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REVIEW

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Help from the past to cope with the future: *Vitis sylvestris* as a resource for abiotic stress resilience

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Societal Impact Statement

Viticulture is facing increasing challenges due to climate change. The focus on fast growth and sweet berries has come at the expense of stress resilience. Grafting onto Phylloxera-resistant rootstocks from American species has been the most successful form of ecological pest management. However, there is still a significant reliance on chemical plant protection. Additionally, abiotic stress has not been a primary concern in rootstock breeding efforts so far. To identify genetic factors that contribute to abiotic stress tolerance, we propose to explore the potential of the wild ancestor of grapevine, *Vitis sylvestris*. By identifying resilience factors, we can develop a new generation of rootstocks or enhance grafted cultivars to protect viticulture from the impact of abiotic constraints.

Summary

There is an urgent need to explore wild germplasm resources for resilience traits that enhance stress tolerance in grapevines. The challenges posed by climate change, including heat and drought stress, salinity, rising temperatures, and untimely cold snaps in spring, are intensifying. Traditional grapevine varieties often lack the resilience to withstand environmental threats because conventional breeding has historically prioritized yield and flavor over stress tolerance. In this review, we highlight the potential of the European Wild Grapevine, *Vitis sylvestris*, as a valuable genetic resource for resilience traits. Understanding the underlying mechanisms is crucial for developing molecular markers to support resilience breeding. Such traits can be directly integrated through introgression into productive cultivars. Alternatively, they can be used to develop a new generation of rootstocks that protect the scion from environmental stresses without compromising desirable oenological qualities. These markers may support the development of gene editing strategies to engineer more resilient genotypes.

KEYWORDS

abiotic stress, epigenetic, gene editing, marker-assisted selection, resilience factors, sustainable viticulture, *Vitis sylvestris*, wild grapevine

1 | VITICULTURE – A SHOWCASE FOR COSTS AND BENEFITS OF GLOBALIZATION

Although not a staple crop essential for food security, grapevines hold significant economic importance, having one of the highest cash yields per area of any fruit crop. Despite a slight decline in recent years, 7.3 million hectares still produce around 232 million hectolitres of wine (OIV, 2023). However, this productivity comes at a cost, as domestication has selected against resilience, making the grapevine vulnerable to various stressors and parasitic organisms for review, see (Dolferus, 2014). So far, resistance to these pathogens has been the main focus of resilience breeding. Most of these organisms reached Europe in the 19th century, coming from North America. In their region of origin, a long co-evolution between host and pathogen has established a kind of evolutionary armistice. However, the European Grapevine (*Vitis vinifera* L.), lacking this co-evolutionary history, is a naïve host, lacking efficient defense mechanisms. This encounter led to the almost complete collapse of European winegrowing in the second half of the 19th century. The introduction of the insect pest grape phylloxera (*Daktulosphaira vitifoliae* Fitch), destroyed over 40% of European vineyards (Banerjee et al., 2010). Grafting on rootstocks derived from wild American grape species, resistant to this pest, intercepts the asexual propagation cycle of phylloxera at the roots and is considered to be one of the most economically successful cases of Ecological Pest Management in history. The development of rootstocks in the viticulture sector serves as a paradigmatic example of the potential of a Crop Wild Relatives (CWRs) as a source of resilience.

The potential of CWRs as resilience sources for breeding has been understood only recently. While most crop plants perform poorly in unfavorable environments, their wild ancestors or relatives often cope better because they prioritize resilience overgrowth. CWRs have been used to improve disease and pest resistance in wheat, rice, potato, tomato, and other major crops (for a review, see Hajjar & Hodgkin, 2007). This approach offers promising opportunities for sustainable agriculture by reducing reliance on chemical inputs for plant protection. Unfortunately, this strategy is under threat due to the rapid loss of biodiversity, especially agrobiodiversity (for a recent review see (Khoury et al., 2022)). In this review, we investigate the use of the highly endangered ancestor of domesticated grapevine, the European Wild Grapevine *V. vinifera* subsp. *sylvestris*, (hereafter referred to as *Vitis sylvestris*), a valuable genetic resource for both breeding a novel generation of rootstocks and improving abiotic stress tolerance in cultivated grapevines. There are basically two reasons why *V. sylvestris* germplasm is preferred as a resilience donor over other wild grapevine species. First, the European Wild Grapevine is the same species as the domesticated Grapevine, meaning that introgression of genes is just following the natural gene flow. In fact, numerous studies have shown that the migration of viticulture from the two domestication centers in the Caucasus and the Near East (Dong et al., 2023) have resulted in extensive spontaneous introgression between *V. vinifera* and wild populations of *V. sylvestris* (Freitas et al., 2021; Zhou et al., 2019) contributing substantially to the expansion of the European grapevine gene pool (Myles et al., 2011). The expansion of both *V. sylvestris* and its domesticated descendant, *V. vinifera*, occurred during a period of considerable climate change over the transient global warming around a millennium ago, ranging from hibernation in glacial refugia through to the mild and humid conditions of the Atlanticum. These differences were accentuated by extensive migration over several climatic zones (Marrano et al., 2018). Thus, the gene pool of *V. sylvestris* is expected to harbor genes promoting climate resilience. The close genetic relationship between *V. sylvestris* and domesticated grapevines also avoids incompatibility, often encountered in interspecific hybrids, as well as between graft and scion (Assunção et al., 2019; Nazir et al., 2022).

