

Review

Which American Wild Species Could Be Used in Grapevine Breeding Programs? A Review

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Abstract

Plant domestication has led to a series of morphological and physiological changes aimed at making species more suitable for human use and consumption. In *Vitis vinifera* ssp. *sativa*, these changes include increased sugar content and berry size, modifications in seed morphology, and the transition from dioecy to hermaphroditism. This process, which began approximately 6000–8000 years ago in the Transcaucasian region, unfolded in multiple stages and involved the natural abandonment of wild *Vitis* populations. While it contributed to the phenotypic diversification of modern grapevine cultivars, it also came at the expense of biodiversity. Selection for yield and quality has resulted in the loss of resilience traits in cultivated grapevines. In this study, 23 *Vitis* species of American origin were examined, analyzing for each their native range, susceptibility to biotic and abiotic stresses, and their suitability for propagation. The study, characterization, and compilation of these American *Vitis* species provide a valuable resource for consultation and use in targeted grapevine breeding programs. These efforts aim to recover adaptive traits from wild progenitors, enhance the resilience of cultivated grapevines, and address the challenges posed by modern agriculture and sustainability.

Keywords: abiotic stresses; biotic stresses; breeding; disease resistance; interspecies; PIWI; plant development; propagation aptitude; *Vitaceae*; *Vitis*



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1. Introduction

The Vitaceae family comprises 16 genera and around 950 species, predominantly distributed across tropical regions spanning Africa, Asia, the Pacific Islands, and the Neotropics [1,2], with a limited number of genera extending into temperate zones. *Vitaceae* is distinguished from other angiosperm families by its leaf-opposed tendrils, which contribute to its success as a climbing liana in diverse tropical and temperate vegetation types [1]. The grape is one of the main horticultural crops worldwide and is taxonomically classified within the genus *Vitis* [3]. Grape berries are one of the most economically valuable fruit crops. In addition to their use in the production of wine, table grapes, raisins, juices and distillates, in recent years, interest has also extended to the antioxidant properties and health benefits associated with grape products [4]. Their significance is also rooted in their long-standing connection with the evolution of human civilization. Wine, as the principal derivative of grape cultivation, held a revered status in ancient societies, often

regarded as a divine beverage and closely linked to mythological deities such as Dionysus and Bacchus [3]. Centers of *Vitis* spp. diversity are primarily located in the southeastern United States [5,6] and East Asia [7,8]. Eastern Asia—including regions such as China, Japan, and Java—harbors up to 30 native species, while two subspecies, belonging to the widely cultivated *Vitis vinifera* species, are distributed across Central Asia and Europe [9]. Additionally, up to 28 species are native to a broad area encompassing the eastern and southwestern United States as well as Mexico [9]. Knowledge of these centers of diversity is essential to understand the origins and the domestication process of grapevine.

Plant domestication is an evolutionary process, driven by human intervention, that has led thousands of plant species to diverge morphologically and genetically from their wild ancestors [10,11]. This phenomenon has affected numerous plant species, including the grapevine (*V. vinifera*), with the aim of selecting characteristics favorable to cultivation and human consumption. In the case of *V. vinifera* ssp. *sativa*, domestication has led to substantial modifications compared to the wild form *V. vinifera* ssp. *sylvestris*. Key traits selected during grapevine domestication include increased berry and cluster size, elevated sugar content, modifications in seed morphology, and a shift from a dioecious to a hermaphroditic reproductive system [3,12,13]. These changes are typical examples of the so-called ‘domestication syndrome’, a set of common phenotypic and physiological traits acquired by domesticated plant species [14]. Although these traits have favored fruit productivity and quality, they have often been accompanied by genetic bottlenecks, which have reduced the available genetic diversity and compromised resistance to biotic and abiotic stresses [12]. Artificial selection has therefore led to an unintended loss of traits originally present in wild populations. In addition to the domestication syndrome, another critical factor is vegetative propagation, which has been widely used in grapevines since the birth of their cultivation [15]. While this method of reproduction ensures the preservation of desired agronomic traits, it has blocked the adaptive evolution of the species by limiting genetic recombination and preventing the generation of new genotypes [16].

