



Abiotic Stress Effects on Phenolic Metabolism in *Vitis vinifera*: Implications for Grape Quality

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Abstract

Abiotic stresses represent major constraints in grapevine cultivation and directly influence fruit composition and product quality. Phenolic metabolism in *Vitis vinifera* plays a central role in stress adaptation. It affects both the plant's performance and is closely related to the fundamental quality characteristics of grapes. This review synthesizes current studies on how abiotic stress factors, which are intensifying under climate change, influence the composition and accumulation of phenolic compounds in grapes. Emphasis is placed on phenolic groups, particularly anthocyanins, stilbenes, flavonols, and tannins, which are related to grape and wine quality. Data obtained under controlled conditions or in the field show that the duration and intensity of stress are very important determinants of the effect on phenolics. While phenolic compound content increases in moderately intense stresses, the phenolic balance of the plant can be disrupted in severe and prolonged stresses, and quality characteristics can be negatively affected to a great extent. Our study also examines the extent to which stress-induced changes in phenolic metabolism interact with viticultural experiments such as shading, irrigation programs, and light manipulation. This synthesis links stress responses with quality parameters and proposes adaptive viticultural strategies for climate-resilient production.

Keywords *Vitis vinifera* · Phenolic plasticity · Abiotic stress · Grape quality · Drought · Heat

Introduction

Vitis vinifera, one of the most widely cultivated fruit species worldwide, is under pressure due to climate change, rising temperatures, droughts, ultraviolet (UV) radiation, and increasingly frequent extreme weather events. These pressures threaten the long-term sustainability of viticulture (Costa et al. 2020; Gutiérrez-Gamboa and Verdugo-Vásquez, 2024a). These stressors not only impair growth and yield but also disrupt physiological balance and metabolic regulation. More importantly, they reconfigure defense responses and secondary metabolism, processes that are critical for grape and wine quality (Šuklje et al. 2014; Teixeira et al. 2025a).

Phenolic compounds, including flavonoids (flavonols, flavanols, and anthocyanins), stilbenes, and phenolic acids, constitute a group of secondary metabolites that contribute to the grapevine's response to abiotic stress (Lecourieux et al. 2020; Rodríguez-Lorenzo et al. 2023). Functionally, phenolics act as antioxidants and photoprotective compounds, participate in cellular signaling, and contribute to cell wall architecture. This links stress tolerance to the sensory properties of grapes and wine. Their biosynthesis is largely regulated by the phenylpropanoid pathway. Reactive oxygen species (ROS) serve as key redox signals regulated by environmental cues through interconnected signaling networks involving phytohormones—particularly abscisic acid (ABA)—and stress-sensitive transcriptional components such as the MYB, bHLH, and NAC families (Sun et al. 2024; Konecny et al. 2025).

Recent studies have highlighted phenolic plasticity, defined as the capacity of grapevines to dynamically adjust the synthesis, accumulation, and distribution of phenolic compounds in response to changing climatic and environmental conditions. This adaptive behavior is closely associated with grapevine resilience. It reflects phenylpropanoid

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reprogramming that contributes to cellular homeostasis under stress (Baltazar et al. 2025). Stresses caused by drought, heat, and UV radiation frequently promote the accumulation of flavonols and stilbenes. This, in turn, strengthens photoprotection and ROS clearance, and also regulates the distribution of phenolic compounds between the berries and other tissues (Joubert et al. 2016; Rodríguez-Lorenzo et al. 2023). These responses arise from coordinated transcriptional and metabolic regulation, highlighting the importance of comprehensive multi-omics approaches for elucidating stress-induced phenolic responses (Konecny et al. 2025).

Recent studies more clearly demonstrate that phenolic responses to stress in grapevines are tissue- and developmental stage-specific, with results varying according to genotype, stress intensity, and exposure duration (Gutiérrez-Gamboa and Mucalo 2025). Berry skins (exocarp) typically exhibit greater phenolic plasticity than pulp or seeds due to localized activation of key biosynthetic genes such as phenylalanine ammonia-lyase (PAL), chalcone synthase (CHS), and stilbene synthase (STS) under stress conditions (Kahn 2023). Furthermore, combined stresses (e.g. heat or UV radiation interacting with drought) frequently produce phenolic profiles that differ from those observed under single stress exposure, indicating coordinated interactions among stress-related signaling pathways (Ali et al. 2023). These responses reflect phenylpropanoid reprogramming that contributes to cellular homeostasis under stress, thereby indicating coordinated cross-talk among stress signaling networks that regulate metabolic adaptation. Consequently, phenolic metabolism should be viewed not merely as a passive antioxidant system but as an active regulatory hub linking environmental perception with metabolic adjustment. To provide a systems-level overview, Fig. 1 summarizes how abiotic stress perception and signaling networks drive phenylpropanoid reprogramming and phenolic plasticity, ultimately modulating grape and wine quality.

Despite extensive research on individual abiotic stresses, integrative syntheses linking stress perception, metabolic reprogramming, and phenolic outcomes under climate change remain comparatively limited. Therefore, this review aims to integrate current knowledge on the regulation of phenolic metabolism in *Vitis vinifera* under increasingly impactful abiotic stresses, particularly focusing on molecular interactions, tissue-specific responses, and the adaptive roles of phenolics in stress resistance. In doing so, it highlights recent omics-based advances that provide a systems-level understanding of grapevine stress adaptation.

Overview of Phenolic Metabolism in Grapevine

Phenolic compounds represent one of the most structurally and functionally diverse classes of plant secondary metabolites and form a central component of the defense, signaling, and adaptive response system of *Vitis vinifera*. Beyond their well-established roles in determining berry color, flavor, and astringency, phenolics contribute decisively to grapevine tolerance against major abiotic stresses, including drought, heat, salinity, and UV radiation (Lecourieux et al. 2020). Their biosynthesis originates from the phenylpropanoid pathway, initiated by PAL, which directs carbon flux from phenylalanine into a wide spectrum of phenolic end products (Bogs et al. 2005).

In grapevine, phenolics are broadly classified into flavonoids (anthocyanins, flavonols and flavan-3-ols), stilbenes and phenolic acids, each fulfilling distinct yet complementary roles in stress adaptation and fruit quality. Anthocyanins enhance photoprotection and antioxidant capacity in berry skins under elevated temperature and solar radiation, flavonols act as efficient UV filters and modulators of oxidative signaling, while stilbenes function as inducible phytoalexins that rapidly accumulate in response to drought, UV-C exposure or pathogen challenge (Agati et al. 2012; Šuklje

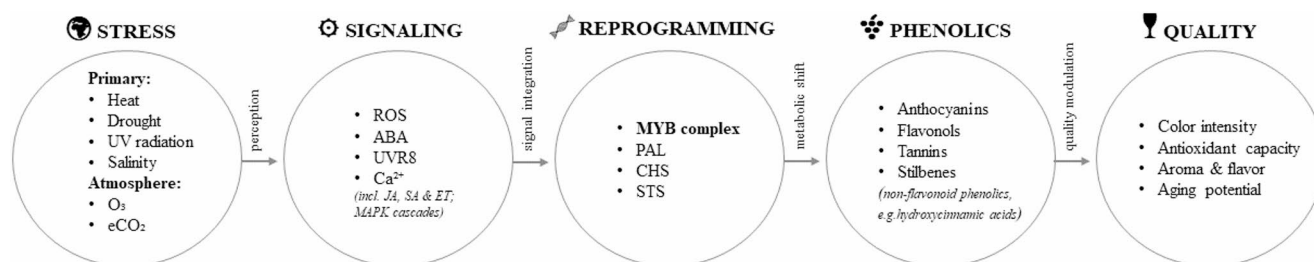


Fig. 1 From stress perception to quality modulation: phenolic plasticity in grapevine under abiotic stress. Conceptual framework illustrating how climate-driven abiotic stresses (heat, drought, UV radiation, salinity, ozone and elevated CO₂ (eCO₂)) are perceived and integrated through ROS- and hormone-mediated signaling networks, leading to phenylpropanoid reprogramming and dynamic redistribution of phe-

nolic compounds. This phenolic plasticity reshapes major phenolic classes and contributes to modulation of grape and wine quality (ROS: reactive oxygen species; ABA: abscisic acid; UVR8: UV resistance locus 8; JA: jasmonic acid; SA: salicylic acid; ET: ethylene; MAPK: mitogen-activated protein kinase; PAL: phenylalanine ammonia-lyase; CHS: chalcone synthase; STS: stilbene synthase)

et al. 2014; Rodríguez-Lorenzo et al. 2023). In addition to flavonoids and stilbenes, hydroxycinnamic acids and other non-flavonoid phenolics represent important components of grapevine stress responses. These compounds contribute to cell wall reinforcement, oxidative buffering and modulation of sensory attributes such as bitterness and aroma precursors, particularly in leaves and berry tissues exposed to environmental stress (Teixeira et al. 2013; Lecourieux et al. 2020; Ali et al. 2010; Rodríguez-Lorenzo et al. 2023).