2 | WHAT WILD SYLVESTRIS CAN TEACH US ABOUT GRAPEVINE RESILIENCE TO ABIOTIC STRESS

Recent climate change impacts, particularly rising temperatures and the increasing frequency of droughts, have significantly intensified evapotranspiration and soil desiccation. These changes pose substantial challenges to agriculture in semi-arid Mediterranean regions (Prada et al., 2024). This area has been identified as a climate change hotspot, experiencing an increased frequency of extreme weather events (Lazoglou et al., 2024; Zittis et al., 2019). One major consequence of these changes is the intensification of soil salinity. Under high evaporative demand, the use of marginal or saline water sources for irrigation further contributes to salt accumulation on the soil surface, accelerating salinization processes and threatening agricultural sustainability (Eswar et al., 2021). Although cultivated grapevines are adapted to a certain level of water deficit, they remain highly sensitive to prolonged salinity stress, particularly in irrigated areas (Santos et al., 2020; Vincent et al., 2007). Salinity disrupts grapevine physiology through osmotic imbalance, ion toxicity (notably Na^+ and Cl^-), and oxidative damage (Shani & Ben-Gal, 2005), resulting in reduced growth, poor photosynthetic efficiency, and lower fruit quality (Al-Taey & abd Al-Ameer, 2023). Salt tolerance mechanisms depend largely on the genotype's ability to sequester toxic ions in the roots, thereby limiting their translocation to the shoots (Storey et al., 2003). Several physiological traits implicated in salinity tolerance overlap with those used to mitigate drought by contributing to the maintenance of water balance. These include hydraulic characteristics such as xylem architecture (Hochberg et al., 2015), aquaporin-mediated water transport (Vandeleur et al., 2009), abscisic acid (ABA) signaling (Soar et al., 2006), and stomatal regulation (Schultz, 2003). The main question is: Are these mechanisms effective in counteracting the exacerbation of environmental pressures predicted under future climate scenarios? While these mechanisms provide some degree of tolerance, they may be insufficient to cope with the intensified climate challenges predicted for the future. This limitation partly arises from the reduced genetic diversity of cultivated varieties, a consequence of selective breeding practices that prioritized agronomic traits such as yield and berry quality over resilience to environmental stresses

