

砧木对葡萄生长发育、果实品质及抗逆性影响的研究进展

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摘要: 砧木作为葡萄栽培的重要基础, 其选择直接影响接穗品种的生长发育、果实品质及环境适应性。近年来研究表明, 不同砧木通过调控根系构型、养分吸收、水分利用效率及激素平衡, 显著影响葡萄的生长势、产量及果实糖酸比、色泽等品质指标。此外, 砧木的抗性基因在增强葡萄对干旱、盐碱及病虫害等生物与非生物胁迫的适应性中起关键作用。砧穗亲和性则通过影响嫁接愈合率及物质运输, 进一步决定葡萄的整体表现。本文总结了近年来有关不同砧木对葡萄生长发育、果实品质及抗逆性影响等方面的主要研究成果, 探讨了砧木选择和应用的未来方向, 以为葡萄栽培中的砧木选择提供理论基础和实践指南。

关键词: 葡萄; 砧木; 生长发育; 果实品质; 抗逆性; 嫁接亲和性

中图分类号: S663.1 文献标志码: A 文章编号: 1009-9980(2026)02-0407-17

Advances in research on the influence of rootstocks on grape growth and development, fruit quality and stress resistance

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Abstract: Grapevine (*Vitis vinifera* L.) is one of the most economically important fruit crops globally, widely cultivated for fresh consumption, wine production, and processing due to its adaptability across diverse climates and high market demand. The selection of appropriate rootstocks is fundamental to sustainable viticulture, as they profoundly influence grapevine growth (including vigor, canopy development, and nutrient uptake), fruit quality (affecting sugar accumulation, acidity, phenolic content, and aromatic compounds), and stress resilience (enhancing tolerance to drought, salinity, pests, and diseases). By mediating physiological interactions between the scion and soil environment, rootstocks optimize vineyard performance under varying agroecological conditions. This review synthesizes current research on rootstock effects, highlighting their role in growth regulation, fruit quality enhancement, and stress adaptation mechanisms, thereby providing a scientific foundation for informed rootstock selection and targeted breeding programs to advance sustainable grape production. Rootstocks serve as critical determinants of grapevine growth and productivity by profoundly modulating key physiological and morphological traits. Their influence extends to vine vigor, canopy architecture, and metabolic processes, with distinct rootstock genotypes eliciting markedly different growth responses. For instance, vigorous rootstocks such as 1103 Paulsen and 140 Ruggeri stimulate robust cane elongation and enhance photosynthetic efficiency by optimizing leaf area development and stomatal conductance. In contrast,

收稿日期: 2025-07-01 接受日期: 2025-07-25

基金项目: 宁夏回族自治区重点研发计划项目(2025BBF02019); 宁夏自然科学基金优秀青年项目(2024AAC05049); 宁夏回族自治区农业育种专项项目(NXNYYZ202101)

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dwarfing rootstocks like 101-14 Mgt and SO4 restrict vegetative growth, promoting earlier berry maturation through improved carbon partitioning to reproductive structures. Rootstocks also exert significant effects on yield components, with 110 Richter and 3309 Couderc increasing cluster numbers and berry size, while 420A and 161-49 Couderc enhance fruit uniformity by regulating sink strength and assimilate distribution. At the physiological level, rootstocks mediate nutrient partitioning and hormonal balance, as demonstrated by 110R and 5BB rootstocks, which enhance soluble sugar and starch accumulation in scions through optimized phloem transport and cytokinin signaling. These mechanisms collectively fine-tune resource allocation between vegetative growth and reproductive development, underscoring the pivotal role of rootstocks in balancing vine productivity with fruit quality. The profound influence of scion interactions on fruit quality parameters—including sugar-acid equilibrium, phenolic composition, and volatile aroma profiles—has emerged as a critical factor in premium grape production. Vigorous rootstocks such as 110 Richter and 140 Ruggeri demonstrate remarkable capacity to enhance sugar accumulation (particularly glucose and fructose) while simultaneously stimulating anthocyanin biosynthesis in red varieties, thereby improving both fermentation potential and wine color stability. However, certain rootstock genotypes that facilitate excessive potassium uptake can inadvertently elevate juice pH, potentially compromising the fresh acidity essential for balanced wines. Cutting-edge research reveals that rootstocks exert sophisticated control over secondary metabolite pathways, modulating the production of health-promoting compounds like resveratrol and flavanols, which significantly contribute to the antioxidant capacity and mouthfeel characteristics of wines. A striking example is observed in Shine Muscat grapes grafted onto Summer Black rootstock, where terpene biosynthesis is enhanced through upregulation of key genes (*VvLoXA* and *VvADH*), resulting in a 2.3-fold increase in linalool content that imparts distinctive floral notes to the berries. These findings underscore how strategic rootstock selection can serve as a powerful tool for precision viticulture, enabling targeted manipulation of biochemical pathways to achieve desired quality benchmarks while maintaining vine health and productivity. Stress resistance is a pivotal criterion for rootstock selection, particularly under climate change. Drought-tolerant rootstocks develop deeper root systems and improve water-use efficiency, sustaining physiological activity during water deficit. Salt-resistant genotypes like Salt Creek and 140 Ruggeri limit Na^+ and Cl^- translocation, preserving photosynthetic integrity. Cold-hardy rootstocks upregulate cryoprotectants (proline, and soluble sugars) and antioxidant enzymes (SOD and POD), mitigating frost damage. Additionally, rootstocks confer partial resistance to biotic threats; for instance, 41B and Gravesac reduce susceptibility to phylloxera and nematodes, while SO4 enhances scion resistance to powdery mildew and downy mildew via elevated POD and PPO activities. Molecular mechanisms underlying rootstock effects involve hormone signaling (ABA and jasmonates), nutrient transporters, and stress-responsive genes such as *VvWRKYs* and *VvCBFs*. Transcriptomic analyses reveal that rootstocks modulate phenylpropanoid biosynthesis and ion homeostasis pathways. For example, *VhWRKY44* in Beta rootstock enhances cold and salt tolerance by regulating antioxidant enzyme expression, while *VvMYBPA1* in 1103P improves drought resilience through ABA-mediated stomatal closure. This study analyzes major grape rootstock cultivars (1103P, SO4, 5BB and Beta) and their vital roles in growth regulation, fruit quality, and stress resistance. While current rootstocks show single-stress tolerance (cold, drought, or salinity), few possess comprehensive resilience to combined stresses. We propose developing multi-resistant varieties by integrating superior traits such as Beta's *VhWRKY44* for cold tolerance, 1103P's *VvMYBPA1* upregulation for drought adaptation, and 101-14's ion selectivity for salt resistance through hybridization, marker-assisted selection, or gene editing. Multi-omics approaches should elucidate resis-

tance mechanisms to guide precision breeding. Imported rootstocks such as Fercal and 1103P require regional adaptation trials for China's diverse conditions including arid northwest and coastal saline areas. Native species such as *V. amurensis* and *V. davidii* offer valuable stress-resistant genes for developing proprietary cultivars. Future research should adopt an "introduction-breeding-utilization" strategy to create resilient and high-quality rootstocks supporting sustainable viticulture in China.

