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外源物质提高葡萄抗寒性的作用机制及其应用进展

王志磊^{1,4,5} 翟肖宇¹ 李超³ 薛婷婷^{1,4,5} 徐国前^{1,4,5} 要菲^{2*} 张军翔^{1,4,5*}

(1. 宁夏大学 葡萄酒与园艺学院, 银川 750021;

2. 山西如燕酒庄有限公司, 山西 太谷 030899;

3. 银川市河东生态园艺试验中心, 银川 750021;

4. 葡萄与葡萄酒教育部工程中心, 银川 750021;

5. 宁夏葡萄与葡萄酒工程技术中心, 银川 750021)

摘要 低温是制约全球葡萄越冬栽培发展的主要挑战之一, 随着越冬保护措施的不断完善, 越来越多的外源物质被用于增强葡萄的越冬抗寒性, 认识和理解不同外源物质增强葡萄越冬抗寒性的作用机制能够有效帮助实施越冬保护措施。本研究通过检索国内外聚焦外源物质与葡萄抗寒性的相关文献, 综述外源物质提高葡萄抗寒性的作用机制及应用进展。结果表明: 1) 葡萄的抗寒性受自身的遗传特性与外在因素的双重影响; 2) 外源物质通过影响抗寒相关基因的表达以及表达产物的运输与分配, 增强葡萄的抗寒性; 3) 外施适宜浓度的外源物质能够有效增强葡萄的抗寒性。综上, 不同外源物质增强葡萄抗寒性的作用机制不尽相同, 外施适宜浓度的外源物质均可以不同程度地提高葡萄的抗寒性。本研究为如何增强葡萄抗寒性提供了一些策略和见解。

关键词 外源物质; 生长调节剂; 无机盐离子; 葡萄; 抗寒性

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Mechanism and application of exogenous substances to improve cold resistance of *Vitis* L.

WANG Zhilei^{1,4,5}, ZHAI Xiaoyu¹, LI Chao³, XUE Tingting^{1,4,5}, XU Guoqian^{1,4,5},
YAO Fei^{2*}, ZHANG Junxiang^{1,4,5*}

(1. College of Enology and Horticulture, Ningxia University, Yinchuan 750021, China;

2. Shanxi Ruyan Wine Industry Co., Ltd., Taigu 030899, China;

3. Hedong Ecological Horticulture Experimental Center of Yinchuan, Yinchuan 750021, China;

4. Engineering Center of Grape and Wine Education Ministry, Yinchuan 750021, China;

5. Ningxia Grape and Wine Engineering Technology Center, Yinchuan 750021, China)

Abstract Low temperature is one of the major challenges restricting the development of global viticulture during the overwintering period. With the continuous improvement of overwintering protection measures, more and more exogenous substances are used to enhance the cold resistance of grapevines during the overwintering period. Understanding the mechanism of different exogenous substances to enhance the

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第一作者: 王志磊(ORCID:0009-0008-6679-249X), 副教授, 主要从事葡萄与葡萄酒学研究, E-mail: wangzl1994@nxu.edu.cn

通讯作者: 要菲(ORCID:0009-0006-2143-2226), 助理酿酒师, 主要从事葡萄与葡萄酒学研究, E-mail: yaofei@nwafu.edu.cn

张军翔(ORCID:0000-0002-9487-0247), 教授, 主要从事葡萄与葡萄酒学研究, E-mail: zhangjunxiang@126.com

winter resistance of grapevines can effectively help us implement overwintering protection measures. In this paper, the mechanism and application progress of exogenous substances to improve grapevine cold resistance were reviewed by collating domestic and foreign literature. The results showed as follows: 1) The cold resistance of grapevine was influenced by both its genetic characteristics and external factors; 2) Exogenous substances enhance the cold resistance of grapevine by affecting the expression of cold-resistance-related genes, and the transport and distribution of expression products; 3) Application of appropriate concentration of exogenous substances can effectively enhance the cold resistance of grapevine. In conclusion, the mechanism of enhancing grapevine cold resistance by different exogenous substances is not the same. The application of exogenous substances with appropriate concentration can effectively improve grapevine cold resistance. This study provides some strategies and insights on how to enhance the cold resistance of grapevines.