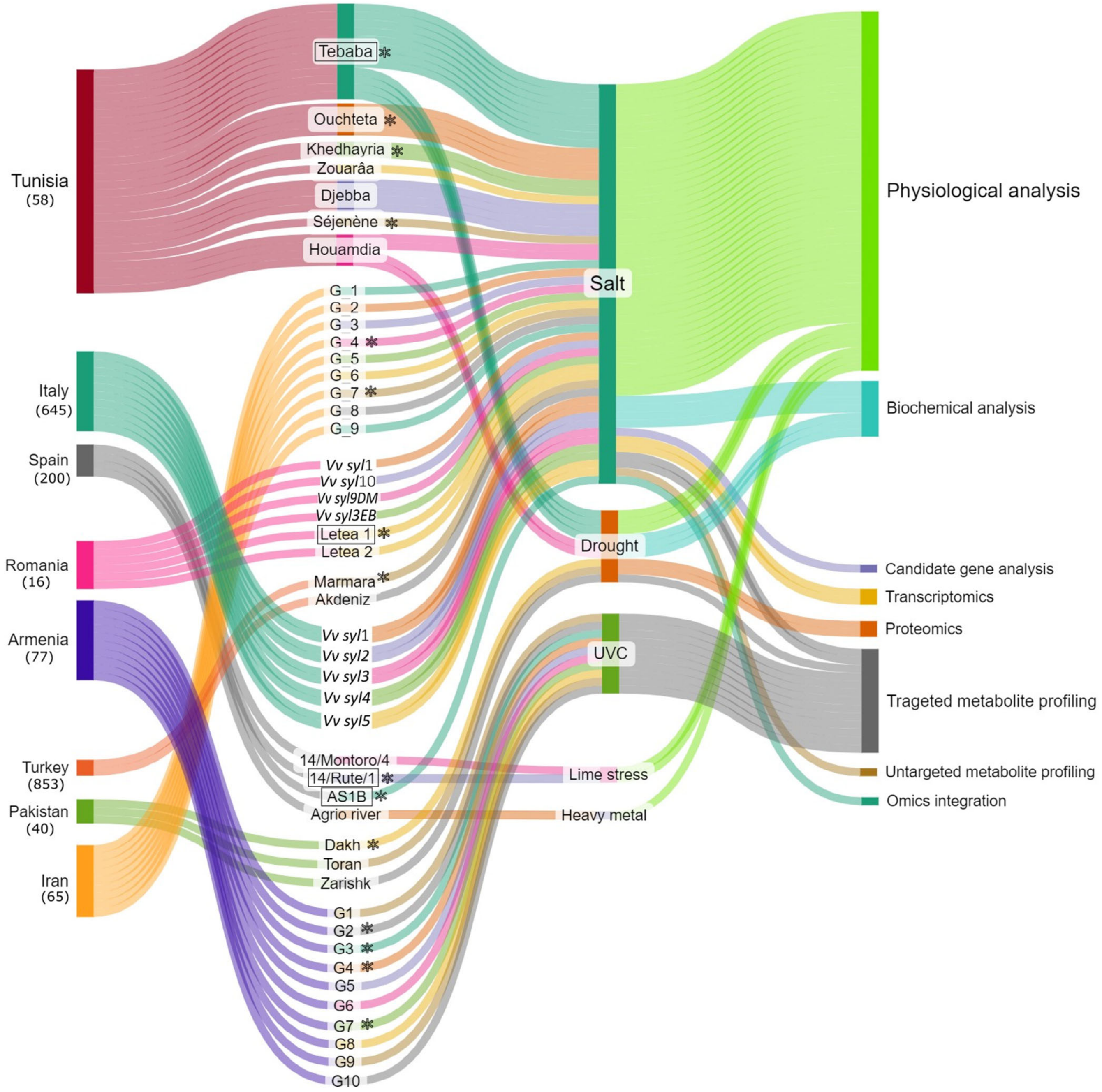

FIGURE 1 Sankey diagram illustrating a review of various *Vitis sylvestris* accessions from different countries, under diverse abiotic stress conditions. Accessions from North Africa (Tunisia), West of Europe (Italy, Spain), East of Europe (Romania, Armenia), Asia (Turkey, Pakistan, and Iran) are represented on the left side. The number below each country corresponds to the total number of *V. sylvestris* accessions. These accessions were subjected to various abiotic stresses, including salt, drought, UV-C, lime, and heavy metal stress. The analysis approaches, including physiological, biochemical, candidate gene, transcriptomics, proteomics, targeted and untargeted metabolite profiling, and omics integration, are represented on the right. This figure highlights the range of stress responses analyzed in each accession and the methodologies applied to elucidate the underlying physiological and molecular mechanisms. Accessions marked with stars (*): represent the most tolerant to stress conditions. Accession inside a frame: denote those exhibiting higher tolerance compared to conventional rootstocks. The diagram was generated using https://sankeymatic.com/build/.

(Marrano et al., 2018; Zhou et al., 2017). In contrast, wild grapevines such as *V. sylvestris* possess a wealth of adaptive traits that have been shaped by millennia of natural selection under fluctuating and often harsh environmental conditions (Daldoul et al., 2023). Their broad distribution across various climates and soil types underscores their phenotypic plasticity and strong adaptive capacity (Figure 1). Whole-genome comparisons between wild and cultivated grapevines have revealed "signatures of selection," including genes critical for adaptation such as *SOS1* (Na^+/H^+ antiporter), *HRE1* (*hypoxia-responsive* transcription factor), ankyrin repeat-containing proteins, soluble starch synthases, and *AP2/ERF*-domain transcription factors (Marrano et al., 2018). These findings raise a critical question: How can the traits that have evolved in wild grapevines to withstand various environmental stresses provide valuable insights for enhancing the resilience of cultivated grapevines under stressful conditions? "Tebaba," a salt-tolerant accession of *V. sylvestris*, provides a compelling answer to this question. Its dynamic regulatory capacity demonstrates how lost adaptive traits can be harnessed to improve stress resilience. Salt tolerance in "Tebaba" does not rely on a single genetic determinant but instead arises from a coordinated network of synergistic metabolic fluxes. Metabolomic profiling revealed a multifaceted adaptive strategy, including reduced cell wall degradation to sustain growth, stabilized central carbon metabolism, and a metabolic shift toward the accumulation of antioxidants and compatible osmolytes (Daldoul et al., 2023). Complementary transcriptomic analyses further revealed the upregulation of genes involved in root architectural plasticity and cell wall remodeling, such as *Expansins*, *Xyloglucan endotransglucosylases* (*XyG*), *Cinnamyl alcohol dehydrogenase* (*CAD*), and *laccase* (*LAC*). These genes may play a crucial role in adapting to salinity (Daldoul et al., 2022). Environmental adaptability is increasingly recognized as being, in part, governed by epigenetic mechanisms, including stress-induced DNA methylation and histone modifications, which can modulate gene expression in response to environmental stresses (Venios et al., 2024). One of the important questions is how epigenetic mechanisms regulate the stress response and enhance the stress tolerance of the grapevine. Epigenetic memory, established during stress exposure and reactivated during recurrent stress, enhances survival potential in fluctuating environments (Berger et al., 2023). Several genes linked to phenotypic plasticity and regulated by epigenetic modifications were identified in the Chinese wild grapevine *V. amurensis* as part of its response to cold stress (Zhu et al., 2023). These include genes encoding chitinase-related proteins, G-type lectin S-receptor-like serine/threonine-protein kinases, *glucosyltransferases* (*GTFs*), *peroxidases* (*PODs*), and *NAC* domain transcription factors (*NAM*, *ATAF1/2*, and *CUC2*). Findings from *V. amurensis* provide valuable insights into the epigenetic mechanisms underlying the resilience of *V. sylvestris* populations in the Mediterranean basin. In Tunisian *V. sylvestris*, resveratrol accumulation was reported as a biomarker of salt stress tolerance (Hanzouli et al., 2024). Although Hanzouli et al. (2024) did not investigate the epigenetic regulation of resveratrol, studies on *V. amurensis* suggest that resveratrol biosynthesis may be influenced by epigenetic modifications (Zhu et al., 2023). Thus, we can speculate that similar epigenetic mechanisms may be involved in resveratrol-mediated stress tolerance in Tunisian *V. sylvestris*. Furthermore, *NAC* transcription factors, which have been identified among the master regulators in salinity tolerance in *V. sylvestris* (Daldoul et al., 2024), were also found to be modulated epigenetically in other grapevine species (Zhu et al., 2023).