Key words: Grape; Rootstock; Growth and development; Fruit quality; Stress resistance; Graft compatibility

葡萄(*Vitis vinifera* L.)是葡萄科(Vitaceae)葡萄属(*Vitis*)的多年生落叶植物,广泛分布于世界各地^[1]。作为世界上最具经济价值的果树之一,葡萄在农业经济中占有重要地位。根据国际葡萄与葡萄酒组织(OIV)最新数据,全球葡萄栽培面积稳定在730万hm²左右,年产量约7700万t,是广泛应用于鲜食果品、葡萄酒酿造、果脯加工等各个领域的主要水果之一。然而,葡萄对气候和土壤条件表现出高度敏感性,需要充足的阳光、适宜的温度和良好的排水条件,并且容易受到干旱、霜冻、盐碱和其他环境压力的影响,因此砧木嫁接技术在葡萄栽培中具有重要作用。选择合适的砧木可以提高品种的适应性和稳定性,让更多的自根苗保持嫁接品种的优良特性,改善生长和田间表现,提高果实品质^[2]。近年来,由于气候和土壤条件的不断恶化,砧木的研究和应用已成为葡萄栽培领域的一个重要课题,通过筛选和培育适应性强的砧木品种可有效提升葡萄植株对于干旱、高温、盐碱等环境胁迫的抵抗能力,为应对全球气候变化和土壤退化提供关键解决方案。笔者综述了不同砧木对葡萄生长发育、果实品质形成及抗逆性调控的最新研究进展,以为葡萄高效栽培提供理论参考。

1 国内外葡萄砧木育种历史

20世纪初,欧美因根瘤蚜危机开启砧木育种,随后在抗逆性(如耐旱、抗盐)方面取得突破,并将其应用到实际生产中,为全球葡萄种植业的发展做出了重大贡献。葡萄砧木种质资源有6种:沙地葡萄(*V. rupestris* S.)、河岸葡萄(*V. riparia* M.)、冬葡萄(*V. berlandieri* P.)、欧洲葡萄(*V. vinifera* L.)、香宾尼葡萄(*V. champinii* P.)和沙罗尼斯葡萄(*V. solonis* L.)^[3]。这些砧木都具有较强的抗性。例如,圆叶葡萄最抗根瘤蚜虫;沙地葡萄抗根瘤蚜虫、抗病、抗寒、抗旱;冬葡萄是欧洲非常重要和稳定的砧木,具有抗

旱、抗根瘤蚜虫、抗真菌特性,最抗石灰性土壤;山葡萄最耐寒;美洲葡萄耐寒且耐热;香宾尼葡萄非常耐旱等^[4]。

目前,欧洲对砧木的选择主要集中在对根瘤蚜虫和线虫的抗性方面,但在提高砧木抗旱、抗盐碱能力方面也取得了重大进展^[5]。德国和法国是世界上葡萄砧木育种研究的先驱,通过将河岸葡萄、冬葡萄和沙地葡萄作为亲本杂交,培育出了具有抗根瘤蚜、耐旱和耐石灰土壤的优良砧木品种。然而,目前在德国种植的砧木品种的抗性仍不理想,因为根瘤蚜虫也开始进化,使砧木抗性无效,德国品种Börner对根瘤蚜虫和线虫都有极强的免疫力^[6]。相比之下,美洲的科学家选取了河岸葡萄和沙地葡萄,直接用作抗性砧木^[7]。我国对葡萄砧木的研究起步较晚,许多地区选用葡萄自根繁育,葡萄栽培面临低温、干旱、盐害等难以解决的问题,严重影响了葡萄生产及相关产业的发展^[8]。20世纪60年代,科学家发现山葡萄在-40℃的低温可以维持生理活性,以河岸葡萄和美洲葡萄为亲本,杂交培育出的贝达砧木,具有良好的耐寒性,在我国北方地区,这两种砧木作为耐寒砧木被用于生产。除冻害外,干旱也是西北和华北地区葡萄栽培的主要威胁,而燕山-1和刺葡萄作为耐旱的中国野生葡萄被用于生产或育种,以抵御干旱对葡萄生长的影响^[9]。目前,我国葡萄砧木育种主要以提高嫁接葡萄的抗寒、抗旱、抗盐能力为目标,但由于我国葡萄主产区分布广泛,土壤条件和气候差异较大,砧木品种的选择受环境因素的影响较大,因此应考虑和培育适合栽培地区的砧木品种,以充分发挥其优势,促进我国葡萄产业的健康发展。

2 砧木对葡萄生长发育的影响

砧木作为葡萄栽培的基础,通过根系对嫁接葡萄的生长表现有重要影响。研究表明,不同砧木品种在调节葡萄生长势、光合特性及生理代谢等方面

存在显著差异,这些差异直接影响葡萄的栽培表现和生产效率。

在生长势方面,砧木主要影响葡萄的枝条发育和树体结构。研究表明,3309M和抗砧3号砧木可显著增强阳光玫瑰葡萄的生长势,与自根苗相比,其枝条粗度和长度都有明显改善^[10]。这种促进作用可能与砧木的激素合成能力有关,特别是生长素和细胞分裂素的生产和运输。值得注意的是,砧木对接穗生长势的影响因品种而异。而SO4砧木在克瑞森无核葡萄上表现出明显的生长抑制效应,与自根苗相比,新梢长度减少达54.60%,这可能是由于其调节了内源激素平衡或改变了水分利用效率^[11]。砧木选择可显著影响葡萄的生长势,最优砧木能使产量、修剪质量和Ravaz指数提升50%以上,主要通过促进水分吸收实现浆果增重,且该效应在不同年份和品种间表现稳定,证实了砧木是调控葡萄生长势的关键因素^[12]。

砧木对葡萄光合特性的影响同样不容忽视。SA15砧木能明显提高赤霞珠和脆光葡萄的净光合速率(分别提高11.75%和12.06%)和叶绿素含量^[13],这种提升可能是由于接穗对矿物质的吸收得到改善,以及光合酶的活性得到提高。此外,砧木的树龄也会影响光合速率,嫁接在多年生砧木上的阳光玫瑰葡萄叶片结构更发达,叶绿素含量更高^[14],为生产优质葡萄奠定了生理基础。SO4砧木显著提升红地球葡萄的穗质量、单果质量及可溶性固形物含量,而1103P砧木促进叶片P、K、Ca、Mg等矿质元素吸收,但不同砧木(41B、SO4、1103P)对光合速率和蒸腾速率的影响无显著差异^[15]。

在生理代谢层面,砧木通过调节养分分配影响葡萄生长。110R和5BB砧木能显著提高克瑞森无核葡萄枝条的可溶性糖和淀粉含量^[16],表明优质砧木能提高接穗积累养分的能力。在巴西地区的长相思葡萄栽培中,砧木选择显著影响生理代谢,其中106-8砧木可提高80%产量,而IAC 766砧木结合低篱架系统能显著提升酚类、黄酮类含量及抗氧化活性,说明砧木通过调控代谢途径直接影响葡萄的营养品质与产量^[17]。不同砧木通过调控赤霞珠葡萄果皮中赤霉素(GA₃)、生长素(IAA)和脱落酸(ABA)的动态平衡,影响花青素合成关键基因(*VvCHS*、*VvDFR*、*VvUFGT*)的表达,从而介导果实转色期的生理代谢进程,其中140R砧木组合显著促进果皮着

