al[108]
<i>OsASLI</i>	编码 ASL, <i>OsASLI</i> 有 2 个可变剪接的转录本 <i>OsASLI.1</i> 和 <i>OsASLI.2</i> , <i>OsASLI.1</i> 在整个生长季大多数器官中都有表达, <i>OsASLI.2</i> 仅在根中表达	水稻	Xia et al[76]
<i>ARGAH1(At4g08900)</i>	编码 Arginase, 两者均位于线粒体中, 拟南芥中 Arginase 活性急剧增加主要是 ARGAH2 起作用; 超表达拟南芥中 ARGAH2, 拟南芥中精氨酸和鸟氨酸的含量均降低	拟南芥	Flores et al[101] Brauc et al[102]
<i>LeARG1, LeARG2</i>	编码 Arginase	番茄	Palmieri et al[48]

注: NAGS. N-乙酰谷氨酸合成酶; NAGK. N-乙酰谷氨酸激酶; NAGPR. N-乙酰谷氨酸-5-磷酸还原酶; NAOAT. N-乙酰鸟氨酸转移酶; GAT. N-乙酰鸟氨酸谷氨酸转移酶; NAOD. N-乙酰鸟氨酸脱乙酰基酶; OTC. 鸟氨酸氨甲酰转移酶; ASS. 精氨酸琥珀酸合酶; ASL. 精氨酸琥珀酸裂解酶; Arginase. 精氨酸酶。

实现的^[83-84],此外 NAGK 也可以被 N-乙酰谷氨酸激活^[85];鸟氨酸氨甲酰转移酶(OTC)^[86]被证实在许多植物中存在^[87-90],多位于植物叶绿体^[91]和线粒体中,有些也位于细胞质中^[92],是瓜氨酸合成途径的关键酶^[93],OTC 的活性是可逆的,拟南芥中 OTC 基因(*Atlg75330*)在所有部位都有表达^[85],OTC 插入突变导致突变植物对外源提供的鸟氨酸高度敏感,而对瓜氨酸不敏感^[94]。在西瓜基因组有一个 *OTC-like* 基因(*Clao20781*),相应的预测蛋白质序列与之前报道的 OTCases 高度同源;N-乙酰谷氨酸-5-磷酸还原酶(NAGPR)研究的较少^[95-96],拟南芥中 NAGPR 由单基因 *At2g19940* 编码;N-乙酰鸟氨酸谷氨酸转移酶(GAT)是叶绿体酶,具有较高的热稳定性和不敏感性,在高浓度的精氨酸和瓜氨酸的条件下不会被反馈抑制;N-乙酰鸟氨酸转移酶(NAOAT)主要于叶绿体中,与根系表型有关,拟南芥中 NAOAT 由 *TUMOR PRONE* 编码,*TUMOR PRONE* 隐性突变材料中精氨酸显著减少,表现出短根现象,这种现象可通过补充精氨酸和其前体物质恢复^[97];水稻中精氨酸琥珀酸裂解酶(ASL)基因(*OsASLI*)表达具有组织特异性,*OsASLI* 有 2 个可变剪接的转录本 *OsASLI.1* 和 *OsASLI.2*,*OsASLI.1* 在整个生长季大多数器官中都有表达,而 *OsASLI.2* 仅仅只在根中表达^[76],*ASL* 基因突变,可能导致精氨酸的含量减少,进而使水稻表现出短根现象^[76, 97];NAOD 调节植物细胞中鸟氨酸的含量^[98],并通过多胺合成调控碳氮平衡,在植物开花和坐果过程中发挥作用;N-乙酰谷氨酸乙酰转移酶(NAOGAcT)最初被认为和 NAOD 相同,但拟南芥中,在没有功能性 NAOD 的情况下,鸟氨酸积累的减少不能通过 NAOGAcT 活性得到补偿^[98],表明 NAOGAcT 功能可能次于 NAOD;精氨酸酶(Arginase)活性在拟南芥^[99]和其他一些植物^[100]幼苗发育过程中急剧增加,拟南芥中 Arginase 活性急剧增加主要是 *ARGAH2* 在起作用^[101],拟南芥中 *ARGAH2* 的过表达会导致精氨酸和鸟氨酸的含量降低^[102];精氨酸琥珀酸合酶(ASS)和精氨酸琥珀酸裂解酶(ASL)的亚细胞定位因植物类型而异^[103],一般定位于质体、细胞质或细胞核^[73, 97, 103-107],精氨酸琥珀酸合酶(ASS)和精氨酸甘氨酸裂解酶(ASL)基因突变植物与野生型植物相比,精氨酸显著减少^[108];动物中 NOS 将精氨酸转化为 NO 和瓜氨酸^[109],植物中精氨酸依赖性 NOS 也促进 NO 产生^[101, 110],仅少量研究表明可能同时产生瓜氨酸^[63]。

5 瓜氨酸在蔬菜作物抗逆中的作用

逆境胁迫条件下,蔬菜作物对瓜氨酸的含量进行调节,维持正常生长^[28]。在植株受到干旱等胁迫时,西瓜和一些瓜类植物叶片中瓜氨酸会在一些酶如(N-乙酰谷氨酸转移酶)GAT 的参与下大量积累^[10-12, 111-112],维持水分状态^[9],清除体内多余的自由基,抵御逆境的伤害^[10];外施瓜氨酸能够提高受胁迫种子的活性,促进种子萌发^[113];西瓜中谷氨酰胺酰基转移酶基因在干旱胁迫下会上调^[114];用抗病性南瓜砧木嫁接西瓜,嫁接苗果实的瓜氨酸含量高于自根苗,且瓜氨酸含量维持时间更长^[3, 115-116]。干旱胁迫和低温处理会诱导瓜氨酸在甜瓜叶片和韧皮部汁液中积累,而其他氨基酸相对没有变化^[65];黄瓜中西瓜同源基因 *CsNOAI* 的直系同源物已被证明在低温胁迫中发挥作用^[117],但尚未对其与瓜氨酸的关系进行验证;Cao 等^[118]验证表明,ABA 和瓜氨酸之间具有强相关性。对非葫芦科植物物种的几项研究揭示了在干旱或盐胁迫下参与瓜氨酸生物合成的基因显著富集,如番茄^[119]、水稻^[120]、野生小麦^[121]、鹰嘴豆^[122]和过表达 DOF(DNA binding with one finger)转录因子的拟南芥^[123]。