These insights highlight the potential of extrapolating epigenetic regulatory mechanisms from related species to deepen our understanding of grapevine resilience. They provide a solid foundation for future research focused on targeted epigenetic interventions to improve grapevine stress tolerance (Tan & Rodríguez López, 2023). However, the study of epigenetic regulations in *V. sylvestris* is still limited. While further epigenetic studies are needed to elucidate the molecular basis of *V. sylvestris* resilience, physiological analyses are providing critical insights into how these mechanisms translate into adaptive traits under real-world stress conditions. The remarkable ability of *V. sylvestris* to adapt to various abiotic stresses highlights its potential as a genetic resource for improving the resilience of cultivated grapevines. Indeed, studies of Iranian wild grape populations reveal significant salt sensitivity, with some accessions unable to tolerate even 50 mM NaCl, while others succumb to severe leaf burning/defoliation at 100 mM NaCl (Baneh et al., 2014). In contrast, Turkish ecotypes show variable levels of salinity tolerance, with greater resilience at 80 mM NaCl (Demir, 2007). However, Tunisian accessions were found to tolerate higher salinity concentrations of up to 150 mM NaCl, through activation of different adaptive strategies such as leaf sodium sequestration (Hamrouni et al., 2011), osmotic balance adjustment, antioxidant defense system induction (Askri et al., 2018; Azri et al., 2020), and secondary metabolite accumulation (Hanzouli et al., 2024). These findings highlight that *V. sylvestris* is a valuable genetic resource with several adaptive responses to various stresses, making it an important asset for future breeding programs (Table 1). A review analysis, illustrated by the Sankey diagram (Figure 1), highlights the diverse responses of grapevine accessions from multiple countries to various abiotic stresses, as revealed through different analytical approaches. The accessions originated from Tunisia, Italy, and Spain and are categorized based on their tolerance levels, with the most stress-tolerant ones marked by stars and framed to indicate their superior resilience compared to conventional rootstocks. The abiotic stresses studied were salt, drought, exposure to UV-C, lime, and heavy metals. Salt stress was the most studied stress for Tunisian accessions.

Physiological analysis remains the most used approach, highlighting its fundamental role in identifying initial tolerance traits. However, more in-depth omics analyses such as transcriptomics, proteomics, metabolite profiling, and epigenetics are still needed to uncover the molecular mechanisms and pathways underlying stress resilience in these accessions. Expanding such omics-based studies could provide a more comprehensive understanding of the biochemical and genetic processes involved in stress tolerance.

3 | HARNESSING THE RESILIENCE OF *VITIS SYLVESTRIS* FOR DEVELOPING RESILIENT ROOTSTOCKS TOWARD ABIOTIC STRESS ADAPTATION

The development of grapevine rootstocks, which began over a century ago, was primarily driven by the need for Phylloxera resistance (Nesbitt, 1974). However, this historical focus has resulted in a limited gene pool among commercial rootstocks. Modern viticulture faces new pressures from climate change, including emerging pathogens

TABLE 1 Overview of the traits and mechanisms related to abiotic stress tolerance in *Vitis sylvestris*.