色^[18]。此外,砧木对葡萄生长的调控还涉及赤霉素(GA₃)和茉莉酸(JA)等植物激素的相互作用。例如,葡萄VvGAI1蛋白作为赤霉素信号途径的调控因子,与VvJAZ9蛋白互作,共同参与低温胁迫响应^[19]。

在地域适应性方面,选择砧木时应考虑环境因素。在新疆的北疆地区,1103P和5BB砧木表现出良好的适应性^[20],而5BB砧木在江汉平原的生长表现最好^[21](表1)。在得克萨斯高平原地区,嫁接在1103P砧木上的歌海娜葡萄从主芽萌发的枝条比从副芽萌发或使用其他砧木的植株表现出更好的枝条质量、产量和果实成熟度,说明1103P砧木可能有助于提高葡萄对晚霜冻害的适应能力^[22]。

3 砧木对葡萄果实品质的影响

砧木与接穗的互作关系深刻影响葡萄果实的品质形成。一般来说,葡萄果实品质可分为三类:外观品质、内在品质和贮运品质。外观品质包括果实大小、形状和颜色等;内在品质包括果实糖酸、矿物质、花色苷和维生素含量等;贮运品质包括果实贮藏条件、果肉硬度和货运寿命等。正确选择砧木可以大大改善葡萄果实的外观和内在品质,不同砧木嫁接也会影响葡萄果实的穗质量和粒质量。

砧木通过影响果实膨大与色素合成,显著改善葡萄外观品质。在阳光玫瑰葡萄中,夏黑砧木由于其砧穗之间的亲和性好,可以加快成熟,提高单粒和果穗质量,同时显著改善果实的玫瑰香味,其芳樟醇含量达到43.20%,显著高于3309和5BB砧木的芳樟醇含量^[23]。不同砧木显著影响阳光玫瑰葡萄的品质与香气特性,其中QN和3309砧木通过上调*VvLoXA*、*VvADH*等基因表达,显著提升果实总香气含量与单果质量,而SB砧木则通过激活MEP途径促进芳香物质合成,整体优化果实风味品质^[24]。类似地,抗砧3号砧木在郑州地区表现出增强树势、提高果实维生素C含量和固酸比的特点^[25],这表明砧木的选择不仅会影响果实的外观和口感,还会通过调节生理活性物质来提高营养价值。

果实色泽调控是砧木影响外观品质的另一重要方面。在赤霞珠酿酒葡萄品种中,砧木的影响更为明显。SO4和5BB砧木虽降低了可溶性固形物含量,但却显著提高了花色苷和单宁含量^[26],而花色苷和单宁对葡萄风味和抗氧化性能非常重要。在巴西

表1 砧木对葡萄生长发育的影响
Table 1 Effects of rootstocks on grape growth

砧木品种 Rootstock variety	影响方面 Implications	具体效应 Concrete effect	参考文献 Reference
3309M、抗砧3号 3309 Millardet, Kangzhen No.3	生长势 Growth momentum	显著提高阳光玫瑰葡萄枝条粗度和长度,与激素合成相关 Significantly increases the thickness and length of Shine Muscat grape branches, which is related to hormone synthesis	[10]
SO4	生长势 Growth momentum	对克瑞森无核葡萄表现生长抑制,新梢长度减少54.60% Inhibits the growth of Kresen seedless grape, reducing new shoot length by 54.60%	[11]
SA15	光合特性 Photosynthetic characteristics	提高赤霞珠和脆光葡萄净光合速率(11.75%~12.06%)及叶绿素含量 Increase the net photosynthetic rate(11.75%-12.06%)and chlorophyll content of Cabernet Sauvignon and Crisp Light grape	[13]
SO4	果实品质 Fruit quality	提升红地球葡萄穗质量、单果质量及可溶性固形物含量、酸度比 Improving the bunch mass, individual fruit mass, and soluble solids content, acidity ratio of Red Globe grape	[15]
1103P	矿质元素吸收 Mineral absorption	促进红地球葡萄叶片P、K、Ca、Mg吸收,但对光合速率无显著影响 Promotes the absorption of P, K, Ca, and Mg in Red Globe leaves, but has no significant effect on photosynthetic rate	[15]
110R、5BB	生理代谢 Physiological metabolism	提高克瑞森无核葡萄枝条可溶性糖和淀粉含量 Increase the soluble sugar and starch content of Kresen Seedless grape shoots	[16]
106-8	产量 Yield	使长相思葡萄产量提高80% Increase the yield of Changxiangsi grape by 80%	[17]
IAC 766	营养品质 Nutritional quality	结合低篱架系统提升酚类、黄酮类含量及抗氧化活性 Combining low trellis systems to increase phenolic and flavonoid content and antioxidant activity	[17]
140R	果着色 Fruit coloration	调控赤霞珠葡萄果皮激素(GA ₃ 、IAA、ABA)平衡,促进花青素合成基因表达 Regulate the balance of Cabernet Sauvignon fruit skin hormones(GA ₃ , IAA, ABA) to promote anthocyanin synthesis gene expression	[18]
1103P、5BB	地域适应性 Regional adaptability	在北疆地区表现良好 Performing well in the northern border region	[20]
5BB	地域适应性 Regional adaptability	在江汉平原生长表现最佳 Grows best in the Jiangnan Plain	[21]

半干旱条件下,早熟伊莎贝尔葡萄在 IAC 313 和 IAC 766 砧木上表现出更优的果实品质,其可溶性固形物、花色苷和糖含量在转色后 28 d 达到峰值,果穗质量则在 24 d 最大,表明该品种适合鲜食与酿酒用途^[27]。此外,贝达和 5BB 砧木显著提高了果实的抗氧化活性,与贝达砧木相比,5BB 砧木的总酚、花色苷和单宁总含量分别提高了 12.62%、2.61% 和 19.29%^[28]。以上结果表明,砧木通过调节次生代谢途径影响果实的化学成分,从而决定其酿酒潜力。

砧木对果实糖酸代谢的调控直接影响风味品质。110R、SO4 和抗砧 3 号砧木通过提高赤霞珠葡萄的 NAD-MDH 酶活性和基因表达水平,促进苹果酸积累,同时降低草酸和柠檬酸含量,从而优化果实糖酸平衡,提升酿酒品质^[29]。在河西走廊地区,110R 砧木显著提高了小芒森葡萄的固酸比,而 SO4 和 3309M 砧木对维欧尼葡萄也有类似的影响^[30]。这一现象可能与砧木对根系吸收能力和光合效率的调节有关。例如,赤霞珠/110R 组合的净光合速率和水

分利用效率明显高于自根苗^[31],这表明砧木可通过优化光合作用间接促进果实的糖分积累。然而,砧木的效果存在品种和地域差异。在南方湿热地区,5BB 砧木能够显著降低阳光玫瑰葡萄的气灼病发生率^[32],而在新疆地区,101-14 和 3309M 砧木则更适合赤霞珠葡萄的栽培^[33]。