Keywords exogenous substance; growth regulator; inorganic salt ions; *Vitis L.*; cold resistance

葡萄是我国重要的果树经济作物,在全国32个省份均有种植,其中北方干旱、半干旱地区受温带大陆性气候的影响,低温成为限制我国北方地区葡萄生产发展的一个重要因素,选择合适的越冬保护措施,实现葡萄的安全越冬,对于葡萄与葡萄酒产业可持续和高质量发展具有重要的意义^[1]。覆盖防寒是当前葡萄栽培主要的越冬方式,尤其是埋土防寒越冬,但埋土越冬带来的植株损伤、生态破坏和成本上升制约了葡萄与葡萄酒产业的发展^[2]。此外,采用保温仓、保温被、保温膜和草帘等保温材料覆盖也取得了明显的保温效果,但保温效果有限,无法应对极端低温,且多数覆盖材料为非环保材料,堆积占用的空间大^[3]。综合当前越冬保护措施的优点,北方地区采用免下架越冬栽培可避免葡萄植株在下架和上架过程中的损害,应用前景广泛^[4]。

目前生产中比较常用的免下架栽培办法是使用外源物质来提高葡萄在越冬期间对低温的耐受性,如外施生物刺激素腐殖酸(HA)、植物激素脱落酸(ABA)、褪黑素(MT)、无机盐离子 Si^{2+} 、 Se^{2+} 和 Ca^{2+} 等。这些外源物质搭配抗寒性较高的葡萄品种有望实现中国北方葡萄的免埋土越冬栽培^[5-6]。因此,本研究针对葡萄免下架越冬栽培技术,综述了影响葡萄抗寒性的内因和外因,并对可以提高葡萄抗寒性的外源物质进行总结,概括其作用机制及应用进展,提出未来葡萄防寒越冬的研究方向,进而为葡萄的越冬栽培模式提供理论依据和技术支撑。

1 影响葡萄抗寒性的因素

抗寒性是植物在长期适应低温环境的过程中,

通过自然选择和自身遗传变异获得的一种抗寒能力,是果树的一个重要性状^[1]。葡萄的抗寒性除受自身遗传特性控制外,还与葡萄的树龄、长势、生长发育阶段、营养积累,枝条的形态结构、粗度、成熟度,外界的温度、光照、水分及抗寒锻炼等有关。

1.1 外在因素

1.1.1 温度

低温是重要的环境刺激信号,是冷驯化过程的主导因子。葡萄冷驯化过程是渐进累积的,抗寒力随着冷驯化气温的降低而增强,葡萄抗寒力指数与低温存在典型的Logistic非线性关系。在气温 $< -18.0\text{ }^{\circ}\text{C}$ 时,葡萄启动冷驯化过程,抗寒力随温度降低而增强;在气温 $< -12.0\text{ }^{\circ}\text{C}$ 后,葡萄抗寒能力迅速增大;在气温 $< -3.0\text{ }^{\circ}\text{C}$ 时,葡萄枝条的抗寒力缓慢增大,至埋土前,葡萄抗寒力趋于最大^[7]。此外,低温可以刺激葡萄休眠芽中水杨酸的合成以及 $VvCBFs$ 的过表达,引起葡萄枝条含水率降低, Ca^{2+} 和蔗糖含量增加,致使葡萄越冬抗寒性提高^[8]。

1.1.2 光照

短日照在诱导植物抗寒性增强方面具有非常重要的作用。有研究表明,葡萄枝条的脱落酸含量与日照时间存在显著的正相关关系,13 h的日照长度可使美洲种葡萄进入休眠诱导期^[7]。在自然低温条件下,短日照增加葡萄植株的总呼吸速率,并加速植株进入休眠,暗示了短日照光周期对自然休眠诱导有促进作用^[9]。研究表明,欧美杂种‘夏黑’葡萄冬芽的自然休眠诱导受光周期和温度影响,13.4 h左右的短日照和 $17.6\text{ }^{\circ}\text{C}$ 左右的自然低温单独或联合作用均能诱导冬芽进入休眠,越冬抗寒性开始升高^[9]。

1.1.3 水分

植物含水量与抗寒性密切相关,自由水含量愈高,植物代谢活动愈强,生长也较快;束缚水是植物体内与原生质胶体紧密结合的水分,不参与代谢,也不易结冰和蒸发。葡萄在自然低温胁迫下束缚水含量增加,且随着温度的降低,束缚水与自由水的比值升高,越冬抗寒性升高^[10]。然而,含水量过高或过低都不利于越冬抗寒性的提高。研究表明,降水(灌溉)明显降低了葡萄枝条的越冬抗寒力,而含水量过低会因影响植株正常生长而不利于越冬抗寒性提高^[7]。同时,植物在干旱条件下比在潮湿条件下越冬抗寒性更高^[11]。