Depict traits and mechanisms	Abiotic constraint	Approach of study	Key finding	References
Seed germination	Salt temperature	Physiology analysis	• Enhanced the seed germination capacity	Santo et al., 2019
Photosynthetic efficiency	Heat	Physiology analysis	• Regulation of stomatal behavior associated to leaf thermoregulation and water conservation	Faralli et al., 2022
	Salt	Physiology analysis	• Maintain regular photosynthetic rates	Askri et al., 2012
Osmotic adjustment	Salt	Physiology analysis	• Maintain of turgor pressure and cellular hydration by accumulation of osmolytes	Baneh et al., 2014, 2015; Askri et al., 2018
Ion homeostasis	Salt	Physiology analysis	• Regulation of potassium and sodium transport	Askri et al., 2018; Popescu et al., 2015
Antioxidant capacity	Salt Drought	Proteomics Transcriptomics Biochemistry analysis	• Induction of transcripts encoding enzymes of reactive oxygen species (ROS) scavengers and non-enzymatic antioxidant pathways • Accumulation of ROS scavenging proteins APX, ASR2 and GRXS17 • Upregulation of POD, APX, SOD, and catalase enzymes activities	Azri et al., 2020; Daldoul et al., 2022; Nazir et al., 2022
Stress associated regulator hubs	Salt	Omics integration	• Activation of stress-responsive genes • Recruitment of specific transcription factors	Daldoul et al., 2022; Daldoul et al., 2024
			• Tuning ABA-signaling pathway	Daldoul et al., 2024
Metabolite reprogramming	Salt Drought UVC	Targeted metabolite profiling	• Rechanneled of metabolic pathways toward antioxidants and compatible osmolytes, • Buffered photosynthesis • Decreased of cell-wall breakdown	Daldoul et al., 2023; Hanzouli et al., 2024; Margaryan et al., 2019
Cell wall remodeling	Salt	Transcriptomics	• Upregulation of cell wall-loosening genes (Expansin and xyloglucan). • Down-regulation of cell wall stiffening genes (cellulases, Pectinesterase)	Carrasco et al., 2022; Daldoul et al., 2022

and abiotic stresses that were not significant concerns in the past. Most commercial rootstocks are derived from North American *Vitis* species, leading to a narrow genetic base in viticulture (Arrigo & Arnold, 2007). The majority of cultivated grapevines rely on fewer than 10 rootstocks for grafting (Serra et al., 2014). While these rootstocks provide some level of stress tolerance, they are becoming increasingly vulnerable to unpredictable environmental factors (Serra et al., 2014), making the limited genetic diversity a significant barrier to adaptation. As environmental challenges continue to intensify, breeding new and diverse rootstock genetic resources has become essential for ensuring the resilience of grapevine cultivation. Incorporating species like *V. sylvestris* is particularly promising, as it has evolved under natural selection in harsh Mediterranean environments, developing strong resilience to drought, salinity, and temperature fluctuations (Daldoul et al., 2020). This natural adaptability makes *V. sylvestris* an essential genetic reservoir for breeding new climate-resilient rootstocks. Recent studies have explored the use of *V. sylvestris* accessions as rootstocks, revealing their capacity to confer both salt and drought stress tolerance to grafted grapevines. For example, the Romanian accession ‘Letea 1’ shows superior salt tolerance compared to commercial rootstocks by maintaining a high K/Na ratio (Popescu et al., 2015). The Tunisian wild grapevine ‘Tebaba’ achieves greater salt tolerance than the rootstock 1103P by redirecting metabolic flux toward the synthesis of compatible osmolytes and flavonoids, which play a crucial role in protecting photosynthesis and maintaining cellular integrity (Daldoul et al., 2023). In Spain, the coastal wild accession ‘AS1B’ demonstrates a better capacity for maintaining cell wall extensibility under prolonged salinity stress compared to the rootstock 110R, highlighting its enhanced adaptive capacity (Carrasco et al., 2022). These accessions exhibiting higher salinity tolerance than the conventional rootstocks are highlighted in Figure 1. In Pakistan, the wild grapevine ‘Dakh’ conferred drought tolerance when used as a rootstock for cultivated grapevines. This tolerance is attributed to enhanced enzymatic activities that mitigate oxidative stress under drought conditions (Nazir et al., 2022). In Bulgaria, exploratory research on *V. sylvestris* as a rootstock showed that the wild accession (S-1) had a strong affinity with grafted local and introduced cultivars. It showed faster early growth than the standard rootstocks SO4 and Fercal (Tsvetkov et al., 2016).

The high tolerance of the Spanish wild *V. sylvestris* 14/Rute/1 to calcareous soil conditions as compared to the lime-tolerant rootstock 41B was attributed to its ability to preserve photosynthetic integrity and sustain growth rates. This was achieved via more efficient Fe uptake and translocation to the leaves, even under extreme lime conditions (40% $CaCO_3$), along with the maintenance of essential mineral nutrient levels (Cambrollé et al., 2015). Such germplasm would be an appropriate genetic resource to overcome lime-induced chlorosis, a major problem in Mediterranean viticulture.

In-depth investigations into rootstocks have revealed various aspects of scion behavior, particularly its adaptation to abiotic stresses. These adaptations are influenced not only by the characteristics of the rootstock but also by rootstock-scion interactions. Recent discoveries suggest that rootstocks with enhanced salt-exclusion properties can alleviate salt stress in grapevine plants by promoting photosynthesis and providing ionic and oxidative protection (da Silva et al., 2024).