此外,砧木对果实色泽和质地的影响也不容忽视。蜜光/3309M 组合的果实硬度和可溶性固形物含量显著高于其他砧穗组合^[34],而天工墨玉葡萄在 1103P 砧木上表现出更深的果皮颜色和更高的糖酸含量^[35](表 2)。这些差异可能与砧木对内源激素(如 IAA、GA₃ 和 ABA)的调控有关。不同砧木(如 140R)通过调控赤霞珠葡萄果皮中 IAA、GA₃ 和 ABA 的动态平衡,显著促进 *VvCHS*、*VvDFR* 和 *VvUFGT* 等花青素合成基因的表达,从而加速果实转色并提升色泽积累水平,同时影响果实质地发育^[18]。砧木通过降低转色后果实的 IAA 含量来抑制发育,同时提高 ABA 含量以促进成熟^[36]。而茉莉酸在葡萄果实的

表 2 砧木对葡萄果实品质的影响
Table 2 Effects of rootstocks on grape fruit quality

砧木品种 Rootstock variety	影响方面 Implications	具体效应 Concrete effect	参考文献 Reference
110R、SO4、抗砧3号 110 Richter, SO4, Kangzhen No.3	苹果酸含量 Malic acid content	提高赤霞珠NAD-MDH酶活性,促进苹果酸积累,降低草酸、柠檬酸,优化糖酸平衡 Increase Cabernet Sauvignon NAD-MDH enzyme activity, promote malic acid accumulation, reduce oxalic acid and citric acid, optimize sugar-acid balance	[29-30]
110R, SO4, 3309M	可溶性固形物含量 Soluble solids content	显著提高固酸比 Significantly increase the solid-acid ratio	[30]
1103P	糖酸平衡 Sugar-acid balance	更高的糖酸含量 Higher glycolic acid content	[35]
SO4, 5BB	花色苷、单宁含量 Flower glycosides, tannins content	增加花色苷和单宁含量,但降低可溶性固形物含量 Increases anthocyanins and tannins content, but decreases soluble solids content	[26, 28]
140R	果皮颜色 Fruit skin color	上调 <i>VvCHS</i> 、 <i>VvDFR</i> 等基因,促进花青素合成,加速转色 Up-regulation of genes such as <i>VvCHS</i> and <i>VvDFR</i> promotes anthocyanin synthesis and accelerates color transitions	[18]
IAC 313, IAC 766	花色苷峰值 Anthocyanin peak	转色后 28 d 达峰值 Peak 28 days after color change	[27]
夏黑砧木 Xiahei rootstock	芳樟醇含量 Linalool content	芳樟醇含量达 43.20%, 显著高于 3309、5BB, 增强玫瑰香味 Linalool amounted to 43.20%, which was significantly higher than 3309 and 5BB, and enhanced the rose flavor	[23]
QN, 3309	总香气含量 Total aroma content	上调 <i>VvLoXA</i> 、 <i>VvADH</i> 基因,提升单果质量与总香气 Up-regulation of <i>VvLoXA</i> and <i>VvADH</i> genes to enhance single fruit mass and total aroma	[24]
SB Salt Creek Rootstock	芳香物质合成 Aromatic substance synthesis	激活 MEP 途径,优化风味品质 Activating the MEP pathway to optimize flavor quality	[24]
3309M	果实硬度 Fruit hardness	显著高于其他砧穗组合 Significantly higher than other rootstock combinations	[34]
抗砧3号 Kangzhen No.3	维生素C含量 Vitamin C content	提高维生素C含量与固酸比 Increase vitamin C content and solid-acid ratio	[25]

着色和软化过程中发挥着重要作用,其作用机制通过提高与果实成熟、软化和芳香相关的多个基因的转录水平来实现^[37]。这种激素水平的动态变化进一步影响了果实的成熟进程和品质形成。

4 砧木对葡萄抗逆性的影响

我国西北地区(新疆、甘肃、宁夏、陕西等)具备种植优质葡萄的独特自然地理条件,但干旱、寒冷、病虫害等因素常影响葡萄种植面积、产量、品质及经济效益。通过嫁接抗性砧木,可显著提升葡萄的抗逆能力。

4.1 砧木对葡萄耐寒性的影响

砧木耐寒性研究在寒冷地区葡萄栽培中至关重要,不同砧木品种的耐寒性差异显著。砧木对葡萄耐寒性的影响不仅体现在生理生化层面及半致死温度(LT₅₀)的差异方面,分子调控机制的研究也取得了重要进展(表3)。

首先,砧木的耐寒性与其生理生化特性密切相

关。在低温胁迫下,砧木枝条的相对电导率及丙二醛(MDA)、游离脯氨酸、可溶性糖和可溶性蛋白质含量都会发生变化。常强等^[38]研究了12个葡萄砧木品种,发现耐寒砧木品种(如贝达、山河2号)在低温下的相对电导率较低,渗透调节物质含量较高,对细胞膜的损害较轻。马晓燕等^[39]利用高低温交替的试验箱模拟低温环境,发现耐寒性强的砧木(如SO4、196-17)在低温胁迫下的生理指标变化呈现出更稳定的趋势。研究还发现,Beta砧木中的Vh-WRKY44转录因子通过调控抗氧化酶(SOD、POD、CAT)活性及渗透调节物质(脯氨酸、MDA)含量,显著增强葡萄对盐和冷胁迫的抗性,为砧木抗寒机制研究提供了新靶点^[40]。这些研究表明,通过调节渗透物质含量和保护酶活性来提高砧木的耐寒性是适应低温环境的一个重要机制。

其次,半致死温度(LT₅₀)是评价砧木耐寒性的重要指标。多项研究通过Logistic方程计算LT₅₀,并结合隶属函数法或主成分分析法对耐寒性进行综合

表3 砧木对葡萄耐寒性的影响
Table 3 Effects of rootstocks on cold tolerance of grape

砧木品种 Rootstock variety	评价指标 Evaluation indicators	具体效应 Concrete effect	参考文献 Reference
贝达、山河2号 Beta, Shanhe No.2 Rootstock	相对电导率、渗透调节物质 Relative electrical conductivity, permeability regulating substance	低温下电导率低,脯氨酸、可溶性糖含量高,细胞膜损伤轻 Low conductivity at low temperature, high proline and soluble sugar content, minimal cell membrane damage	[38]
SO4, 196-17	低温胁迫稳定性 Low-temperature stress stability	生理指标(MDA、保护酶活性)变化更平稳 Physiological indicators (MDA, protective enzyme activity) show more stable changes	[39]
贝达 Beta	抗氧化酶与渗透调节 Antioxidant enzymes and osmotic regulation	调控SOD、POD、CAT活性及脯氨酸、MDA含量,增强冷胁迫抗性 Regulate SOD, POD, CAT activity, and proline and MDA content to enhance cold stress resistance	[40]
CFS57-34	LT ₅₀ =-25.86 °C	耐寒性最强 Most cold-tolerant	[41]
P40-151	LT ₅₀ =-21.85 °C	耐寒性较弱 Weak cold tolerance	[41]
3309C, 101-14	LT ₅₀ 与耐寒性呈正相关 LT ₅₀ is positively correlated with cold tolerance	耐寒性显著优于其他砧木 Significantly more cold-tolerant than other rootstocks	[42]