1.1.4 其他外因

枝条的营养水平与葡萄的越冬抗寒性密切相关,越冬期间,可溶性糖等渗透调节物质增加,有助于增加细胞液浓度,降低冰点温度,从而提高葡萄自身的越冬抗寒性^[10]。土壤中水分和养分的异质供应通过各种信号过程影响植物的生长、形态和生理,如土壤孔隙大小影响根系的吸水过程,土壤干燥度直接影响气孔导度和叶生长速度,这些因素直接或间接影响葡萄的抗寒性^[12]。内生菌广泛存在于各种植物组织内,直接或间接地参与了植物生长发育的各个阶段,并能增强宿主对非生物胁迫的抗性,维持宿主在逆境条件下正常生长^[13]。研究表明,*Burkholderia phytofirmans* PsJN降低了低温对植物光合作用的影响,并增强葡萄对低温的耐受性^[14]。已知芽孢杆菌属、假单胞菌属、变形杆菌属和根瘤菌属的许多细菌菌株可从硅酸盐中释放硅并促进植物生长,增强植物抗逆性^[15]。随着可持续种植系统的需求日益迫切,内生菌可能是今后研究的一个热点。

1.2 内在因素

1.2.1 遗传学基础

通常而言,野生种山葡萄(*Vitis amurensis*)抗寒性最强,美洲种葡萄(*Vitis labrusca*)次之,欧亚种葡萄(*Vitis vinifera*)抗寒性最差。其中,山葡萄的枝蔓可耐-40℃低温,根系可耐-15℃低温,是抗寒育种的重要种质资源^[16]。导致葡萄种间抗寒性的巨大差异可能与种质资源的起源地及地理分布区密切相关,起源地极端低温越低,种质抗寒性可能越强^[17]。

1.2.2 生长周期

植物有着抗寒性发育的内在节律,葡萄生长期的抗寒性比休眠期弱。以欧亚种葡萄为例,春季膨大的芽眼能忍受-1℃的低温,温度下降到-3~-4℃时常发生冻害,休眠期的芽眼则能忍受-15℃的低温^[2]。一旦芽在脱驯化过程中开始萌芽膨大,它们的耐寒性就会迅速降低,并且物候期的提前可能会增加新生葡萄芽遭受倒春寒的风险^[18]。

1.2.3 细胞结构

葡萄对低温胁迫的适应包括膜结构的变化、渗透调节物质的积累、抗氧化系统的调节以及抗寒基因的表达。抗寒性强的葡萄品种低温下细胞渗透性小,发生渗透性变化的细胞可逆转恢复正常;相反,抗寒性弱的品种细胞发生严重冷害不易恢复正常,极易导致植株死亡^[19]。渗透调节物质本质上是亲水性的,因此它们很容易与膜蛋白和其他复杂的蛋白质系统相互作用,从而稳定酶、膜、蛋白质和复合物,而不会在胁迫条件下改变其结构和功能^[20]。

2 外源物质提高葡萄抗寒性的作用机制

外源物质通过影响植物内部相关基因的表达以及表达产物的运输与分配,调控植物生长发育,增强葡萄的抗寒性。葡萄抗寒栽培中使用的外源物质主要分为三大类:使用外源激素或相关活性物质影响调节网络的表达,如脱落酸、茉莉酸、乙烯、水杨酸和油菜素内酯等;使用含钙离子调节剂,改善低温信号转导,激活下游基因的表达;使用其他无机盐离子,如硅、钾和硒等。

2.1 活性物质提高葡萄抗寒性的作用机制

2.1.1 腐殖酸类物质

腐植酸类物质是由动物、植物残体在微生物以及地球化学作用下分解和合成的一类天然有机高分子聚合物,其主要的成分是生理活性物质和黄腐酸,作为主要生物刺激剂,它可以调节植物的代谢过程,促进植物生长发育^[21]。其主要成分黄腐酸通过提高保护酶活性来缓解氧化损伤,通过提高脯氨酸和可溶性糖等渗透调节物质的含量进而提高植物抗性^[22]。HA可以激活与应激防御机制有关的多种基因集,经HA处理之后,脱水反应元件结合蛋白2A(DREB2A)、氧化应激3(OXS3)和热应激诱导的热休克蛋白(HSPs)等相关基因上调^[23]。DREB2A和OXS3过表达赋予了葡萄对干旱、寒冷、重金属和氧