Further studies have shown that certain *V. sylvestris* accessions exhibit resistance to Phylloxera infection, possibly due to the favorable edaphic conditions in their natural habitat, such as permanent or temporary anoxic conditions and gravelly or sandy soils, which do not support Phylloxera development (Ocete et al., 2011). Therefore, harnessing the resilience of the wild ancestors of *V. sylvestris* may offer an effective strategy to adapt agriculture to climate change.

4 | HOW CAN *VITIS SYLVESTRIS* GENETIC RESOURCES HELP BREEDING PROGRAMS?

Genomics will play a key role in facilitating the integration of resistance signatures from wild *Vitis* species for breeding studies. This will be achieved using more sensitive SNP and genome sequencing tools (Butiuc-Keul & Coste, 2023). Breeders may be able to select offspring with desired traits inherited from wild relatives by combining markers associated with key traits with genomic ancestry information. The germplasm of *V. sylvestris*, the wild ancestor of cultivated grapevines, serves as a valuable genetic resource for enhancing grapevine breeding programs. There is an increasing recognition that historical introgression events have contributed to the development of important agronomic traits. Specifically, gene pathways involved in the synthesis of aromatic compounds were found to be enriched in regions that have undergone both selection and introgression. This suggests that wild *V. sylvestris* grapevines have played a crucial role in enhancing the flavor profile of cultivated grape varieties (Xiao et al., 2023). In this context, genetic factors enabling strong stilbene inducibility are still present in *V. sylvestris* (Hanzouli et al., 2024; Margaryan et al., 2019). Molecular analyses revealed larger genomic regions enriched with functional genes associated with responses to biotic and abiotic stresses in *V. sylvestris* compared to cultivated varieties (Freitas et al., 2021). Notably, *V. sylvestris* exhibits natural tolerance to multiple abiotic stresses, including calcareous soil (Cambrollé et al., 2015), salinity (Askri et al., 2018), and drought (Azri et al., 2020).

The diverse stress tolerance mechanisms among *V. sylvestris* genotypes require a targeted approach to harness their resilience in viticulture. Depending on the specific trait, this could involve either direct scion selection or rootstock introgression. For instance, certain *V. sylvestris* genotypes exhibit dynamic stomatal responses that enhance their ability to cope with heat stress and maintain leaf water balance, thereby improving thermotolerance (Faralli et al., 2022). This trait is particularly valuable for grafted scions, as its benefits are primarily scion-related, making direct grafting onto existing rootstocks a more suitable approach than rootstock breeding. Conversely, other *V. sylvestris* genotypes possess root system traits that enhance drought tolerance. Research indicates that wild grapevine *V. sylvestris* has been utilized as rootstock to improve drought resilience in cultivated varieties (Nazir et al., 2022). These wild species often develop extensive root systems that enhance water uptake and confer greater resilience under water-limited conditions. In this context, the introgression of beneficial root traits into existing rootstock genotypes represents a promising strategy for breeding drought-tolerant rootstocks capable of sustaining grapevine hydration in arid environments.

These findings consolidate the hypothesis of the role of *V. sylvestris* as a reservoir of adaptive traits largely lost during domestication. These observations highlight a critical question: Can cultivated grapevines be “rewilded” through targeted breeding or genetic engineering to restore lost adaptive traits and enhance resilience to environmental challenges?

Although grape breeders have utilized conventional breeding to develop abiotic-resistant cultivars with high-quality fruit, successfully introgressing resistance traits into susceptible grapevine cultivars remains a time-consuming challenge. Molecular genetic tools, such as marker-assisted selection (MAS), can expedite this process by enabling the identification of genomic regions harboring resistance genes from different genetic backgrounds. MAS is particularly valuable for pyramiding resistance genes from wild grapevines, facilitating their introgression into elite cultivated grapevine varieties (for review see (Daldoul et al., 2020)). In addition, the integration of genome editing technologies, particularly the CRISPR/Cas9 system, into breeding programs would enable targeted genetic modifications, accelerating the enhancement of desirable traits while preserving the genomic integrity of elite cultivars (Ren et al., 2024). This editing technology is highly effective in overcoming the limitations of traditional breeding, such as linkage drag, where undesirable traits are co-introduced with beneficial ones. Recent studies have demonstrated the potential of genome editing in improving abiotic stress tolerance in grapevines. For instance, CRISPR/Cas9-mediated inactivation of *VvEPFL9–1* has been shown to enhance water-use efficiency and drought resilience in table grapes (Clemens et al., 2022). Similarly, targeted mutagenesis of *VvbZIP36*, a key transcription factor, increases anthocyanin accumulation, which may contribute to better oxidative stress defense (Tu et al., 2022). Moreover, in *V. amurensis*, genome editing of *VaDof17d*, a gene linked to the raffinose family oligosaccharides, has improved cold stress tolerance (Wang et al., 2021). Beyond simple gene modifications, genome editing has the potential to address complex traits by targeting regulatory networks, facilitating genomic rearrangements, and stacking multiple traits within a single variety to fine-tune stress responses (Scheben et al., 2017).