评价。郭艳兰等^[41]对6个砧木品种的研究显示,CFS57-34砧木的LT₅₀为-25.86 °C,表现出最强的耐寒性;而P40-151砧木的LT₅₀为-21.85 °C,耐寒性较弱。刘钰玺等^[42]在对13种砧木的研究中,发现LT₅₀和耐寒性呈明显相关性,3309-C、101-14和其他砧木都是非常耐寒的类型。这些研究结果为寒冷地区抗寒葡萄砧木选择提供了科学依据。

此外,砧木还调控葡萄耐寒性的分子机制,涉及基因表达与信号转导等关键途径。研究发现,耐寒山葡萄砧木中的VaCOLD1蛋白通过与VaGPA1互作激活CBF-COR通路,显著增强植物的低温耐受性,为砧木选育和抗寒分子育种提供了新方向^[43]。贝达砧木中的VhMYB60转录因子通过调控逆境响应基因表达及抗氧化系统活性,显著增强植物的耐寒性与耐盐性,为砧木抗逆性改良提供了关键基因资源^[44]。同时,外源MeJA通过激活苯丙氨酸合成途径关键基因VvPAL10及激素信号转导通路,显著增强葡萄抗氧化能力和低温胁迫耐受性,为砧木抗寒性研究提供了新的激素调控策略^[45]。笔者课题组对VaCOI1初步进行了生物信息学分析和低温诱导表达分析,以验证VaJAZ9与VaCOI1蛋白之间的相互作用,并对过表达VaJAZ9和VaCOI1的拟南芥植物进行了抗寒功能验证和qRT-PCR分析,旨在为提高葡萄的耐寒性及培育耐寒品种提供理论依据^[46]。

4.2 砧木对葡萄耐旱性的影响

砧木对葡萄耐旱性的影响是葡萄栽培研究的一个重要课题,尤其是在干旱或半干旱地区,砧木的选

择直接关系到葡萄的生长发育和产量及品质。实践证明,嫁接到耐旱砧木上能显著提高葡萄对干旱的适应能力。焦淑珍^[47]研究表明,嫁接到1103P砧木上的阳光玫瑰葡萄在干旱条件下表现出较高的叶片相对含水量、光合效率、抗氧化酶活性和较低的氧化损伤标记物积累水平。此外,转录组分析表明,VvMYBPA1基因在干旱响应调控中起重要作用,其过表达能显著增强转基因植株的抗旱能力。Ren等^[48]研究表明,贝达砧木上的转录因子VhMYB2通过调节脯氨酸、叶绿素和MDA含量,提高POD、SOD和CAT等酶活性,显著增强了葡萄对盐和干旱胁迫的耐受性。Koc等^[49]研究表明,洛特河岸砧木通过显著促进脯氨酸的积累和调节水通道蛋白基因(VvPIPs/VvTIPs)的表达,有效缓解了叶片相对含水量的减少,与霍罗兹卡拉瑟葡萄相比,对干旱的耐受性更强。这些结果不仅证实了砧木通过生理和分子生物学机制提高葡萄的耐旱性,还为砧木选择提供了理论依据。

砧木耐旱性的差异与其生理特性密切相关。马龙等^[50]比较了嫁接在110R砧木上的黑比诺和自根苗,发现嫁接苗在干旱条件下表现出更高的新梢生长量、叶片水势和光合参数,且主成分分析证实,110R砧木显著提高了接穗的整体耐旱性。由佳辉等^[51]对17个砧木品种的解剖叶片结构分析也表明,栅海比和细胞结构密度等指标与耐旱性密切相关,其中1103P、5BB和河岸9号砧木表现出极强的耐旱性。这些研究表明,砧木的耐旱性可能与叶片结构

的储水能力及其对胁迫的反应效率有关。Li等^[52]还发现,在干旱条件下,耐旱砧木1103P通过提高ABA含量、增加角质层蜡质沉积和减小气孔开度来减少水分损失,同时通过增加H₂O₂清除酶活性以减轻氧化损伤,从而保持较高的光合效率和叶片含水量,明显优于敏感砧木101-14。山葡萄VaCIPK18与VaPYL9的互作关系也揭示了砧木在ABA信号通路中的潜在功能^[53]。

砧木品种的耐旱性评价结果存在一些差异,这可能与试验条件、评价指标和地理适应性有关。王婉妮等^[54]比较了110R、1103P和5BB砧木,发现110R砧木在干旱条件下表现出更高的抗氧化酶活性和脯氨酸积累水平,耐旱性排序为110R>1103P>5BB;而孙茜等^[55]的研究则得出1103P>

5BB>3309C>SO4的结论。这种差异反映了砧木耐旱性的复杂性,需要结合多个指标(光合特性、渗透调节、对氧化应激的反应等)进行综合评价。在西班牙半干旱地区,低活力砧木(41B、161-49C)通过提高水分利用效率和降低整株导水率提高了丹魄品种耐旱性,导致产量降低,但果实糖酸比和多酚含量较高;而高活力砧木(1103P、110R)由于增强了水分运输和养分吸收能力,从而保持了较高的产量,表明砧木选择需权衡抗旱适应性与产量及品质的需求^[56](表4)。