At the enzymatic level, the phenylpropanoid pathway proceeds through key catalytic steps involving cinnamate-4-hydroxylase (C4H), 4-coumarate-CoA ligase (4CL) and CHS, leading to the synthesis of diverse flavonoid compounds. Downstream reactions catalyzed by chalcone isomerase (CHI), flavanone-3-hydroxylase (F3H), flavonoid-3'-hydroxylase (F3'H) and dihydroflavonol-4-reductase (DFR) culminate in anthocyanidin formation, which is stabilized by glycosylation via UDP-glucose: flavonoid-3-O-glucosyltransferase (UGT) (He et al. 2021). In parallel, STS competes with CHS for common precursors; thus, STS activation represents a key regulatory point that can redirect phenylpropanoid flux toward stilbene biosynthesis (Lecourieux et al. 2020; Rienth et al. 2021).

Phenolic biosynthesis in grapevine exhibits pronounced spatial regulation, with berry skins preferentially accumulating anthocyanins and flavonols, seeds enriched in flavan-3-ols and condensed tannins, and leaves characterized by high levels of hydroxycinnamic acid derivatives (Gutiérrez-Gamboa et al. 2024b). This compartmentalization enables tissue-specific optimization of protection and signaling under environmental stress. For example, UV-B exposure enhances flavonol biosynthesis in leaves through activation of the UV-responsive transcription factor *VvMYB1*, whereas drought stress induces *VvSTS* expression in berry skins, promoting stilbene accumulation (Martínez-Lüscher et al. 2016; Teixeira et al. 2025b).

Regulation of phenolic metabolism is governed by a complex transcriptional network dominated by MYB, bHLH and WD40 transcription factors, commonly assembled into the MYB-bHLH-WD40 (MBW) complex. These regulators integrate hormonal and environmental signals to fine-tune phenylpropanoid gene expression. R2R3-MYB transcription factors such as *VvMYB5a*, *VvMYB5b* and *VvMYB1* primarily regulate late steps of anthocyanin biosynthesis, whereas *VvMYB14* and *VvMYB15* control STS genes under stress conditions (Höll et al. 2013; Corso et al. 2015; Savoi et al. 2017; Tan et al. 2023). Transcriptomic studies further highlight the interaction of these transcriptional regulators with hormone signaling pathways—particularly ABA, jasmonic acid (JA) and ethylene (ET)—as a central driver of phenolic plasticity under drought and combined stress scenarios (Ribalta-Pizarro et al. 2021; Rienth et al. 2021).

Together, this regulatory architecture enables *Vitis vinifera* to dynamically adjust phenolic production in response to environmental fluctuations, reinforcing phenolic metabolism as a core component of climate resilience. Understanding these control mechanisms therefore provides a critical framework for interpreting how distinct and interacting abiotic stresses reprogram phenolic metabolism, as addressed in the following sections.

Abiotic Stress-Driven Regulation of Phenolic Metabolism in Grapevine

Abiotic stresses intensified by climate change—most notably drought, heat, enhanced solar radiation (including UV), salinity, and atmospheric ozone—reshape phenolic metabolism in *Vitis vinifera* in stress- and tissue-dependent ways. Across primary studies, these stresses are associated with consistent shifts in the abundance and composition of major phenolic classes (e.g., anthocyanins, flavonols, stilbenes and hydroxycinnamates), with outcomes strongly modulated by genotype, phenological stage, and stress intensity and exposure duration. Responses also differ between white and red cultivars, reflecting differences in anthocyanin capacity and phenylpropanoid allocation (Deluc et al. 2007).

A common early feature across stresses is modulation of the phenylpropanoid pathway, including changes in expression of upstream enzymes (e.g., PAL, C4H, 4CL) and branch-associated gene families (e.g., CHS and *VvSTS* clusters) (Corso et al. 2015; Savoi et al. 2017; Tan et al. 2023).

Accordingly, the following subsections synthesize stress-specific phenolic outcomes and representative quantitative findings across key organs (leaves, roots, berry skins and seeds), emphasizing that phenolic plasticity reflects selective, context-dependent reallocation within the phenylpropanoid network rather than uniform increases in total phenolics. The shared signaling and transcriptional mechanisms underpinning these patterns are integrated in Sect. 3.

Drought Stress

Drought represents one of the most pervasive and economically significant abiotic stresses affecting *Vitis vinifera* across viticultural regions. Water deficit triggers coordinated physiological and metabolic adjustments aimed at maintaining cellular homeostasis, osmotic balance, and redox stability, with phenylpropanoid metabolism constituting a major regulatory target of this adaptive response (Buesa et al. 2022; Cabral et al. 2022; Xu and Wang 2025).

Drought-induced accumulation of ROS, including hydrogen peroxide and superoxide radicals, functions not only as a source of oxidative pressure but also as a key signaling

mechanism activating phenolic biosynthesis. Transcriptomic analyses consistently report differential regulation of core phenylpropanoid genes such as PAL, CHS, F3H and STS in leaves and berry skins under water deficit, with expression patterns varying according to genotype, tissue type and stress severity (Savoi et al. 2016; Rienh et al. 2021; Rodríguez-Lorenzo et al. 2023).

In grapevine, ABA functions as a central drought-stress signal that induces phenylpropanoid biosynthetic gene expression and promotes flavonoid and anthocyanin accumulation, thereby linking water deficit signaling to secondary metabolism reprogramming (Jeong et al. 2004; Koyama et al. 2010; Conde et al. 2016). In parallel, stress-responsive transcription factors contribute to activation of stilbene-associated pathways, supporting reinforcement of antioxidant phenolic branches under water limitation without implying uniform activation across all derivatives (Höll et al. 2013; Savoi et al. 2017; Tan et al. 2023).

Consequently, often exhibit increased concentrations of flavonols, flavan-3-ols and stilbenes, compounds that enhance ROS scavenging, membrane stability and overall phenolic resilience (Lecourieux et al. 2020). The magnitude and direction of phenolic accumulation under drought depend strongly on stress intensity, duration and developmental timing. Moderate water deficit generally stimulates phenolic synthesis and anthocyanin accumulation, improving berry color and antioxidant potential, whereas severe or prolonged drought imposes metabolic constraints associated with limited carbon availability and reduced precursor supply (Teixeira et al. 2023).

Field studies under regulated deficit irrigation (RDI) have reported moderate increases in skin-localized flavonols and stilbenes, although responses vary among cultivars and environments. Extended or severe drought beyond veraison has been associated with altered expression of late anthocyanin biosynthetic genes in a genotype-dependent manner, potentially resulting in reduced pigmentation (Gashu et al. 2023).

Drought-driven phenolic reprogramming also exhibits pronounced tissue specificity. Leaves preferentially accumulate hydroxycinnamic acids and flavonols that function as UV screens and redox modulators, whereas berry skins display strong induction of stilbene derivatives such as resveratrol, piceid and viniferins (Valletta et al. 2021). Flavonols and stilbenes are predominantly localized in berry skins, pulp tissues contain comparatively low concentrations, and seeds are enriched in flavan-3-ols, highlighting the importance of tissue-specific responses. Seed phenolics may also vary in concentration and polymerization degree, influencing astringency and wine sensory properties (Gutiérrez-Gamboa et al. 2025).