胁迫下的生长,被称为“胁迫激素”或“逆境激素”。在葡萄冷驯化和脱驯化过程中,外源 ABA 的应用可以通过直接渗透,或通过上调 9-顺式-环氧类胡萝卜素双加氧酶(NCEDs)介导的间接正反馈来增加细胞内的游离 ABA 含量。游离 ABA 的积累会触发 ABA 信号转导,并刺激下游 ABA 响应代谢途径或基础代谢途径(图 1),如棉子糖家族系列寡糖(RFO)代谢,生长素代谢和核糖体生物合成^[35]。一定浓度的 ABA 对其生物合成存在正反馈,但随着浓度的增加,这种正反馈被 AREB(ABA 应答元件结合蛋白)和 NAC 蛋白复合物介导的另一个 ABA 依赖的负反馈系统平衡^[36]。植物脱落酸受体(PYL/RCARs)在与 ABA 结合后,与 2C 类蛋白磷酸酶(PP2C)形成一个三元复合物,PP2C 在三元复合物中失活,促进蔗糖非发酵-1-相关蛋白激酶 2(SnRK2)成员的自磷酸化,进而磷酸化 AREB/abf(ABA 的响应元件)等转录因子。在细胞核中,激活的 AREB/abf 通过结合 NCED 的上游启动子区域,负调控 ABA 应答基因的表达(图 1)。

有研究称 2 个编码 NCED 的基因在葡萄冷驯化与脱驯化试验中均被外源 ABA 上调^[35]。在葡萄冷驯化试验中,外源 ABA 处理上调了催化 RFO 前体(半乳糖醇)或 RFOs(蜜子糖或水苏糖)合成的 3 个关键酶编码基因的表达^[35]。ABA 的施用可能会对生长素的生物合成产生负面影响,抑制生长素的积累,从而减缓芽萌发的过程^[37]。此外,低温处理和对葡萄休眠芽施用外源 ABA 都上调了 *VvCBF2*、*VvCBF3*、*VvCBF4* 和 *VvCBF6* 的表达,增加了超氧化物歧化酶编码基因(*VvSOD1*, *VvSOD3*)、过氧化氢酶编码基因(*VvCAT1*)以及谷胱甘肽过氧化物酶(GPx/GSH-Px)编码基因(*VvGPx3*)的表达^[37]。综上,正常条件下施用外源 ABA 可调节一系列防御反应,提高植物的抗寒性,而在逆境条件下施用外源 ABA 可改善植物的防御机制。晚秋(冷驯化)葡萄叶面施用 ABA 可提高冬芽的抗寒性,早春(脱驯化)在葡萄芽上施用 ABA 可推迟萌芽。

2.2.2 其他植物激素

乙烯(ET)是一种气态植物激素,调节植物生命周期的许多方面。ET 对植物的抗寒作用在不同的物种中有所不同,研究证实 ET 对葡萄的抗寒性具有积极影响,低温胁迫会促进葡萄藤中 ET 的释放,外源性氨基环丙烷处理提高葡萄低温应激期间的

抗寒性,相反生物合成抑制剂氨基乙氧基乙烯甘氨酸的外施应用降低葡萄的抗寒性^[38]。茉莉酸(JA)属于植物的内源生长调节物质,在应对低温等非生物胁迫起着重要的作用,研究表明 VaPAT1 通过调节 JA 生物合成在葡萄的冷应激反应中发挥着关键作用^[39]。水杨酸(SA)处理的葡萄叶面可以增加细胞间隙或液泡中 Ca^{2+} 回流,从而保护叶绿体免受破坏。2 mmol/L SA 溶液喷洒葡萄叶面后,叶片中抗氧化酶活性、可溶性糖和脯氨酸含量显著增加,暗示了水杨酸可通过 Ca^{2+} 稳态和一个更高的抗氧化活性系统来调控葡萄的抗寒性^[40]。同样,外施油菜素内酯可以结合钙信号调节增强葡萄的抗寒性,减轻低温带来的冷冻损伤^[41]。

2.3 无机盐离子提高葡萄抗寒性的作用机制

2.3.1 硒

硒可以通过调节活性氧水平来缓解低温对植物造成的氧化应激,其作用方式如下:刺激 O_2^- 歧化为 H_2O_2 ,调节抗氧化系统,通过含硒酶直接消除活性氧^[42]。如图 1 所示,硒还可以促进褪黑素的合成,在正常和冷应激条件下,褪黑素生物合成基因 *T5H* 和 *COMT* 的表达随着硒处理的增加而显著增加,褪黑素含量增加,植物抗寒性提高^[43]。硒通过调节抗氧化酶相关基因(*GPX1*、*GPX4*、*CATa* 和 *CATc*)的表达增强抗氧化系统,从而促进活性氧降解,最终减轻胁迫对植物的不利影响^[44]。硒促进有丝分裂原激活蛋白激酶和钙依赖蛋白激酶基因的表达,这些基因作为改善抗氧化防御系统成分的信号来提高植物抗寒性^[45]。