However, despite successful genome editing in grapevine, several challenges remain. One of the major constraints is the clonal

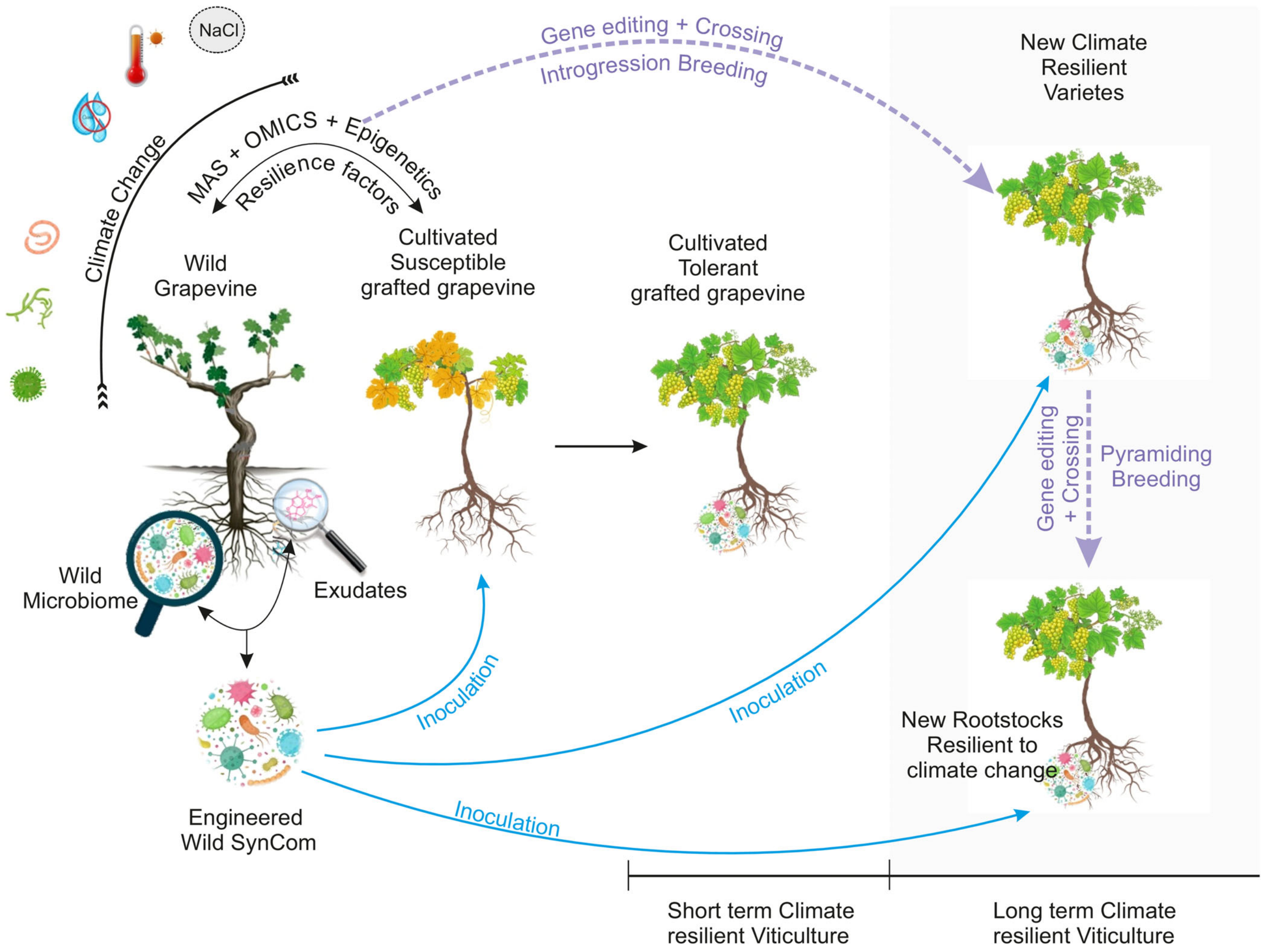

FIGURE 2 Harnessing wild grapevines (*Vitis sylvestris*) for resilient viticulture. Our proposed strategy harnesses the rich genetic diversity and adaptive resilience inherent in wild grapevines (*V. sylvestris*). Wild species were continually evolving under natural selection across diverse environments and serve as crucial reservoirs of genetic resources. Marker-assisted selection (MAS) and OMICs tools strategy has revolutionized plant breeding by refining the process of identifying and selecting beneficial traits to transfer from wild species into domesticated varieties or rootstocks, facilitating the incorporation via introgression (Intogression breeding) or pyramidization of desirable characteristics such as climate resilience to biotic and abiotic stresses (pyramiding breeding). This strategy attempts to promote long-term resilience in viticulture. Moreover, we recognize the limitations imposed by intensive cultivation practices on domesticated grapevine varieties, which often diminish their ability to adapt to changing environments. These insights from wild and cultivated grapevines' responses to environmental stimuli pave the way for novel breeding strategies, ensuring the sustainability and adaptability of viticulture in a changing climate. Solid blue arrows illustrate the use of engineered wild SynCom inoculum which could enhance the resilience of grapevine varieties and rootstocks. Dashed purple arrows indicate the transfer of resilience factors through advanced plant breeding approaches.