Although drought-associated phenolic plasticity is primarily coordinated through ABA-linked transcriptional regulation, additional hormonal and redox interactions contribute to fine-tuning pathway activity. Epigenetic regulation has been proposed as an additional control layer; however, direct evidence for stable chromatin-level regulation of specific phenylpropanoid loci in grapevine remains limited, with current data supporting dynamic transcriptional regulation and potential priming effects under recurrent drought exposure (Bulgakov 2024). From a viticultural perspective, moderate drought can enhance berry quality by concentrating phenolic compounds and increasing skin thickness, whereas excessive or late-season water deficit may disrupt phenolic balance, yield and sensory coherence (Petoumenou and Liava 2025).

Overall, drought emerges as a major modulator of phenylpropanoid regulation in *Vitis vinifera*, contributing to integrated redox-, hormone- and transcription-dependent adjustments within the phenylpropanoid network. This phenolic plasticity underpins both stress tolerance and grape quality, highlighting the critical trade-offs that accompany adaptive responses to water limitation. The redox-hormonal and transcriptional mechanisms coordinating these drought-associated outcomes are synthesized in Sect. 3.

Heat Stress

Rising temperatures associated with climate change impose major constraints on grapevine physiology and berry metabolism. Heat stress typically develops when canopy or berry temperatures exceed cultivar-specific thresholds—commonly around 32–35 °C for leaves and 35–40 °C for berries—although these limits are strongly influenced by genotype, phenological stage, water status and vineyard microclimate (Williams et al. 2018). Exceeding these thresholds disrupts photosynthesis, membrane stability and cellular redox balance, with phenolic metabolism emerging as a particularly heat-sensitive target.

Thermal stress reconfigures phenylpropanoid flux through both enzymatic limitations and transcriptional modulation. In berry skins, elevated temperatures are frequently associated with reduced anthocyanin accumulation. While downregulation of late biosynthetic genes (e.g., DFR, LDOX/ANS, UFGT) has been reported in some cultivars, controlled experiments indicate that enhanced anthocyanin degradation and reduced pigment stability also contribute substantially to color loss under high temperature conditions (Mori et al. 2007; Pillet et al. 2015; He et al. 2021). In contrast, flavonol biosynthesis is often maintained or moderately enhanced, particularly under high irradiance, supporting photoprotection when heat coincides with intense solar radiation (Cabral et al. 2023; Zhao et al. 2024).

Stilbene responses appear context dependent, with short-term activation observed under combined heat and oxidative cues, whereas prolonged heat exposure may constrain accumulation through carbon reallocation toward primary metabolism (Carbonell-Bejerano et al. 2014; Rienth et al. 2021).

Phenolic outcomes under heat stress are strongly shaped by thermal timing and developmental stage. Moderate warming during pre-veraison may accelerate berry development and transiently concentrate skin phenolics through reduced berry size, although this effect can be offset by irrigation-driven berry expansion (Gutiérrez-Gamboa et al. 2021a). In contrast, heatwaves occurring between veraison and harvest—characterized by daytime temperatures exceeding 35–38 °C—are consistently associated with anthocyanin decline and reduced color density, reflecting both transcriptional modulation and post-synthetic instability mechanisms (Mori et al. 2007; Cataldo et al. 2023). Elevated night-time temperatures may further exacerbate these effects by sustaining ROS levels and modulating late anthocyanin gene expression, even when daytime temperatures return to permissive ranges (Rienth et al. 2014). Recent field comparisons further indicate that cultivar sensitivity varies markedly, with some red cultivars (e.g., Tempranillo) exhibiting stronger anthocyanin decline under elevated thermal load than more heat-resilient genotypes, highlighting genotype-dependent thermal plasticity (Gashu et al. 2023).

Heat-driven phenolic reprogramming exhibits pronounced tissue specificity. Leaves preferentially accumulate flavonols and hydroxycinnamic acids that function as non-enzymatic photoprotectants, whereas berry skins—characterized by limited heat dissipation—display heightened susceptibility to pigment instability and metabolic imbalance (Czemmel et al. 2017; Gouot et al. 2019). Structural alterations in berry skin tissues, such as membrane disorder and cuticular microcracking, may further influence phenolic extractability and oxidative reactions, ultimately affecting fruit composition and wine quality (Jolliffe et al. 2023). Seed phenolics are comparatively buffered; nevertheless, heat exposure can modify proanthocyanidin concentration and polymerization degree, with implications for astringency and bitterness perception (Kallithraka et al. 2016; Basalekou et al. 2019; Gombau et al. 2020; Wang et al. 2023).

At the cellular level, heat stress induces oxidative imbalance and interacts with hormone-mediated signaling networks that influence stress-responsive transcriptional activity. Elevated temperatures may reduce transcriptional support for anthocyanin biosynthesis in susceptible genotypes while maintaining photoprotective flavonol pathways, reflecting selective metabolic prioritization rather than uniform pathway suppression (Gouot et al. 2019; LaFountain

and Yuan 2021). Molecular integration of thermal stress signals with redox and transcriptional regulation is discussed in Sect. 3.

In vineyard environments, heat stress rarely occurs in isolation and frequently interacts with high irradiance, water deficit and salinity (Teixeira et al. 2013; Carvalho et al. 2015; Rienth et al. 2021). Combined heat and solar load typically suppress anthocyanin biosynthesis while promoting UV-screening flavonols, whereas the interaction of severe heat with drought or salinity imposes strong metabolic constraints that may down-regulate multiple phenolic branches (Blancquaert et al. 2019; Hewitt et al. 2023; Shtai et al. 2024; Lu et al. 2022). From a viticultural perspective, maintaining berry temperatures below ~35 °C during ripening is critical for preserving color integrity, highlighting the importance of canopy microclimate management and genotypic plasticity in safeguarding phenolic composition under warming conditions (Marín et al. 2021; Torregrosa et al. 2017).

Overall, heat stress generates a distinct phenolic signature in grapevine, characterized by anthocyanin decline driven by both transcriptional modulation and post-synthetic instability, the relative maintenance of flavonols under high irradiance and context-dependent modulation of stilbenes. These responses reflect integrated regulation by thermal intensity, exposure timing, tissue specificity and interacting stresses, positioning phenolic plasticity as a key determinant of grape quality in a warming climate.

UV Radiation

Climate change is altering not only the intensity but also the spectral composition of solar radiation reaching vineyard canopies, with fluctuations in UV-B (280–315 nm) and UV-A (315–400 nm) emerging as key drivers of phenolic plasticity in grapevine. Field experiments and altitude gradients indicate that variation in incident UV radiation can markedly influence the accumulation of flavonols, anthocyanins and stilbenes in berry skins and, consequently, in wines (Carbonell-Bejerano et al. 2014; Del-Castillo-Alonso et al. 2020b; Mansour et al. 2022).

UV signals in grapevine are primarily perceived through the UVR8–COP1–HY5 signaling module, which interfaces with ROS and hormone-mediated pathways to modulate phenylpropanoid metabolism. This signaling cascade exerts well-documented regulatory control over flavonol biosynthesis via the *VvUVR8*–HY5–*VvMYB1* axis, while also influencing stilbene-related branches under elevated or pulsed UV exposure (Carbonell-Bejerano et al. 2014; Loyola et al. 2016; Tossi et al. 2019; Cao et al. 2024). UV-B perception via UVR8 promotes HY5 accumulation and induces flavonoid biosynthetic genes together with UV-responsive

MYB regulators such as *VvMYB1*, thereby enhancing flavonol-based photoprotection (Czemmel et al. 2017; Martínez-Lüscher et al. 2019). UV-induced ROS signaling also intersects with hormone-mediated pathways, contributing to stress-responsive phenolic regulation (Rodríguez-Lorenzo et al. 2023). Rather than representing uniform pathway activation, these responses appear to reflect context-dependent reallocation within the phenylpropanoid network.

UV-driven phenolic responses are highly dose- and timing-dependent. Low to moderate UV-B levels generally act as priming signals, favoring flavonol accumulation and epidermal UV screening, whereas intense or abrupt UV exposure can elicit phytoalexin-type stilbene responses characteristic of defense activation (Rienth et al. 2021). Experimental UV-C treatments further illustrate this response, triggering pronounced oxidative and physiological responses in grapevine tissues (Tahmaz and Küskü 2024). Accordingly, flavonols—mainly quercetin, kaempferol and myricetin glycosides—represent the phenolic class most consistently stimulated by UV-B, reinforcing photoprotection under high irradiance (Martínez-Lüscher et al. 2014, 2019; Matus 2016; Del-Castillo-Alonso et al. 2020a).