硒元素是谷胱甘肽过氧化物酶(GSH-Px)的组成成分,能调节 GSH-Px mRNA 的稳定性,提高抗坏血酸-谷胱甘肽(AsA-GSH)循环中脱氢抗坏血酸还原酶(DHAR)、单脱氢抗坏血酸还原酶(MDHAR)、GSH-Px 和谷胱甘肽还原酶(GR)的活性,增加了 AsA 的再生能力和还原谷胱甘肽(GSH)的合成能力^[46]。如图 2 所示,APX(AsA-GSH 循环中的关键酶类组分)利用 AsA 作为特定的电子供体,将 H_2O_2 还原为水,同时产生单脱氢抗坏血酸(MDHA)。MDHA 自发转化为 AsA 和 DHA(2,3-二酮古洛糖酸),DHA 在 DHAR 的作用下迅速还原为 AsA, DHAR 首先利用 GSH 降低 DHA。氧化型谷胱甘肽(GSSG)在 GR 作用下通过还原型辅酶 II(NADPH)再生 GSH^[47]。甲基乙二

醛(MG)是一种高度反应性的细胞毒性化合物,它主要被乙醛酶系统中中和^[48]。综上,硒在胁迫下对植物的保护作用主要归因于4种机制:通过增强根系

吸水来调节植物水分状态,保护细胞免受氧化损伤,刺激渗透调节物质的积累,调节植物相关基因的表达。

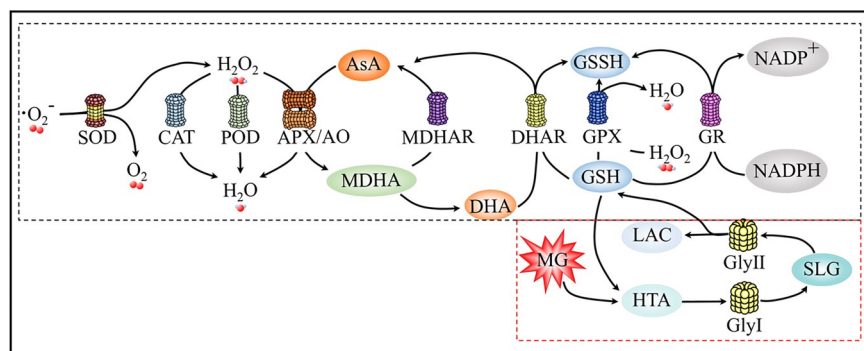


图2 AsA-GSH循环和乙醛酶系统

Fig. 2 AsA-GSH cycle and acetaldehyde enzyme system

2.3.2 硅

硅与角质间形成“角质-硅质”双层结构,增强了植物细胞壁的机械强度,从而提高了植物抗冻害能力^[49]。硅与叶表皮细胞壁中的木质素-碳水化合物有关,硅施用量的增加会导致木质素的产生,致使叶组织变厚,从而提高了植株的耐冷性^[50]。硅诱导的木质部导管细胞壁特征的变化可以调节水的运输,硅与细胞壁半纤维素的结合提高植物结构稳定性^[51]。冬季出现了更多细长的植硅体,沉积在表皮、内胚层、中柱体和木质部的细胞壁中,有助于保持叶片的水分,减轻冷害^[52]。此外,植物吸收的凝胶态硅或可溶性硅可以改变细胞膜的膜脂含量和脂肪酸配比,提高清除活性氧自由基的抗氧化酶的活性和非酶物质的含量,降低膜脂过氧化作用,从而提高植物的抗寒性^[49]。硅还通过与其他激素相互作用,调节植物抗寒性^[53-54]。

外源硅增加抗氧化防御相关基因的表达,如过氧化物酶(POX)、查尔酮合酶(CHS)、几丁质酶和AsA-GSH循环中的酶,下调根和芽中参与ABA合成的基因^[55]。Si还增加了参与酚类和类黄酮生物合成的系统获得性反应苯丙烷途径的基因的表达^[56]。Si通过上调脱落酸响应元件结合蛋白(AREB)、富含半胱氨酸类受体激酶(CRK1)、脱落酸和环境应激诱导蛋白(TAS14)和NCED3基因的表达来缓解胁迫^[57](图1)。综上,硅提高植物抗寒性的作用机制主要体现在以下5点:形成“角质-硅质”双层结构,增强植物细胞壁的机械