4.3 砧木对葡萄耐盐性的影响

砧木对葡萄耐盐性的影响是葡萄栽培中应对盐碱地的一个重要研究领域。通过生理和生化调节、维持离子平衡和保护光合作用等机制,将葡萄嫁接

表4 砧木对葡萄耐旱性的影响

Table 4 Effects of rootstocks on drought tolerance of grape

砧木品种 Rootstock variety	评价指标 Evaluation indicators	具体效应 Concrete effect	参考文献 Reference
砧木1103P 1103 Paulsen	叶片含水量、光合效率、抗氧化酶 Leaf water content, photosynthetic efficiency, antioxidant enzymes	干旱下维持较高叶片相对含水量、光合速率及SOD、POD、CAT活性,降低氧化损伤程度; <i>VvMYBPA1</i> 基因调控抗旱响应 Maintaining high relative leaf water content, photosynthetic rate, and SOD, POD, and CAT activity under drought conditions, reduces oxidative damage; the <i>VvMYBPA1</i> gene regulates drought resistance responses	[47]
贝达 Beta	脯氨酸、叶绿素、MDA含量 Proline, chlorophyll, and MDA content	上调 <i>VhMYB2</i> , 促进脯氨酸积累及增强抗氧化酶活性, 提高耐旱性 Upregulation of <i>VhMYB2</i> enhances proline accumulation and antioxidant enzyme activity, improving drought tolerance	[48]
110R	新梢生长量、叶片水势、光合参数 New shoot growth, leaf water potential, photosynthetic parameters	嫁接黑比诺后显著提高干旱条件下的生长量和水势, 主成分分析证实整体耐旱性提升 Grafting Pinot Noir significantly improves growth and water potential under drought conditions, and principal component analysis confirms overall drought tolerance improvement	[50]
1103P、5BB、河岸9号 1103 Paulsen, 5BB, Riparia No.9 Rootstock	叶片解剖结构 Leaf anatomical structure	耐旱性与储水结构呈正相关 Drought tolerance is positively correlated with water storage structure	[51]
1103P、101-14	ABA含量、角质层蜡质、气孔调节 ABA content, stratum corneum wax content, and stomatal regulation	1103P通过增加ABA和蜡质沉积减少水分流失, 提高H ₂ O ₂ 清除能力, 优于101-14M 1103P reduces water loss by increasing ABA and wax deposition, improves H ₂ O ₂ clearance capacity, and outperforms 101-14M	[52]
110R、1103P、5BB	抗氧化酶活性、脯氨酸积累 Antioxidant enzyme activity, proline accumulation	耐旱性排序: 110R>1103P>5BB Drought tolerance ranking: 110R>1103P>5BB	[54]
1103P、5BB、3309C、SO4	综合耐旱性评价 Comprehensive drought resistance evaluation	耐旱性排序: 1103P>5BB>3309C>SO4 Drought tolerance ranking: 1103P>5BB>3309C>SO4	[55]
41B、161-49C	水分利用效率、导水率 Water use efficiency, hydraulic conductivity	降低导水率, 提高糖酸比和多酚含量, 但减产 Lower water conductivity, increase sugar-acid ratio and polyphenol content, but reduce yield	[56]
1103P、110R	水分运输、养分吸收 Water transport, nutrient absorption	维持较高产量, 因改善了水分和养分运输 Maintain high yield by improving water and nutrient transport	[56]
洛特河岸 Rupestris du Lot	脯氨酸积累、水通道蛋白基因 Proline accumulation, aquaporin gene	上调 <i>VvPIPs</i> 、 <i>VvTIPs</i> 表达, 缓解叶片含水量下降, 耐旱性优于‘Horozkarasi’ Upregulating <i>VvPIPs</i> and <i>VvTIPs</i> expression, alleviates leaf water content decline and improves drought tolerance compared to ‘Horozkarasi’	[49]

到耐盐砧木上可显著增强葡萄对盐胁迫的适应性。

多项研究表明,不同砧木品种的耐盐性差异较大。邢志淦等^[57]发现,嫁接到SO4砧木上的阳光玫瑰葡萄对盐和低温的复合胁迫具有很强的耐受性,丙二醛(MDA)含量显著降低,渗透调节物质(如可溶性蛋白、可溶性糖和脯氨酸)含量和抗氧化酶(CAT和POD)活性明显升高。这表明,SO4砧木可通过增强渗透调节能力和激活抗氧化防御系统,有效减轻盐胁迫引起的植物损伤。郑聪丽^[58]研究表明,与其他砧木组合相比,阳光玫瑰葡萄与夏黑砧木表现出更高的耐盐性,生长指数和激活光合参数降低较少,果实品质更好。这表明,砧木的选择不仅会影响植株的耐盐性,还会对接穗果实的品质产生积极影响。

耐盐砧木的生理机制包括离子选择性吸收和抗氧化系统激活。刘迎^[59]比较了101-14和SO4砧木在NaCl胁迫下的表现,发现耐盐101-14砧木植株能够通过根系截留Na⁺,从而抑制Na⁺向地上部分的转移,同时保持较高的K⁺/Na⁺、Ca²⁺/Na⁺和Mg²⁺/Na⁺比例,维持细胞内的离子平衡。此外,101-14砧木的抗氧化酶(如SOD、POD、CAT)活性和抗坏血酸-谷胱甘肽循环的效率明显高于SO4砧木,从而有效地清除活性氧(ROS),减轻氧化损伤。王瑞等^[60]的研究也证实了这一点,他们发现耐盐110R和101-14砧木

在盐胁迫条件下能通过根系选择性地吸收K⁺、Ca²⁺和Mg²⁺,并限制Na⁺和Cl⁻的积累,从而维持正常的新陈代谢。Yuan等^[61]研究表明,101-14砧木通过抑制Na⁺和Cl⁻的向上运输,促进对K⁺的吸收,提高叶片抗氧化酶SOD和POD活性,从而显著提高了玫瑰香葡萄的耐盐性,而188-08和5C砧木则增大了盐害的影响。

然而,砧木的耐盐性评价需结合多指标综合分析。史晓敏^[3]通过对13种葡萄砧木的研究,提出相对电导率、F_v/F_m、G_s和PIabs可作为评价耐盐性的重要指标。耐盐砧木(如110R和101-14)能够在盐胁迫下保持较高的光合效率和膜稳定性,而盐敏感砧木(如188-08和3309C)则会加速叶绿素降解并抑制光合作用。此外,陈丽靓^[62]利用聚类分析将砧木分为强耐盐性、中度耐盐性和弱耐盐性3类,发现和田红和木纳格砧木表现出较强的耐盐性,膜渗透性和有机渗透物质的变化与耐盐性密切相关。Lo'ay等^[63]研究表明,1103P砧木通过维持火焰无核葡萄在盐渍土壤中较高的叶绿素含量、光合效率(F_v/F_m)及抗氧化酶活性,显著增强其果实发育期的耐盐性,成为干旱-半干旱地区新建葡萄园的理想砧木选择(表5)。

4.4 砧木对葡萄耐热性的影响

砧木对葡萄耐热性的影响是葡萄栽培研究中的一个重要课题,尤其是在经常出现高温的地区,选择

表5 砧木对葡萄耐盐性的影响

Table 5 Effects of rootstocks on salt tolerance of grape

砧木品种 Rootstock variety	评价指标 Evaluation indicators	具体效应 Concrete effect	参考文献 Reference
SO4	渗透调节、抗氧化防御 Permeability regulation, antioxidant defense	降低MDA含量,提高可溶性蛋白、糖、脯氨酸含量及CAT、POD活性,缓解盐-低温复合胁迫 Reduce MDA content, increase soluble protein, sugar, proline content and CAT, and POD activity, and alleviate salt-low temperature composite stress	[57]
IAC 313, IAC 572	生长指数、光合参数 Growth index, photosynthetic parameters	盐胁迫下生长和光合效率下降较少,果实品质更优 Under salt stress, growth and photosynthesis decline less, and fruit quality is better	[58]
101-14	离子选择性吸收、ROS清除 Ion selective absorption, ROS scavenging	根系截留Na ⁺ ,维持K ⁺ 、Na ⁺ 、Ca ²⁺ 、Mg ²⁺ 平衡,增强SOD、POD、CAT活性及提高抗坏血酸-谷胱甘肽循环效率 The root system retains Na ⁺ , maintains the balance of K ⁺ , Na ⁺ , Ca ²⁺ , and Mg ²⁺ , enhances the activity of SOD, POD, and CAT, and improves the efficiency of the ascorbic acid-glutathione cycle	[59]
110R, 101-14	离子选择性运输活性 Ion-selective transport activity	选择性吸收K ⁺ 、Ca ²⁺ 、Mg ²⁺ ,限制Na ⁺ 、Cl ⁻ 积累 Selectively absorbs K ⁺ , Ca ²⁺ , and Mg ²⁺ , while limiting the accumulation of Na ⁺ and Cl ⁻	[60]
1103P	光合保护、抗氧化酶 Photosynthetic protection, antioxidant enzymes	维持叶绿素含量、F _v /F _m 及抗氧化活性 Maintaining chlorophyll content, F _v /F _m , and antioxidant activity	[63]
110R, 101-14	光合效率、膜稳定性 Photosynthetic efficiency, membrane stability	盐胁迫下保持高F _v /F _m 和G _s Maintaining high F _v /F _m and G _s under salt stress	[3]