Anthocyanin responses to UV radiation are more context dependent. Moderate UV-B exposure around fruit set or veraison may enhance anthocyanin accumulation through induction of early flavonoid genes such as CHS and F3H. However, intense or prolonged UV exposure—particularly when combined with elevated temperature or water deficit—often reduces extractable anthocyanins or alters their compositional profile, even when flavonol accumulation is maintained (Martínez-Lüscher et al. 2014; Del-Castillo-Alonso et al. 2020a; Narra et al. 2023). Stilbenes, including resveratrol, piceid and viniferins, display dose-responsive induction under UV-B and UV-C exposure associated with modulation of *VvSTS* gene families, with short high-intensity pulses producing sharp accumulation peaks and repeated moderate exposure sustaining elevated baseline levels (Teixeira et al. 2013; Yin et al. 2016; Hasan and Bae 2017; Sheng et al. 2018).

Phenolic responses to UV radiation are further shaped by developmental stage and tissue specificity. During pre-veraison, UV-B exposure promotes flavonol biosynthesis in both leaves and developing berry skins, with effects typically more pronounced in leaves (Martínez-Lüscher et al. 2014, 2019; Del-Castillo-Alonso et al. 2021). From veraison to ripening, UV outcomes become increasingly dependent on berry temperature and water status. Moderate UV-B maintained under a well-managed canopy can preserve color development and enhance copigmentation through flavonol accumulation, whereas high UV combined with elevated berry temperature increases sunburn risk and

constrains anthocyanin biosynthesis (Martínez-Lüscher et al. 2016; Gambetta et al. 2021; Cataldo et al. 2023).

UV radiation rarely acts alone in vineyard environments and frequently interacts with light intensity, heat and water availability. Under high photosynthetically active radiation (PAR), UV and visible light act synergistically to promote flavonol accumulation via sustained activation of flavonol-associated regulatory pathways (Martínez-Lüscher et al. 2019). In contrast, elevated berry temperatures exceeding ~35 °C antagonize anthocyanin accumulation even when UV exposure is sufficient to maintain flavonol biosynthesis (Campos-Arguedas et al. 2022). Interactions between UV and drought further modulate stilbene responses through ROS- and ABA-linked signaling, with outcomes highly dependent on cultivar, irrigation regime and canopy microclimate (Deluc et al. 2011; Teixeira et al. 2013; Carbonell-Bejerano et al. 2014; Doupis et al. 2020).

From a viticultural perspective, manipulation of vineyard light spectra represents a powerful lever for steering phenolic composition. Reflective ground covers, precision leaf removal, photoselective shade nets and particle films can be used to optimize UV exposure while limiting excessive berry heating, thereby enhancing flavonol accumulation and preserving anthocyanin stability under warming conditions (Ross 2010; Alonso et al. 2016; Martínez-Lüscher et al. 2017; Marigliano et al. 2022; Pallotti et al. 2023). Ultimately, UV radiation shapes a distinct and functionally adaptive phenolic signature in grapevine metabolism, characterized by robust flavonol induction, dose-dependent stilbene activation and a temperature-sensitive anthocyanin branch. The magnitude and direction of these responses are governed by UV dose, exposure timing, tissue specificity and interacting stresses, reinforcing the context-dependent nature of phenolic plasticity under changing radiation environments (Loyola et al. 2016; Matus 2016; Yin et al. 2016; Jeandet et al. 2019). The UVR8–HY5 axis and its interaction with ROS and hormone signaling are integrated in Sect. 3.

Salinity Stress

Soil salinization, increasingly driven by prolonged drought, rising temperatures, and low-quality irrigation water, represents a growing constraint for viticulture, particularly in arid and semi-arid regions. In *Vitis vinifera*, salinity stress primarily disrupts ionic homeostasis through Na^+/K^+ imbalance and reduced cellular osmotic potential, generating both osmotic stress and ion-specific toxicity, which in turn promote oxidative stress and extensive metabolic reprogramming (Munns and Gilliam 2015; Hanin et al. 2016). These two components—osmotic stress occurring rapidly upon salt exposure and slower ionic toxicity resulting from Na^+

and Cl^- accumulation—differentially influence carbon allocation and secondary metabolism. Within this response, the phenylpropanoid pathway plays a central role by supporting antioxidant capacity, membrane stabilization and stress-related signaling through the production of flavonoids and stilbenes (Savoi et al. 2016; Valletta et al. 2021).

Salinity-induced oxidative stress promotes ROS accumulation and is frequently associated with activation of core phenylpropanoid genes, including PAL, CHS and STS, primarily through ROS- and ABA-linked signaling pathways (Almagro et al. 2022). ROS accumulation under salt stress interacts with ABA-dependent signaling and ion homeostasis pathways, indirectly shaping transcriptional responses in secondary metabolism. Under moderate salinity conditions, grapevines often exhibit increased levels of flavonols, hydroxycinnamic acids and stilbenes, enhancing antioxidant protection and membrane stability (Zhao et al. 2024). Transcriptomic and metabolomic studies further show induction of *VvSTS* gene families, resulting in transient resveratrol accumulation analogous to drought-driven defense responses (Yin et al. 2016). In contrast, severe salinity disrupts carbon assimilation and redox balance, which may contribute to reduced expression of anthocyanin-related genes such as DFR, ANS and UFGT and consequent reductions in berry color development (Almagro et al. 2022).

Phenolic responses to salinity display marked tissue specificity. Leaves typically accumulate flavonols and phenolic acids that act as frontline antioxidants under ionic stress, whereas berry skins show enhanced stilbene and flavonol accumulation under moderate salinity but reduced anthocyanin biosynthesis as stress intensity increases (Almagro et al. 2022; Zhao et al. 2024). Root tissues exhibit strong genotype-dependent responses, with salt-tolerant rootstocks such as 140Ru and 1103P maintaining higher antioxidant capacity and more stable phenolic metabolism than sensitive genotypes (Martínez-Moreno et al. 2022). Such genotype-dependent differences are partly linked to variation in Na^+ exclusion efficiency, vacuolar sequestration capacity and maintenance of K^+ homeostasis, which indirectly influence shoot redox balance and phenylpropanoid flux. This root-level regulation is particularly relevant under field conditions, as scion phenolic status is partly shaped by the rootstock's control of ion uptake, hydraulic conductance and stress signaling under saline irrigation.

At the molecular level, salinity activates a complex hormonal network involving ABA, ET and salicylic acid (SA), which collectively modulate ion transport, redox homeostasis and phenylpropanoid gene expression. ABA accumulation promotes MYB-mediated activation of phenylpropanoid genes, reinforcing antioxidant defenses, whereas ET and SA fine-tune growth-defense trade-offs in a tissue- and genotype-dependent manner (Almagro et al. 2022; Zhao et al.

2024). This hormonal crosstalk operates alongside ROS signaling to coordinate antioxidant defenses and phenolic metabolism under ionic stress. Proteomic analyses further reveal increased abundance of major ROS-detoxifying enzymes, highlighting the tight coupling between redox regulation and phenolic flux under ionic stress (Prinsi et al. 2020; Martínez-Moreno et al. 2022).

From a viticultural perspective, moderate salinity may enhance total phenolic content in certain genotypes, particularly under deficit irrigation regimes common in dry climates (Almagro et al. 2022; Martínez-Moreno et al. 2023). However, prolonged or high salinity imposes ionic toxicity, reduces chlorophyll content and disrupts phenolic balance, ultimately impairing berry color and wine sensory quality (Zhao et al. 2024). Mitigation strategies—including the use of salt-tolerant rootstocks, blended irrigation water and soil amendments such as gypsum or biochar—are therefore critical for preserving vine performance and phenolic integrity under saline conditions (Prinsi et al. 2020; Martínez-Moreno et al. 2023).