光呼吸是植物有效利用氮的必要过程,光呼吸受阻,氮同化受抑制^[124]。拟南芥中瓜氨酸含量与光呼吸酶 GGAT 活性密切相关,GGAT 基因过表达会选择性地诱导瓜氨酸含量积累^[64];拟南芥 *GLU1* 突变体中高水平的光呼吸铵部分转移到 CPS 介导的途径,导致精氨酸通过瓜氨酸代谢大量积累^[125];线粒体甘氨酸脱羧酶复合物(GDC)释放的光呼吸铵通过线粒体中的 CPS 重新同化为谷氨酰胺合成酶和氨基甲酰磷酸(CP)^[54],这 2 种酶都参与瓜氨酸合成,瓜氨酸合成的调节被认为是在 CPS 的水平上^[126],拟南芥 *ven3* 和 *ven6* 网状突变体叶片中鸟氨酸和 N-乙酰-L-鸟氨酸的累积量增加,瓜氨酸含量水平降低^[127],这些代谢变化表明,CPS 在提供 CP 底物参与瓜氨酸合成和瓜氨酸在植物光呼吸中发挥作用;在缺乏质体谷氨酰胺合成酶的莲属植物中,CP 水平没有变化,当植株光呼吸活跃时,野生基因型的 CP 水平显著提高^[128]。但蔬菜作物中还未见相关研究。

植物在胁迫条件下电子传递链会被破坏,活性氧(ROS)积累,造成细胞损伤。植物能够利用酶促和非酶促抗氧化剂来清除 ROS,其中氨基酸、糖醇和叔胺等渗透物是强大的抗氧化剂,能增强植物对

胁迫的耐受性^[129]。瓜氨酸被认为是比甘露醇、脯氨酸和甘氨酸甜菜碱更有效的羟基自由基清除剂^[10]，保护绿色组织免受氧化应激^[130]。野生西瓜干旱胁迫叶片中参与瓜氨酸含量生物合成基因上调，参与瓜氨酸含量分解代谢的基因下调^[51]。综上所述，瓜氨酸在逆境胁迫下发挥重要作用，能作为蔬菜作物耐逆境胁迫的代谢标志物加以应用。

6 讨论与展望

随着人们对饮食健康的关注，天然植物瓜氨酸的营养价值被逐渐重视起来。同时瓜氨酸在蔬菜作物抗逆^[28]以及氮代谢^[65]中也发挥了重要作用，如参与氮营养长距离转运^[36]、胁迫期间维持细胞渗透压^[9]、作为光呼吸 NH_4^+ 的清除剂^[125]等，表明瓜氨酸可以作为研究蔬菜作物胁迫耐受性的有效标志物。蔬菜作物中瓜氨酸含量的稳定可能是分解代谢减少、生物合成增加^[40-42]、长距离运输^[36]、跨果皮和果肉组织分配^[41-42]的综合结果。目前人们对蔬菜作物中瓜氨酸的合成代谢已经有了一定的研究基础^[73]，但许多参与瓜氨酸合成代谢的酶尚未进行功能验证，瓜氨酸通过维管系统调节或转运的完整模型尚未建立，对瓜氨酸细胞间/内转运和植物生理作用调节的生化及分子机制还不够清晰，一些调控基因、转录因子在调控瓜氨酸的合成过程中的地位、具体途径也尚不清楚。

目前许多园艺作物的基因组、转录组及代谢组等相关数据正逐渐完善^[131-133]，瓜氨酸合成途径中相关的基因和酶也逐渐被广泛研究^[40,48,71]，一些酶类的亚细胞定位以及相关基因的分离和鉴定技术逐渐成熟。未来可以将重点放在瓜氨酸或鸟氨酸特异性转运蛋白的研究上，有助于对蔬菜中瓜氨酸动态合成和运输的理解。识别更多潜在的瓜氨酸调控酶，获得瓜氨酸亚细胞和长距离分配的精准定位也尤为重要。在蔬菜发育过程中不同营养状态和环境胁迫下进行全植物代谢分析，并结合它们的组织特异性和亚细胞定位实验，发掘游离瓜氨酸的合成、同化、运输和积累位点，对瓜氨酸代谢和运输网络步骤及分子机制进行更好的定性。同时可以对蔬菜作物体内调节瓜氨酸合成代谢的酶及其调控基因以及关于瓜氨酸的信号传导等进行深入研究。西瓜的果实中含有大量的瓜氨酸^[6]，作为一种鲜食水果，人们更容易从中摄取到天然优质的瓜氨酸营养。同时西瓜是一个很具代表性的模型系统，具有可利用的遗传作图资源^[134]、新一代测序数据、

广泛的自然遗传多样性以及基因组信息数据库^[133]，这种全面的数据集可以帮助研究者提高对瓜氨酸动态产生的理解。对西瓜群体进行全基因组关联分析(GWAS)将有助于挖掘与瓜氨酸代谢相关的新基因或有利等位基因，从而有效提高作物中瓜氨酸的含量和稳定性，为培育高瓜氨酸含量的西瓜新品种提供理论依据，为人类营养和健康作出贡献。

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