强度;硅化结构可以调节气孔开闭,减少水分散失;改善抗氧化系统,提高渗透调节物质含量;硅与其他激素的相互作用;硅调节植物相关基因的表达。

2.3.3 钙

钙元素是植物细胞壁、细胞膜的重要组成部分,可以与果胶质结合成果胶酸钙增强细胞壁的机械强度,也可以和磷脂相结合增强细胞膜的稳定性。 Ca^{2+} 通过传递低温信息诱导抗冷基因的表达以提高植物的抗冷力^[58]。如图1所示,冷胁迫由 Ca^{2+} 渗透的机械敏感通道MCA1和MCA2感知,并通过膜流动性和细胞骨架重组进行调节,引发钙内流和钙依赖蛋白激酶(CDPKs)、类钙调蛋白(CMLs)、CBLs及其互作蛋白激酶(CIPKs)和有丝分裂激活蛋白激酶(MAPK)的激活,它们介导COR基因表达^[59-60]。单独的CBLs蛋白能结合 Ca^{2+} ,并通过与CIPKs蛋白互作,CIPK发生磷酸化,解除自身活性抑制,向下游传递信号^[61]。在MAPK信号传递通路中,随着细胞质内 Ca^{2+} 不断积累,通过MAPKKK-MAPKK-MAPK依次磷酸化,将上游的低温信号逐步传递给下游的应答因子,从而调控目的基因的表达^[62]。

钙对抗氧化能力的改善由钙调素(Ca^{2+} 结合蛋白,CaM)介导。研究表明,SOD是一种钙调素依赖酶, Ca^{2+} /钙调蛋白介导的信号传导也被证明通过调节COR基因表达参与诱导冷适应^[63]。VaCPK20过表达通过调节胁迫应答基因,即ABA反应元件结

合因子3(ABF3)或钠/氢交换器1(NHX1)和冷调节基因(*COR47*),表现出对干旱和冷胁迫的高水平耐受性^[64]。此外,多种植物激素信号途径和 Ca^{2+} 信号成分之间存在交叉调节,形成复杂的信号调节网络^[65]。因此,钙是一种对植物的生长和发育必需的营养素,且 Ca^{2+} 作为第二信使,增强植物在各种胁迫条件下的抗性。

3 外源物质在葡萄抗寒中的应用

3.1 外源HA施用对葡萄植株抗寒性的影响

施用外源HA对胁迫条件下许多植物的渗透积累有显著影响,适宜浓度的腐殖酸可以通过调控渗

透调节物质含量以及保护酶活性来减缓胁迫对植株的伤害,提高植株的抗逆能力。如图3所示,HA提高越冬葡萄植株体内POD、SOD、APX、CAT、多酚氧化酶(PPO)、硝酸还原酶(NR)活性^[66]。HA降低越冬葡萄植株体内丙二醛(MDA)含量,调节活性氧含量,减轻膜脂的过氧化水平,从而保持了细胞膜的通透性,增强植株对越冬期间低温的抗性^[67]。HA还能促进植物酚类化合物的产生,调节细胞氧化还原形态,它们也被认为是应对不利环境条件的防御群之一^[68]。此外,施用外源腐植酸可以改良土壤理化性质,优化植物的生长环境,间接提高植物的越冬抗寒性^[69](图3)。