Overall, salinity induces a multi-layered phenolic response in *Vitis vinifera*, characterized by early ROS-mediated activation of the phenylpropanoid pathway, selective enhancement of flavonols and stilbenes under moderate stress, and attenuation of anthocyanin biosynthesis as ionic stress intensifies. These shifts reflect context-dependent redistribution of metabolic resources under ion- and osmotic-driven constraints rather than uniform upregulation of secondary metabolism. The magnitude and direction of these responses depend on genotype, stress intensity and tissue specificity, underscoring phenolic plasticity as a key component of salt tolerance in grapevine. How ionic stress signaling converges with redox and hormonal networks to shape phenylpropanoid allocation is summarized in Sect. 3.

Ozone and CO_2 Enrichment

Rising tropospheric ozone (O_3) concentrations and elevated atmospheric CO_2 have emerged as major atmospheric drivers shaping grapevine physiology and secondary metabolism. O_3 primarily acts as a potent oxidative stressor that compromises photosynthetic efficiency and membrane integrity, whereas eCO_2 generally enhances carbon assimilation and water-use efficiency and may partially buffer oxidative damage. Together, these atmospheric factors modulate phenylpropanoid metabolism in *Vitis vinifera*, reshaping flavonol and stilbene pools as well as broader antioxidant defenses (Fumagalli et al. 2019).

Ozone stress is initiated when tropospheric O_3 enters leaves through stomata and rapidly decomposes into ROS, including hydrogen peroxide and singlet oxygen. This oxidative burst disrupts chloroplast function and cellular

membranes, triggering phenolic-based defense responses. Several experimental studies have reported altered regulation of phenylpropanoid metabolism and shifts in flavonol-related branches under moderate O₃ exposure (Agati et al. 2013; Csepregi and Hideg 2018). Field and controlled studies further illustrate these responses. For instance, controlled preharvest ozone treatments in cv. Bobal demonstrated dose-dependent modulation of berry phenolics, where a single O₃ application increased anthocyanin concentration by approximately 30%, whereas repeated exposure reduced anthocyanins by nearly 47%, while flavonols increased by ~9% and total phenolic index rose by ~34% (Campayo et al. 2019). Similarly, leaf-level ozone exposure experiments revealed enhanced flavonol accumulation and activation of antioxidant enzyme systems (SOD, CAT, APX), supporting a coordinated redox-phenylpropanoid response under oxidative challenge (Modesti et al. 2021). These findings suggest that short-term O₃ exposure may transiently enhance antioxidant-related phenolic branches, whereas prolonged exposure can shift metabolism toward oxidative damage control rather than sustained secondary metabolite production.

Phenolic responses to ozone are strongly duration-dependent. Short-term O₃ exposure often induces transient increases in flavonols and stilbenes, strengthening ROS-scavenging capacity and functioning as an additional oxidative shield in exposed tissues (Hasan and Bae 2017; Campayo et al. 2021). In contrast, chronic O₃ exposure impairs photosynthetic performance and is frequently associated with reductions in total phenolic content, likely due to oxidative overload and diversion of carbon toward repair processes (Fumagalli et al. 2019; Wang et al. 2020). Cultivar-dependent tolerance is evident, with ozone-tolerant genotypes maintaining higher basal antioxidant activity and phenolic stability than sensitive ones (Fumagalli et al. 2019).

At the regulatory level, ozone-derived ROS rapidly activate and interact with SA and JA signaling pathways, which converge on redox-responsive transcription factor families such as WRKY, MYB and NAC. These regulators coordinate the induction of antioxidant enzymes—including superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX)—linking ozone-induced oxidative stress with phenylpropanoid reprogramming (Csepregi and Hideg 2018; Nowroz et al. 2024). Rather than representing uniform upregulation of secondary metabolism, O₃ exposure appears to drive context-dependent redistribution of metabolic resources under oxidative constraint.

eCO₂ (~500–700 ppm) generally enhances photosynthetic carbon gain, vegetative growth and water-use efficiency in grapevine, yet its effects on phenolic metabolism are inconsistent. Evidence from Free-Air CO₂ Enrichment

(FACE) and controlled-environment studies indicates that eCO₂ does not uniformly increase berry phenolics and may even dilute anthocyanin and total polyphenol concentrations through altered source–sink relationships and accelerated berry growth (Gonçalves et al. 2009; Morales et al. 2020; Kahn 2023). For example, FACE experiments in Sangiovese reported increases in vegetative growth and yield under ~550 ppm CO₂, while berry anthocyanin concentrations exhibited year-dependent responses and in some cases remained unchanged or decreased relative to biomass accumulation, highlighting dilution and source–sink effects (Bindi et al. 2001; Arrizabalaga-Arriazu et al. 2020). These results indicate that eCO₂ influences phenylpropanoid metabolism primarily through modification of carbon availability and growth dynamics rather than direct transcriptional activation of phenolic biosynthetic genes.

Interactions between O₃ and eCO₂ add further complexity. eCO₂ often partially mitigates ozone toxicity by reducing stomatal conductance and O₃ uptake while sustaining photosynthesis and antioxidant capacity (Paoletti and Grulke 2010; Fumagalli et al. 2019). Under these conditions, O₃-induced phenolic responses—particularly flavonol and hydroxycinnamate accumulation—are moderated rather than eliminated. In long-term or multi-stress scenarios, however, stilbene-type phytoalexins may remain elevated while anthocyanin accumulation declines if additional stresses such as heat or drought constrain carbon allocation (Arrizabalaga-Arriazu et al. 2020; Fumagalli et al. 2019).

From a viticultural perspective, limiting canopy O₃ uptake through irrigation management, selection of tolerant cultivars and maintenance of antioxidant capacity is critical under polluted atmospheres. eCO₂ may provide partial physiological buffering, yet excessive vegetative growth or inadequate water supply under eCO₂ can dilute berry phenolic concentration by disrupting source–sink balance (Paoletti and Grulke 2010; Arrizabalaga-Arriazu et al. 2020). Overall, O₃ exposure induces an initial stimulation of flavonols and stilbenes but reduces phenolic pools under chronic oxidative load, whereas eCO₂ primarily reshapes phenolic allocation through changes in carbon supply and growth dynamics rather than direct pathway activation. Their combined effects underscore phenolic plasticity as a central axis of grapevine resilience under changing atmospheric conditions. Cross-talk between oxidative signaling, hormonal responses, and carbon allocation constraints under O₃/eCO₂ is integrated in Sect. 3.

While the preceding sections describe stress-specific regulatory mechanisms in detail, a cross-stress quantitative synthesis provides a clearer basis for identifying convergent and divergent phenylpropanoid responses in *Vitis vinifera*. Table 1 summarizes representative experimental studies reporting transcriptional and metabolite-level responses

Table 1 Representative quantitative studies linking abiotic stresses to phenylpropanoid modulation in *Vitis vinifera*

Stress Type	Cultivar	Tissue	Gene/Pathway Response	Quantitative Phenolic Response	Key Mechanistic Insight	Reference
Prolonged water deficit (−1.25 to −0.8 MPa)	Cabernet Sauvignon	Whole berry	<i>STS</i> transcripts ↑	trans-piceid ↑ 5-fold	Cultivar-specific activation of stilbene branch under drought	Deluc et al. 2011
Prolonged water deficit	Tocai Friulano (white)	Whole berry	4,889 DE genes; phenylpropanoid pathway modulated	20/27 phenolics altered; cinnamic & benzoic derivatives ↑	Broad transcriptional reprogramming of secondary metabolism	Savoi et al. 2016
High temperature (35 °C vs. 25 °C)	Cabernet Sauvignon	Berry skin	Anthocyanin biosynthetic genes <2-fold transcriptional change	Anthocyanins ↓ >50–60%	Heat promotes anthocyanin degradation rather than transcriptional repression	Mori et al. 2007
Field heat (+1.5 °C warmer site)	20 red cultivars	Berry skin	Genotype-dependent modulation	Flavonols ↓; Anthocyanins ↓	Temperature-driven phenolic plasticity is cultivar-specific	Gashu et al. 2023
Solar UV-B exposure (field)	Tempranillo	Berry skin	121 genes modulated; <i>VvFLS1</i> ↑	Flavonol accumulation ↑	UV-B signaling activates flavonol branch	Carbonell-Bejerano et al. 2014
Salinity (100 mM NaCl)	Syrah vs. Razegui	Leaf	Stilbene pathway activation (sensitive genotype)	Resveratrol & piceid ↑ (Syrah)	Genotype-dependent stilbene induction	Soudi et al. 2019
Salinity (gradual NaCl)	Cabernet Sauvignon	Leaf	Large-scale transcriptional reprogramming	Distinct metabolite profiles vs. drought	Salt triggers stress-specific signaling	Cramer et al. 2007
Ozone (preharvest spraying)	Bobal (red)	Berry	ROS-mediated modulation	Anthocyanins ↑30% (single); ↓47% (repeated); Flavonols ↑9%; TPI ↑34%	Dose-dependent oxidative signaling; overstimulation reduces phenolic stability	Campayo et al. 2019
eCO ₂ (550–700 ppm; FACE)	Sangiovese	Berry & wine	Photosynthetic carbon assimilation ↑	Polyphenols ↑8–30%; Anthocyanins variable (year-dependent); Yield ↑40–45%	Phenolic response constrained by source–sink balance	Bindi et al. 2001