表 5 (续) Table 5 (Continued)

砧木品种 Rootstock variety	评价指标 Evaluation indicators	具体效应 Concrete effect	参考文献 Reference
188-08, 3309C	叶绿素降解、光合抑制 Chlorophyll degradation, photosynthetic inhibition	加速叶绿素降解,抑制光合作用 Accelerates chlorophyll degradation and inhibits photosynthesis	[3]
和田红、木纳格 Hetian Red, Munage	膜渗透性、有机渗透物质 Membrane permeability, organic permeable substances	强耐盐性,膜稳定性与渗透调节物质变化显著相关 Strong salt tolerance, membrane stability, and osmotic regulation substances are significantly correlated	[62]
188-08, 5C	盐害加重 Salt damage intensifies	加重玫瑰香盐胁迫损伤 Enhancing rosefragrance salt stress damage	[61]

合适的砧木对葡萄的生长和产量至关重要。研究表明,砧木通过调节葡萄的生理和生化特性,对葡萄的耐热性有较大影响。户金鸽等^[64]评价了15个葡萄砧木品种的耐热性,发现不同砧木在高温下的表现差异显著。在40℃高温下,110R和Fercal砧木叶片卷曲,山河2号砧木叶片轻微卷曲,而其他砧木的叶片正常,这表明山河2号砧木的耐热性较强,140R砧木的耐热性较弱。研究结果不仅显示了砧木耐热性的多样性,也为筛选耐热砧木提供了科学依据。

进一步的研究表明,砧木的耐热性与叶绿素荧光参数密切相关。砧木叶片的净光合速率和叶绿素荧光参数(如 F_0 、 F_m 、 F_v/F_0 、 F_v/F_m)在高温胁迫下发生了显著变化。110R、188-08、140R和Valliant砧木的净光合速率呈单峰曲线,而其他砧木则呈双峰曲线,并在午后出现典型的“午休”现象。此外, F_0 值随温度升高而增加,但在40℃以上趋于稳定; F_m 、 F_v/F_0 和 F_v/F_m 的日变化呈“U”形曲线^[65]。这些参数的变化反

映了砧木对高温的生理反应机制。模糊隶属函数分析表明,BR No.2和5C砧木表现出较高的综合耐热性,再次证实了高温条件下砧木适应性的差异。

砧木对葡萄耐热性的影响还体现在对水分和细胞膜稳定性的调节方面。砧木叶片的相对含水量和相对电导率在高温下都有所下降,这表明高温可能会导致细胞膜通透性增加和水分流失。耐热砧木通过保持较高的叶片含水量和减少电解质流失,减轻高温对细胞造成的损害。山河2号砧木在高温条件下叶片卷曲现象减少^[64],表明其对水分调节和细胞膜稳定性有较强的调节作用。

研究表明,HTH砧木通过提升赤霞珠葡萄叶片光系统II与光系统I的电子传递效率、稳定类囊体结构及优化能量分配,显著增强其在高光高温胁迫下的光化学活性及提高质体蓝素氧化还原速率,从而有效缓解光合损伤,凸显其作为耐热砧木的优异性能^[66](表6)。

表 6 砧木对葡萄耐热性的影响
Table 6 Effects of rootstocks on heat tolerance of grape

砧木品种 Rootstock variety	评价指标 Evaluation indicators	具体效应 Concrete effect	参考文献 Reference
山河2号 Shanhe No.2 Rootstock	叶片形态变化 Changes in leaf blade morphology	40℃高温下叶片轻微卷曲,耐热性强 Slightly curled blades at 40℃, heat resistant	[64]
110R, Fercal	叶片形态变化 Changes in leaf blade morphology	40℃高温下叶片卷曲,耐热性中等 Leaf curl at 40℃, medium heat resistance	[64]
140R	叶片形态变化 Changes in leaf blade morphology	40℃高温下耐热性较弱 Weak heat resistance at high temperatures of 40℃	[64]
BR No.2, 5C	叶绿素荧光参数 Chlorophyll fluorescence parameters	模糊隶属函数分析显示综合耐热性高 Fuzzy affiliation function analysis shows high integrated heat resistance	[65]
110R, 188-08, 140R, Valliant	光合日变化模式 Patterns of daily changes in photosynthesis	净光合速率呈单峰曲线,无“午休”现象 Net photosynthesis rate has a unimodal curve with no“nap” phenomenon	[65]
HTH	光系统稳定性(PSII/PSI) Optical system stability (PSII/PSI)	提高电子传递效率,稳定类囊体结构,增强光化学活性 Improvement of electron transfer efficiency, stabilization of vesicle structure and enhancement of photochemical activity	[66]
山河2号 Shanhe No.2 Rootstock	水分调节、细胞膜稳定性 Water regulation, cell membrane stability	高温下保持较高叶片含水量,减少电解质流失 Maintains high leaf water content under high temperature to minimize electrolyte loss	[66]

4.5 砧木对葡萄抗病性的影响

作为葡萄栽培的基础,砧木对嫁接品种的健康和产量有直接影响。研究表明,砧木通过各种方式影响葡萄对最主要真菌病害(如白粉病、霜霉病和黑痘病)的抗性,这主要体现在遗传性状、生理调节以及砧木与接穗之间的相互作用方面。

在遗传性状方面,李妍琪^[67]的研究揭示了砧木抗病性的复杂遗传机制。研究结果表明,砧木对白粉病和霜霉病的抗性表现为数量性状遗传,而对黑痘病的抗性则表现为显性遗传。值得注意的是,可以通过杂交选育出抗多种病害的砧木品种,如101-14、110R和3309等砧木对3种主要病害都有抗性。这种选择多种抗病砧木品种的方法为葡萄病害防控提供了新的遗传资源。Nguyen^[68]研究发现,圆叶葡萄与101-14杂交培育的新砧木(如07107系列)及抗线虫砧木GRN-1,在控制扇叶病症状(如坐果率下降)方面与O39-16砧木相当,同时兼具抗根瘤蚜和

线虫特性,为扇叶病毒防控提供了兼具抗病性与农艺适应性的砧木替代方案。

在生理调节方面,砧木通过影响接穗的抗氧化酶系统来提高抗病性。薛晓斌等^[69]研究表明,嫁接SO4砧木的组合具有更高的POD和PPO活性,这与更高的黑痘病和霜霉病抗性密切相关。相比之下,贝达砧木组合显示出更高的PAL活性,这表明不同的砧木可能通过不同的生理途径增强抗病性。Vondras等^[70]的研究证实,在赤霞珠葡萄果实中,脱落酸(ABA)信号、苯丙烷代谢和细胞骨架重塑相关基因的表达受不同砧木的调控,从而显著影响它们对葡萄卷叶病毒感染的反应,这表明ABA信号在砧木介导的抗病性中发挥着核心作用。这些发现为理解砧木抗病机制提供了重要的生理学依据(表7)。