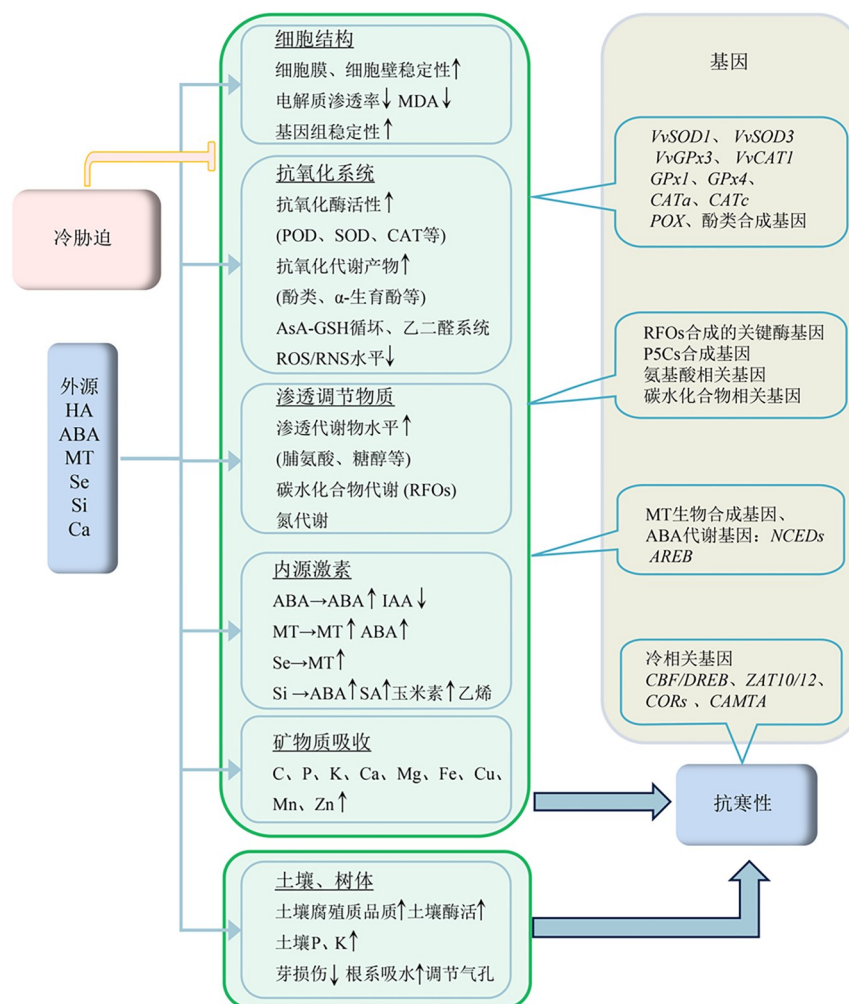


图3 不同外源物质对葡萄植株抗寒性的影响

Fig. 3 Effects of different exogenous additives on cold resistance of grapevines

3.2 外源ABA施用对葡萄植株抗寒性的影响

ABA通过诱导芽组织脱水而增加芽的抗冻性,

减少芽组织的可冻水量^[70]。在葡萄冷驯化的过程中,关键的变化是叶片的衰老以及芽基部到顶端周

皮形成过程,经ABA处理的葡萄叶片衰老提前、植株周皮形成率增加,芽损伤率降低,抗寒性增强^[71]。应用于葡萄园的ABA适宜浓度在100~1 000 mg/L,因基因型、栽培方式以及施用部位的不同而不同,施用ABA可有效诱导‘品丽珠’‘灰比诺’‘霞多丽’等葡萄的冷驯化和深度休眠,提高葡萄的抗冻性,提升幅度在2~3.5℃^[72]。此外,施用ABA后,未检测到植物毒性反应以及未对产量和浆果成分产生不利变化,这一发现可能为外源ABA在葡萄园的抗寒栽培实践应用提供依据^[72]。

3.3 外源MT施用对葡萄植株抗寒性的影响

MT通过进入细胞核直接影响遗传物质,提高基因组稳定性和减少可能的突变而增加植物抗性^[73]。低温胁迫下,MT预处理的植物丙二醛含量和电解质渗漏较低^[74]。经胁迫后,用MT预处理的葡萄枝条与对照相比,细胞结构损伤更低^[75]。研究表明,100 μmol/L外源MT可以提高越冬葡萄植株体内SOD、POD和CAT等抗氧化酶的活性,并增强AsA-GSH循环中抗坏血酸过氧化物酶(APX)、脱氢抗坏血酸还原酶(DHAR)、单脱氢抗坏血酸还原酶(MDHAR)和谷胱甘肽还原酶(GR)活性,增加AsA和GSH含量,为抗坏血酸-谷胱甘肽(AsA-GSH)循环系统提供充足底物,加速活性氧清除效率,减轻活性氧对膜脂的伤害,保持细胞完整性,从而缓解越冬期间低温对葡萄的伤害^[76-77]。MT通过调节渗透势和维持离子稳态来提高葡萄抗逆性,MT预处理后,可溶性蛋白和脯氨酸的水平显著提高(图3)。MT处理增加了Δ1-吡咯啉-5-羧酸合成酶(P5CS)基因的表达,促进脯氨酸的生物合成。

3.4 外源硒的施用对葡萄植株抗寒性的影响

外源硒的施用促进AsA-GSH循环和乙二醛酶系统的协同上调,诱导葡萄叶片抗氧化酶(SOD、POD、APX和CAT)活性的增加,并抑制了丙二醛的积累以及脂质的过氧化水平^[47-48]。硒可以改变与代谢活动相关的矿物质的吸收和积累,直接影响膜转运蛋白的活性^[78]。外源硒的添加改善了铁、锌和锰等矿物质向幼苗地迁移,且这些矿物质是SOD、POD和CAT等抗氧化酶的结构成分^[79]。硒的施用可通过与二氨基亚胺脱羧酶的相互作用,调节氨基酸的生物合成^[80]。硒处理还显著增加了受到冷胁迫幼苗的花青素、黄酮类化合物和多酚类化合物的含量,它们具有清除自由基和抑制膜脂过氧化的能