Values represent representative responses reported under controlled or field conditions and may vary with cultivar, phenological stage and stress intensity. Arrows indicate direction of change (↑ increase; ↓ decrease). TPI=total phenolic index; FACE=Free-Air CO₂ Enrichment. Midday stem water potential (Ψ_{stem}) values are reported where available (e.g., RDI studies) as indicators of vine water status

under drought, heat, UV radiation, salinity, ozone and eCO₂. Rather than implying uniform responses, this comparative framework highlights the context-dependent, genotype-specific and pathway-selective nature of phenolic plasticity across abiotic stress conditions.

These stress-specific responses align with the conceptual framework presented in Fig. 1, highlighting phenolic plasticity as a dynamic and context-dependent adaptive mechanism. As illustrated in Table 1, moderate abiotic stimuli frequently stimulate specific branches of the phenylpropanoid pathway, such as stilbene accumulation under water deficit or flavonol induction under UV-B exposure. In contrast, prolonged heat stress commonly reduces anthocyanin accumulation through mechanisms not solely explained by transcriptional repression, suggesting enhanced degradation processes and pigment instability. Salinity and ozone exposure further reveal genotype-dependent responses mediated by oxidative signaling, while eCO₂ demonstrates that increased carbon availability does not uniformly translate into higher phenolic accumulation due to source–sink constraints.

Beyond flavonoids and stilbenes, several studies report stress-induced modulation of hydroxycinnamic acids and

other non-flavonoid phenolics, particularly in leaves and berry tissues. These compounds contribute to cell wall reinforcement, oxidative buffering and aroma precursor dynamics, indicating that phenolic plasticity extends across both flavonoid and non-flavonoid branches of the phenylpropanoid pathway (Teixeira et al. 2013; Gutiérrez-Gamboa et al. 2022; Ali et al. 2023).

Collectively, these patterns reinforce the concept of phenolic plasticity as a dynamic, stress-specific reallocation of metabolic flux rather than a universal upregulation of secondary metabolism. This integrative perspective provides a quantitative and mechanistic foundation for understanding how environmental stress reshapes phenolic metabolism under climate change.

Cross-Talk Between Stress Signaling and Phenolic Pathways

Abiotic stresses such as drought, heat, salinity, UV radiation and ozone rapidly reconfigure cellular signaling networks in *Vitis vinifera*. A central feature of this reconfiguration is the integration of redox signaling, hormone perception

and transcriptional control at key regulatory nodes of the phenylpropanoid pathway. Rather than operating as isolated pathways, these signaling modules converge to reshape metabolic flux allocation among flavonoid, stilbene and phenolic acid branches in a stress-specific manner (Rienth et al. 2021; Wang et al. 2024).

ROS as Primary Signaling Integrators

ROS function not merely as damaging by-products but as early secondary messengers of stress perception. ROS accumulation—originating from chloroplast dysfunction, mitochondrial perturbation, NADPH oxidase (RBOH) activation or apoplastic ozone reactions—triggers Ca^{2+} influx and activates mitogen-activated protein kinase (MAPK) cascades, particularly MPK3/MPK6 homologues (Torres et al. 2006; Waszczak et al. 2018; Zandalinas et al. 2020). Activated MAPKs phosphorylate redox-sensitive transcription factors, including MYB, WRKY and NAC families, thereby modulating transcription of phenylpropanoid biosynthetic genes such as PAL, CHS and STS (Mittler 2017; Fichman and Mittler 2020). This ROS–MAPK integration explains rapid flavonol induction under UV-B and transient stilbene activation under ozone or combined heat–oxidative stress. However, when ROS accumulation exceeds buffering capacity, oxidative damage to enzymes and membranes occurs, shifting cellular priorities toward antioxidant defense systems (SOD, CAT, APX) and limiting sustained secondary metabolite production (Hasanuzzaman et al. 2020). Thus, ROS act as bidirectional regulators—initiating phenolic activation under moderate stress but constraining flux under chronic oxidative load.

Hormonal Signal Transduction and Phenylpropanoid Control

ROS signaling is tightly integrated with phytohormonal cascades that refine phenolic responses. Under drought and salinity, ABA accumulates and binds to PYR/PYL/RCAR receptors, leading to inhibition of PP2C phosphatases and activation of SnRK2 kinases (Umezawa et al. 2009; Cutler et al. 2010). Activated SnRK2s phosphorylate ABA-responsive transcription factors (ABFs/AREBs), which bind to ABRE motifs within promoters of stress-responsive genes. Promoter analyses and transcriptomic evidence suggest that ABA-responsive cis-elements occur in upstream regions of PAL and STS gene families, supporting ABA-mediated modulation of phenylpropanoid entry and stilbene-specific branches (Höhl et al. 2013; Savoi et al. 2016). Jasmonate (JA) signaling further integrates oxidative cues through the COI1–JAZ pathway. JA perception promotes degradation of JAZ repressors, releasing MYC2 transcription factors that

interact with MYB regulators to enhance flavonol and stilbene biosynthesis under oxidative or combined stress conditions (Kazan and Manners 2013; Sharma et al. 2019). SA, particularly under ozone exposure, activates NPR1-dependent signaling and WRKY transcription factors, reinforcing defense-associated phenolic accumulation (Csepregi and Hideg 2018). ET contributes to modulation of anthocyanin–flavonol balance during ripening and heat adaptation via ERF-mediated transcriptional regulation (Fuentes et al. 2019). Rather than acting independently, ABA, JA and SA form dynamic antagonistic–synergistic networks that generate stress-specific phenolic fingerprints across tissues (Savoi et al. 2017).

MBW Complex Dynamics and Branch Allocation

At the transcriptional core of phenylpropanoid regulation lies the MBW complex, a conserved regulatory module controlling flavonoid biosynthesis (Xu et al. 2015). In grapevine, activator MYBs such as *VvMYBA1/2* stimulate late anthocyanin genes (DFR, LDOX, UFGT), whereas *VvMYBF1* promotes flavonol biosynthesis and *VvMYB14/15* preferentially activate STS gene clusters associated with stilbene production (Bogs et al. 2007; Höll et al. 2013; Czempl et al. 2017). Stress-dependent modulation of MBW activity—including MAPK-mediated phosphorylation, hormone-responsive promoter regulation and induction of repressor-type MYBs—alters transcriptional balance among competing phenylpropanoid branches. Under heat or ionic stress, destabilization of anthocyanin-promoting MBW complexes may occur despite sustained upstream PAL activity, resulting in selective reinforcement of flavonol or stilbene pathways rather than uniform pathway activation (Gouot et al. 2019; LaFountain and Yuan 2021). This model supports transcriptional prioritization instead of a rigid metabolic “switch” between CHS and STS branches. Rather than representing a strict metabolic switch, stress-induced STS activation reflects context-dependent competition for shared precursors and transcriptional prioritization within the phenylpropanoid network.