砧穗之间的相互作用对抗病性的影响不容忽视。廖凯强等^[71]发现,浙江白刺葡萄与贝达的组合不仅表现出良好的亲和性,还能显著降低霜霉病和

表7 砧木对葡萄抗病性的影响

Table 7 Effects of rootstocks on disease resistance in grape

病害类型 Disease type	砧木品种 Rootstock variety	抗性表现 Resistance performance	参考文献 Reference
白粉病 Powdery mildew	101-14, 110R, 3309	数量性状遗传抗性,多抗性品种 Quantitative traits genetic resistance, multi-resistant varieties	[67]
霜霉病 Downy mildew	101-14, 110R, 3309, SO4	SO4砧木通过提高POD、PPO酶活性增强抗性;其他砧木为数量性状遗传抗性 SO4 rootstocks enhance resistance by increasing POD and PPO enzyme activities; other rootstocks are quantitative traits for genetic resistance	[69]
黑痘病 Black pox	101-14, 110R, 3309	显性遗传抗性 Dominant genetic resistance	[67]
扇叶病毒 Fanleaf virus	07107系列、GRN-1、O39-16 07107 Series Rootstocks, GRN-1, O39-16 Rootstock	控制扇叶病症状(如坐果率下降),兼具抗根瘤蚜和线虫特性 Control of fanleaf symptoms(e.g., reduced fruit setting rate), combined with resistance to phylloxera and nematodes	[68]
卷叶病毒 Leafroll viruses	101-14	通过调控ABA信号、苯丙烷代谢和细胞骨架基因表达,减轻病毒影响 Mitigating viral effects by regulating ABA signaling, phenylpropane metabolism, and cytoskeletal gene expression	[70]

黑痘病的发病率。这表明良好的砧木组合可以通过促进养分运输和信号传递来增强抗病性。陈湘云等^[72]对嫁接高度的研究表明,嫁接不仅促进了花芽分化,还促进了抗病性,这可能是由于激素平衡和养分分配模式发生了变化。Zhao等^[73]研究表明,特定砧木通过维持正常的嫁接体营养生长和光合作用功能,明显减轻了由葡萄卷叶相关病毒和A病毒侵染造成的不亲和性影响,为选择抗病毒砧木和建立葡萄园提供了重要依据。

5 砧木与葡萄嫁接亲和性

葡萄嫁接技术是提升品种稳定性、产量及品质

的核心手段,其中砧穗亲和性是嫁接成功的决定性因素。近年来研究表明,不同砧穗组合在亲和性、生长势、生理特性及抗病性等方面存在显著差异,这些差异是砧木筛选与嫁接实践的重要依据。

砧木与接穗的嫁接亲和性通常从嫁接成活率、生长势、生理生化指标及解剖结构等方面进行评价。SO4砧木与瑞都红玉葡萄表现出极高的亲和性,不仅嫁接成活率高,而且在苗圃和果园中的生长势也较强,从而获得了一定的产量^[74]。类似地,砧木山河1号和接穗苏欣1号的组合在绿枝和硬枝嫁接中也表现出较高的成活率,生理指标(过氧化物酶活性、可溶性蛋白含量等)也表现出显著的相关性^[75]。

Degirmenci 等^[76]将不同的美洲砧木(如 41B、5BB、SO4)嫁接到欧亚种鲜食葡萄品种(如 Razaki、Italia 等)上后发现,砧木类型对整个嫁接苗的成活率有显著影响,且表现出明显的品种与砧木互作效应。此外,在多项研究中,特别是在新疆地区,贝达砧木与威代尔和赤霞珠等酿酒葡萄品种表现出良好的亲和性^[77]。以上研究结果表明,砧木应结合接穗品种特点和地理环境选择。

嫁接亲和性与砧穗愈合过程中的生理生化变化密切相关。研究显示,绿枝嫁接后,砧穗愈合部的过氧化物酶活性、可溶性蛋白和可溶性糖含量与嫁接成活率呈显著正相关,而超氧化物歧化酶活性与嫁接成活率呈负相关^[78]。Gobetti 等^[79]研究发现,IAC 572 雅勒斯砧木与 BRS 卡门葡萄组合通过维持较高的超氧化物歧化酶(SOD)活性及较低的过氧化物酶(POX)活性和过氧化氢(H₂O₂)含量,表现出最优的嫁接成活率与初期生长表现,而 1103P 砧木与早熟伊莎贝尔葡萄的亲和性较差,凸显砧穗组合对氧化应激调控的关键作用。

关于砧木与接穗互作分子机制的研究取得了重要进展,揭示了嫁接技术、不同土壤和砧木类型对接穗转录组的显著影响,为该互作机制提供了新的分子层面的解释^[80]。研究发现,葡萄砧木与接穗互作通过调控二苯乙烯合成影响木质部病原菌抗性,同时,接穗基因型也能显著改变砧木相关真菌群落结构。值得注意的是,外源 dsRNA 虽能抑制病原菌生长,但会扰动木材微生物组,表明其应用可能存在复杂性^[81]。此外,砧木基因型通过调控浆果成熟期苯丙烷类代谢相关基因(如 MYB14)的表达,显著影响黑比诺葡萄果皮次生代谢物(特别是白藜芦醇衍生物)的积累,其中 1103P 砧木的作用尤为突出^[82]。进一步研究发现,不同砧木(如 101-14 和 1103P)通过特异性调控接穗苯丙烷代谢途径关键基因和 miRNA 的表达,显著影响水分胁迫下葡萄浆果酚类物质(特别是花青素)的积累,但对初级代谢无显著作用^[83]。以上研究结果为理解砧木与接穗互作的分子机制提供了新的视角。

6 展 望

笔者通过对现有主栽葡萄砧木的特性分析及适宜品种的归纳,揭示了砧木在葡萄生长、果实品质及抗逆性调控中的关键作用。目前,1103P、SO4、5BB

和贝达等主栽砧木对低温、干旱和盐碱具有单一的耐受性,兼具综合抗性(如耐旱、耐高温、耐盐碱及抗病等)的品种仍较为匮乏。首先,主要目标是培育具有综合抗性的品种。通过杂交育种、分子标记辅助选育或基因编辑技术,将抗寒(如贝达的 *VhWRKY44* 基因)、抗旱(如 1103P 的 *VvMYBPA1* 基因上调)和耐盐(如 101-14 的离子选择性吸收)等优良性状结合起来,克服单一抗性的局限,培育出适应复合胁迫的新品种。同时,应利用多组学技术(如转录组、代谢组)分析砧木抗性的机制,并建立抗性评估系统,作为精准育种的基础。其次,引进和本土化改良需要协同推进。国外优质砧木(如法国的 Fercal、美国的 1103P)具有很好的抗根瘤蚜、抗线虫和适应性,但结合我国产区的生态条件(如西北干旱地区、沿海盐碱地区等),应开展区域试验,选择适宜的品种。此外,为避免过度依赖引进品种,应重视利用当地野生物种(如山葡萄和刺葡萄)的抗性基因,并通过杂交育种和分子育种开发具有自主知识产权的新品种。总之,未来砧木研究应以综合抗性为核心,兼顾遗传改良与实际应用,采取“引进-培育-利用”的策略,培育具有抗逆性和高质量的新品种,为中国葡萄产业的可持续发展提供科技支撑。

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