力^[81]。高浓度硒干扰硫代谢,含硒氨基酸取代含硫氨基酸及其合成的蛋白质,从而改变植物的形态、生理学和生物化学特性^[82]。此外,在施用硒肥以后,‘红提’葡萄果实硒含量可增加4倍以上。

3.5 外源硅的施用对葡萄植株抗寒性的影响

硅通过提高根系质量和密度提高植物活力,还通过提高植物细胞壁强度和细胞膜结构完整性提高抗冻性,缓解低温胁迫对葡萄植株的不利影响^[83]。将硅施加于受冷胁迫的葡萄叶片显著降低了MDA水平,有效提高叶片渗透调节物质(可溶性糖、可溶性蛋白和脯氨酸等)含量,加快蔗糖转运及代谢速率,缓解活性氧累积,增强其耐寒性^[84]。硅还可以增加植物类黄酮、α-生育酚、类胡萝卜素、氨基酸、总蛋白质和总糖含量等抗氧化物质和渗透调节物质的含量,提高单株产量、可溶性固形物百分比、总花青素和总酚,降低总酸度的百分比^[85-86]。如图3所示,外源硅可以增加植物CAT、POX和SOD酶活性,并通过调节抗坏血酸-谷胱甘肽途径,增加AsA和GSH含量以及增强AsA-GSH循环酶(APX、MDHAR、DHAR和GR)活性^[55]。此外,乙二醛酶系统酶(Gly I和Gly II)的活性也在硅的作用下增强^[87-88]。

3.6 外源钙的施用对葡萄植株抗寒性的影响

钙的使用可以增加植株茎中的总果胶含量以及其他细胞壁成分,上调可溶性碳水化合物和总蛋白质含量,进而缓解低温对葡萄植株的伤害,从而增强了葡萄的越冬抗寒性^[89];如图3所示,Ca²⁺可以操纵植物的抗氧化酶系统,调节其清除活性氧的抗氧化水平,外施Ca²⁺后,植物SOD、CAT和APX等酶活性增强^[90];它还参与诱导一些非酶抗氧化剂,如抗坏血酸、α-生育酚、类胡萝卜素和谷胱甘肽等^[63];外源Ca²⁺的施用可以降低MDA含量和H₂O₂含量,增强根系代谢活性,提高糖含量^[91],并增加脯氨酸合成酶的水平来调节脯氨酸积累^[92],以此来抵御越冬期间低温伤害。研究表明,喷施5 mmol/L CaCl₂能够增加葡萄主干中的可溶性糖和脯氨酸含量,增强SOD等酶活性,降低MDA含量,提高葡萄细胞膜的稳定性^[93]。

4 展 望

广泛种植的欧亚种葡萄多对寒冷敏感,本研究综述了目前常用的几种提高葡萄抗寒性的外源物

质,概括了其作用机理和应用研究。通过分析近年来的研究成果,可以看出施用外源物质来提高葡萄植株抗寒性是有效可行的,但针对不同地域具体品种施用外源物质的最佳时间和浓度等不明确。此外,当前的研究多为单一浓度的试验,可能会与田间实际的应用生产相割离,了解这些外源物质如何缓解低温胁迫下葡萄冷害的作用机制有助于选择适宜的物质进行田间复配试验以发挥最大的作用,二者可能是未来的研究方向。

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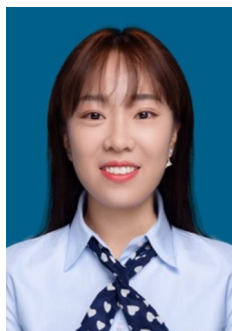
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第一作者简介:王志磊,工学博士,宁夏大学葡萄酒与园艺学院副教授,硕士生导师。主要从事葡萄与葡萄酒学研究。主持国家自然科学基金地区项目和宁夏自然科学基金项目各1项,以第一作者或通讯作者在 *Horticultural Plant Journal*、*Euphytica*、*Frontiers in Plant Science* 等期刊发表SCI论文10篇。



通讯作者简介:要菲,葡萄与葡萄酒学硕士,2023年6月毕业于西北农林科技大学葡萄酒学院。同年入职山西如燕酒庄有限公司,任助理酿酒师一职,主要研究方向为葡萄与葡萄酒学。



通讯作者简介:张军翔,工学博士,宁夏大学葡萄酒与园艺学院教授,博士生导师。主要从事葡萄与葡萄酒学研究。先后主持国家重点研发项目课题、自然科学基金、联合基金等多个项目。获宁夏自治区科技进步一等奖1项。发表论文80余篇,主编教材2部,授权专利2项。