Carbon Allocation, Systemic Signaling and Stress Memory

Phenylpropanoid plasticity is constrained by carbon availability and source–sink dynamics. Under chronic ozone or severe heat stress, impaired photosynthesis reduces carbon flux into secondary metabolism. Conversely, moderate stress may transiently enhance soluble sugar availability, supporting short-term phenolic accumulation. FACE experiments and source–sink analyses in grapevine demonstrate that enhanced vegetative growth under eCO_2

does not necessarily increase berry phenolics, highlighting carbon partitioning as a limiting factor for sustained phenylpropanoid flux (Bindi et al. 2001; Arrizabalaga-Arriazu et al. 2020). Systemic ROS waves and hormone-mediated vascular signaling further coordinate phenolic responses among leaves, roots and berries, integrating redox demand with carbon allocation at the whole-plant level (Miller et al. 2009; Fichman and Mittler 2020). Epigenetic modulation and post-transcriptional regulation add additional layers of control. Stress-associated chromatin remodeling and DNA methylation shifts have been reported in grapevine, although direct locus-specific evidence linking these marks to sustained activation of PAL, CHS or STS remains limited (Luo et al. 2012; Ramakrishnan et al. 2022). MicroRNAs such as miR858 fine-tune R2R3-MYB activity, influencing branch allocation within the flavonoid pathway (Pantaleo et al. 2010; Zombardo et al. 2020).

Cross-talk among ROS signaling, phytohormonal cascades, MBW-mediated transcriptional regulation and carbon allocation dynamics establishes a flexible phenolic regulatory network in *Vitis vinifera*. This multilayered integration enables rapid environmental sensing, stress-specific branch prioritization and restoration of oxidative balance. Rather than uniform upregulation of secondary metabolism, phenolic plasticity emerges as a tightly regulated, context-dependent reconfiguration of metabolic flux under climate-driven stress conditions, linking environmental sensing with biochemical prioritization at the pathway level.

Integrative Omics Insights into Phenolic Plasticity

The multilayered nature of phenolic plasticity in *Vitis vinifera* is increasingly revealed through integrative transcriptomic, proteomic, metabolomic and post-genomic analyses. Multi-omics studies consistently demonstrate that phenolic metabolism is regulated not by isolated gene responses, but by coordinated regulatory modules integrating redox status, hormonal signaling and developmental cues. Under abiotic stress, drought-induced reprogramming of phenylpropanoid and stilbene pathways involves parallel induction of PAL, CHS and STS, antioxidant enzymes and ABA-associated networks, redirecting carbon flux toward specific phenolic subclasses (Cramer et al. 2007; Savoi et al. 2017). These coordinated responses support redox buffering, osmotic adjustment and cellular protection rather than constituting a purely defensive metabolic shift. Small-RNA-mediated regulation further modulates MYB-centered transcriptional networks, reinforcing the systems-level nature of phenolic adjustment (Pantaleo et al. 2010).

Transcriptomic analyses across leaves, roots and berries reveal that drought, salinity and combined drought–heat stress consistently activate early phenylpropanoid genes (PAL, C4H, 4CL), followed by strong induction of *VvCHS*, *VvF3H* and large *VvSTS* gene clusters (Corso et al. 2015; Savoi et al. 2017; Tan et al. 2023). In contrast, heat and UV stress generate distinct transcriptional signatures, with elevated temperature repressing late anthocyanin genes (*VvDFR*, *VvLDOX*, *VvUFGT*) while maintaining flavonol-associated pathways, and UV-B strongly inducing *HY5*, *VvMYBF1* and quercetin-associated flavonol genes (Rienth et al. 2014; Pontin et al. 2010). This divergence reflects stress-specific branch prioritization within the phenylpropanoid network rather than uniform pathway activation. Co-expression network analyses and WGCNA-based studies further identify stress-specific regulatory modules integrating ROS signaling, ABA-responsive transcription factors and phenylpropanoid hubs, with strong genotype- and developmental-stage dependence (Dal Santo et al. 2016; Wu et al. 2023; Dou et al. 2024).

Proteomic analyses highlight that transcriptional plasticity is buffered and reshaped at the protein level. Abiotic stress increases abundance of early phenylpropanoid enzymes together with heat shock proteins and redox-protective components, supporting enzyme stability under oxidative pressure (George 2015; Toups 2021). Chaperone-assisted folding and ROS-detoxifying systems help preserve catalytic activity of phenylpropanoid enzymes under stress-induced protein denaturation. Oxidative modification and selective turnover of vulnerable PAL isoforms, mediated by ubiquitin–proteasome pathways, further redirect metabolic flux toward antioxidant buffering and flavonol accumulation. Comparative proteomics reveal that tolerant cultivars maintain higher baseline levels of phenylpropanoid enzymes, chaperones and antioxidant proteins, emphasizing cultivar-specific proteomic buffering capacity as a determinant of phenolic resilience (Toups 2021; Dou et al. 2024).

Metabolomic profiling provides the functional endpoint of these regulatory layers. Water deficit enhances quercetin glycosides, flavan-3-ols and stilbenes, whereas heat stress suppresses anthocyanins while promoting flavonol accumulation, and UV-B exposure strongly induces quercetin-type flavonols and stilbenes via *HY5*–*MYBF1*–mediated pathways (Pontin et al. 2010; Deluc et al. 2011; Rienth et al. 2021). Multivariate analyses consistently show that metabolomic trajectories segregate according to ROS intensity, ABA levels and carbon allocation between flavonoid and stilbene branches, confirming phenolic metabolism as a flexible, reversible network rather than a fixed stress output (Hochberg et al. 2013; Savoi et al. 2017). These patterns indicate coordinated metabolic reallocation rather than linear upregulation of phenolic synthesis.

Epigenomic and post-transcriptional layers further contribute to phenolic plasticity and stress memory. Abiotic stresses induce dynamic changes in DNA methylation (CpG and CHH contexts) and histone modifications at phenylpropanoid-related loci, modulating chromatin accessibility and transcriptional responsiveness (Fortes and Gallusci 2017; Dal Santo et al. 2018). Although locus-specific regulation of individual phenylpropanoid genes remains under active investigation, these chromatin-level changes are associated with enhanced stress responsiveness. Small RNAs provide an additional regulatory layer: miR858 regulates R2R3–MYB activators of flavonoid biosynthesis, while the Vv-miR156–VvSPL module integrates developmental cues and hormonal signals to modulate anthocyanin accumulation during berry ripening (Pantaleo et al. 2010; Cui et al. 2018; Su et al. 2021).

At the systems level, integrative transcriptome–metabolome–epigenome analyses reposition phenylpropanoid metabolism as a central hub within the grapevine stress-response network. Phenolic derivatives form highly connected metabolic nodes whose network topology shifts with stress intensity, developmental stage and genotype, linking redox demand, carbon availability and metabolic regulatory cost (Cramer et al. 2007; Hochberg et al. 2013; Ciaffi et al. 2019). Network-based models suggest that phenylpropanoid flux is dynamically redistributed to maintain redox homeostasis while minimizing metabolic cost under stress conditions. Together, these convergent multi-omics insights establish phenolic plasticity as an emergent systems property, arising from coordinated reprogramming across molecular layers. This integrative behavior enables *Vitis vinifera* to maintain redox balance, preserve fruit quality and dynamically adapt to climate-driven stress, providing a robust mechanistic framework for predictive viticulture and climate-adaptive breeding strategies.

Implications for Climate-Resilient Viticulture

The pronounced metabolic and phenolic plasticity of *Vitis vinifera* provides a robust molecular and agronomic foundation for climate-resilient viticulture. Although rising temperatures, drought and extreme weather events increasingly threaten grapevine performance and berry quality, recent syntheses indicate that cultivars capable of dynamically reallocating carbon toward antioxidant phenolics—particularly flavonols and stilbenes—tend to exhibit enhanced stress tolerance and physiological stability when supported by appropriate vineyard management (Gutiérrez-Gamboa et al. 2021a; Martínez-Lüscher et al. 2025; Baltazar et al. 2025). Integrating omics-based insights into stress-responsive phenolic pathways with adaptive viticultural practices

therefore represents a central strategy for preserving grape and wine quality under climate change.

Multi-omics studies consistently identify phenolic composition as a sensitive and integrative functional indicator of grapevine resilience. Cultivars and rootstocks that maintain strong induction of regulatory hubs such as the MYB14/15–STS axis and MYBF1-driven flavonol modules maintain superior redox balance, membrane stability and stress tolerance under drought, heat and high radiation (Savoi et al. 2017; Gambetta et al. 2020; Corso et al. 2015). These molecular signatures may serve as predictive indicators of stress adaptation capacity, complementing traditional physiological indicators—including stomatal conductance, chlorophyll fluorescence and canopy temperature—in cultivar selection, vineyard zoning and climate-adaptation modeling.