propagation system used in grapevine breeding, which prevents the elimination of the introduced *Cas9* gene through segregation. Since transgenic grapevines are not permitted for agricultural introduction in many countries, alternative genome editing strategies are necessary. Ribonucleoprotein (RNP)-based protocols using somatic regeneration from protoplasts provide a viable solution. This approach was first demonstrated by Tricoli and Debernardi (2024) as a proof of concept, in which the knockout of phytoene synthase led to leaf bleaching. While this represents a significant advancement, further research is required to refine the methodology for stable and efficient genome editing in grapevines and their wild relatives, such as *V. sylvestris*, to accelerate the development of new climate-resilient varieties.

5 | CHALLENGES AND NEW DIRECTIONS FOR THE FUTURE

Climate change poses a multi-faceted challenge to the vine and wine sector, requiring significant advances in our understanding of the stress resistance of grapevines to develop efficient approaches to combat abiotic threats. Although considerable progress has been made, particularly in the Mediterranean region, there is an urgent need for a more comprehensive effort. A promising direction, as initiated in this review, is to develop a global network of naturally occurring *V. sylvestris* accessions adapted to different climates. This network would enhance our understanding of the genetic and phenotypic diversity within *V. sylvestris* populations and facilitate the identification and conservation of accessions with valuable traits. It would also highlight the critical role that environmental adaptation has played in the resilience of these wild accessions. This has allowed adaptive introgression into domesticated grapevines. Such germplasm resources are invaluable for developing grapevine varieties better adapted to the challenges of a changing climate. Future research should focus on in-depth functional genomic studies and extensive phenotypic screening to elucidate the responses of *V. sylvestris* to various environmental stresses. These wild germplasm resources could serve as models of adaptation mechanisms, which would help to identify specific genomic regions associated with environmental responsiveness. Such research is essential in the quest to discover key genes and understand critical pathways associated with stress tolerance. Furthermore, the adaptability of the wild grapevine *V. sylvestris* may be influenced by epigenetic plasticity, allowing these plants to respond effectively to recurrent stressors. However, there is currently limited data linking epigenetic mechanisms to abiotic stress resilience in *V. sylvestris*. Integrating epigenetic knowledge into breeding strategies offers a valuable opportunity to enhance stress tolerance in cultivated grapevines, providing powerful tools to improve crop resilience in the context of climate change. While the emphasis on epigenetics in *V. sylvestris* is promising, it is essential to address the potential limitations and challenges in translating these findings into practical applications for grapevine cultivation and breeding.

Developing new grapevine cultivars that are resilient to climate change is crucial for introducing competitive varieties. Given that grapevines are typically grafted onto rootstocks to control grape phylloxera, it is essential to incorporate novel resilience factors into these rootstocks. The next challenge is to incorporate desirable traits into the rootstocks of *V. sylvestris* in order to enhance its resilience to climate change. These traits should include resistance to grape phylloxera and nematodes, adaptability to varying pH levels, and tolerance to drought and salinity, as well as promoting the recruitment of beneficial microbes. Integrating rhizomicrobiome engineering using microbiomes derived from wild *V. sylvestris* into grapevine cultivation offers a sustainable strategy that reduces dependence on chemical inputs while promoting a holistic approach to vineyard management. By harnessing the genetic diversity of wild grapevines alongside the rich microbial diversity of their associated microbiomes, this multifaceted approach enhances grapevine immunity and vigor. The result is a more resilient root system in cultivated grapevines, ultimately supporting the longevity and sustainability of viticulture in the face of evolving environmental and biotic challenges. The omics-based technologies, including genomics, transcriptomics, metabolomics, and metagenomics, as well as advanced gene-editing techniques, will play a pivotal role in understanding the critical link between genetics and abiotic stress responses. As gene-editing technologies become more prevalent, addressing ethical concerns and complying with regulatory standards will be imperative. Ensuring that the development of climate-resilient grapevines aligns with ethical standards and regulatory guidelines is essential for fostering acceptance and sustainable implementation of these advancements in viticulture. By modeling the future generation of climate-resilient viticulture, we can pave the way for sustainable and adaptive viticulture under evolving environmental conditions (Figure 2).

AUTHOR CONTRIBUTIONS

S.D; P. N and M. G conceived and designed the review, M. G and I. B created the figures. All authors S.D; I.K; P.N; FH; A.M; M. G contributed to the writing and revision of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

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