Vineyard microclimate management emerges as a powerful lever for steering phenolic outcomes. Canopy architecture, irrigation timing and light exposure directly regulate berry temperature and phenylpropanoid fluxes. Moderately exposed clusters (<30–32 °C) favor stable anthocyanin accumulation and enhanced flavonol synthesis, whereas excessive exposure promotes sunburn and pigment degradation (Martínez-Lüscher et al. 2020; Torres et al. 2020). Reflective ground covers, particle films and photoselective shade nets further modulate the spectral and thermal environment, enabling preservation of color stability and antioxidant capacity under heat and high-radiation conditions (Conde et al. 2016; Marigliano et al. 2022). RDI applied before veraison enhances skin-localized phenolics, while excessive late-season water stress constrains anthocyanin biosynthesis due to enzymatic and carbon limitations (Castellarin et al. 2007; Keller 2020).

The integration of omics platforms with precision viticulture is increasingly transforming phenolic monitoring at vineyard scale. Remote sensing tools—including multi-spectral and hyperspectral indices such as NDVI, PRI and red-edge reflectance—correlate strongly with berry phenolic composition, canopy microclimate and stress intensity, enabling near-real-time phenolic assessment and decision-support systems for irrigation, shading and canopy management (Diago et al. 2016; Giovos et al. 2021; Wong et al. 2025). When combined with transcriptomic and metabolomic fingerprints, these facilitate translation of molecular stress responses into site-specific management decisions.

Sustainable inputs and emerging biotechnological approaches further expand the viticultural toolbox for climate-resilient viticulture. Elicitors such as methyl jasmonate and chitosan stimulate phenylpropanoid metabolism without yield penalties, while biostimulants and soil amendments (e.g., biochar) improve water retention and support long-term redox homeostasis under drought and

salinity (Baronti et al. 2014; Portu et al. 2016; Bulgari et al. 2019). Advances in regulatory genomics, including targeted manipulation of MYB transcription factors and STS gene clusters, are being explored as potential tools to enhance intrinsic phenolic responsiveness (Dalla Costa et al. 2019).

Phenolic reprogramming under climate stress ultimately translates from vine to wine, shaping color stability, mouthfeel, and oxidative buffering capacity. Moderate stress-induced increases in flavonols and stilbenes enhance co-pigmentation and antioxidant protection, whereas excessive heat or prolonged drought accelerates anthocyanin degradation and weakens tannin–anthocyanin interactions (Martínez-Lüscher et al. 2020; Keller 2020; Rustioni et al. 2023). Beyond sensory attributes, elevated levels of resveratrol and quercetin derivatives also enhance the nutritional value of grapes and wines (Hanzouli et al. 2025; Căpruciu 2025).

Overall, climate-resilient viticulture will increasingly depend on harnessing phenolic plasticity as an active management lever rather than a passive stress outcome. By integrating molecular markers of phenylpropanoid activity with microclimate control, precision sensing and sustainable inputs, phenolic metabolism can be strategically steered to preserve grape quality, wine typicity and resilience under accelerating climate change.

Conclusions and Future Directions

Climate change is redefining the physiological and metabolic limits of global viticulture worldwide, placing increasing pressure on *Vitis vinifera* production systems. Accumulating evidence, however, demonstrates that grapevine possess remarkable phenolic plasticity, enabling dynamic reprogramming of secondary metabolism in response to environmental stress. Field and controlled-condition studies consistently show that drought, heat and enhanced summer radiation reshape berry phenolic profiles, often promoting flavonols, stilbenes and skin-bound polyphenols that enhance oxidative buffering capacity and stress tolerance (Chacón-Vozmediano et al. 2021; Šikuten et al. 2025; Pereira et al. 2025).

These adaptive responses do not arise from isolated biochemical reactions but from coordinated, network-level regulation. Phenylpropanoid flux, ROS signaling and hormonal cross-talk adjust in concert to maintain physiological and metabolic homeostasis under limiting environments. Recent climate-oriented multi-omics analyses further demonstrate that phenolic reprogramming closely track microclimatic variability and water availability, positioning phenolic metabolism as a central regulatory hub underpinning

grapevine resilience to climate stress (Pou et al. 2023; Martínez-Lüscher et al. 2025).

Looking forward, advancing climate-resilient viticulture will require a shift from single-stress frameworks toward integrated, predictive approaches. Priority research directions include deciphering multi-stress interactions and their temporal dynamics (e.g. drought × heat × radiation), identifying genotype- and rootstock-specific phenolic architectures, and developing real-time field monitoring tools that integrate biochemical markers with canopy temperature and remote-sensing metrics. In parallel, deeper exploration of epigenetic regulation, stress memory and rhizosphere interactions is needed to understand how phenolic plasticity is stabilized or amplified under recurrent stress. Finally, breeding and biotechnological strategies targeting key regulatory hubs—particularly MYB- and STS-centered modules—offer promising avenues for enhancing intrinsic metabolic adaptability.

From a vineyard management perspective, translating phenolic plasticity into practice requires climate-responsive and cultivar-specific strategies aligned with phenological timing and stress thresholds. RDI applied between fruit set and pre-veraison has been shown to enhance skin phenolics and flavonol accumulation while maintaining yield when vines are maintained under moderate water deficit conditions, typically corresponding to midday stem water potentials near -0.8 to -1.2 MPa, depending on cultivar, soil properties and atmospheric evaporative demand (Castellarin et al. 2007; Keller 2020; Gutiérrez-Gamboa et al. 2021b). Applying water deficits after veraison should be avoided in warm regions, as late-season carbon limitation can suppress anthocyanin biosynthesis and delay ripening.

Under heat stress, maintaining berry temperatures below approximately 35°C during ripening is critical for preserving anthocyanin stability and color density (Spayd et al. 2002; Tarara et al. 2008; Martínez-Lüscher et al. 2020). Canopy shading, delayed or partial leaf removal and 20–30% shade nets can mitigate thermal stress while maintaining sufficient irradiance to support flavonol biosynthesis. Reflective ground covers and particle films such as kaolin reduce radiative heating and sunburn risk while maintaining beneficial UV-induced flavonol synthesis (Glenn et al. 2001; Conde et al. 2016; Marigliano et al. 2022).

Moderate cluster exposure before veraison promotes acclimation and flavonol accumulation, whereas excessive exposure between veraison and harvest accelerates pigment degradation and sunburn risk. Cultivar-dependent responses further underscore the need for tailored management. Heat-sensitive cultivars such as Pinot Noir and Tempranillo frequently exhibit greater anthocyanin degradation under elevated temperatures, whereas Cabernet Sauvignon and Syrah often maintain more stable phenolic profiles under

moderate stress (Mori et al. 2007; Sadras and Moran 2012; Gashu et al. 2023).

Rootstock selection also contributes to resilience; drought- and salt-tolerant rootstocks such as 1103 Paulsen and 140 Ruggeri improve hydraulic conductance, ion balance and antioxidant capacity under stress conditions (Keller 2020; Martínez-Moreno et al. 2022).

Emerging precision viticulture tools—including canopy temperature sensing, thermal imaging and red-edge spectral indices—provide practical means to monitor stress thresholds and guide irrigation and canopy management decisions in real time (Diago et al. 2016; Giovos et al. 2021).

Taken together, these insights redefine phenolic metabolism not as a passive consequence of stress, but as a tractable control point for climate-adaptive vineyard design. Harnessing phenolic plasticity provides a dual opportunity: buffering productivity against climatic extremes while preserving the sensory, nutritional and cultural identity of wines. By integrating molecular knowledge with precision viticulture, the sector can move beyond reactive adaptation toward proactive phenolic management strategies, laying a robust foundation for resilient, quality-driven viticulture in a rapidly warming world. As conceptualized in Fig. 1, phenolic plasticity functions as a central adaptive hub linking environmental perception to metabolic regulation and quality outcomes in climate-resilient viticulture.

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Declarations

Compliance with ethical standards The author declares that there is no conflict of interest.

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