The lack of recombination and the continued preservation of old genotypes have further accentuated the vulnerability of cultivated vines to biotic and abiotic environmental changes and, thus, to the related stresses. Consequently, it is essential to promote genetic improvement strategies that involve the introgression of resistance traits from wild populations [12,17]. Environmental conditions are continuously changing, also as a result of various human activities. Among these, climate change stands out as one of the most significant and widely acknowledged drivers affecting the global distribution and incidence not only abiotic stress but also of plant diseases [18–20]. The current global changes increase the abiotic pressures on agriculture and necessitate the development of solutions to maintain crop production [21]. As described by [22], the process of adaptation consists of the formation, over generations, of new allelic combinations that give rise to genotypes that are better suited to the environment. It is well known that grapevine plants are influenced by many environmental stresses. Among these, the most significant are extreme temperatures, excessive or insufficient light exposure, waterlogging, drought, mineral deficiencies in the soil, and elevated soil salinity [23]. In the upcoming years, changes are expected in the distribution range of infectious plant diseases. As these diseases shift geographically, new interactions between abiotic and biotic factors may influence their distribution, leading to unexpected changes in plant disease risk [24–26]. Human activities have also historically played a key role in the spread and introduction of various pathogens affecting grapevines, as well as harmful insects, such as the grapevine phylloxera *Daktulosphaira vitifoliae*. Native to the northeastern United States [27,28], this insect was accidentally introduced into major European wine-growing regions via American grapevines, which had been imported to control grapevine powdery mildew (*Erysiphe necator*) [29]. Climate change is also impact-

ing grape production in terms of yield, composition, and wine quality. As a result, the geographical landscape of viticulture is shifting due to issues related to drought and other associated abiotic stress factors [30–33]. Under future climate change scenarios, particularly rising temperatures, a study by [34] projected potential increases in the pressure of the disease *Plasmopara viticola* in Italy (Europe), associated with a higher incidence of primary infections occurring in May and June. This would require the implementation of additional strategies to control the pathogen, with plant protection efforts needing to focus more heavily on early-season infections. Consequently, the costs associated with managing the disease are also expected to rise in future scenarios [34]. Similar trends have been observed in other wine-growing regions as well [35]. The impacts of infection may vary depending on the region, but in all cases, plants are expected to become more vulnerable due to abiotic stress. Under climate change scenarios, an increase in the frequency of extreme weather events is expected to negatively affect overall plant health [36]. Additionally, environmental changes are expected to exacerbate the epidemiological risk of infections caused by *Xylella fastidiosa* subsp. *fastidiosa*, the causal agent of Pierce’s disease [20]. Moreover, the association of certain pests such as the grapevine moth (*Lobesia botrana*) and rising temperatures may negatively impact crop yields due to greater asynchrony between plant growth stages and the timing of larval emergence [37]. Fortunately, this does not appear to apply to grapevine powdery mildew (*E. necator*), which, under projected climate change conditions, is expected to show a lower severity of infection in grapevine [37]. These differences in the response of pathogens to environmental changes highlight that the interactions between plants and infectious agents are the result of a long coevolution. The coevolution between plants and pathogens is an important process for maintaining plant species diversity and in the development of plant resistance [38–40]. Genetic differences in plant resistance are advantageous because they make it harder for pathogens to adapt and infect new, susceptible plants [40]. Coevolutionary interactions between plants and pathogens show a high level of variability in resistance, both among different populations and within the same population [38,41–47]. In grapevines, pathogen resistance is inherited across generations, influenced by factors such as geographic origin, species-specific traits, and the nature of host–pathogen interactions [48–50].

One of the greatest challenges facing humanity today is how to make agricultural production more sustainable in the face of climate change. The European Union (EU) has implemented various strategies, such as the European Green Deal, which represents a set of policy initiatives with ambitious goals to overcome the challenges of climate change and environmental degradation. One of the most important policy initiatives for European agriculture was the Farm-to-Fork Strategy whose objectives relate to more sustainable food production [51]. The need to develop strategies to reduce pesticide use in viticulture is linked to evidence that although vineyards occupy only about 5% of European agricultural land, they account for almost 70% of all fungicide applications in agriculture [52]. Moreover, due to the high pest sensitivity of the grapevine, 13% in mass of all synthetic pesticides used in Europe are applied in the wine industry [52]. According to EUROSTAT [53], the three largest grape- and fruit-producing countries, Spain, France and Italy, recorded around 50% of the total amount of fungicides in Europe.

The aim of this study is to analyze and characterize resistance traits in wild grapevine species, in order to assess their potential for the introgression of resistance-associated genes through breeding programs, with the ultimate goal of developing cultivars with enhanced resilience to biotic and abiotic stresses.

2. *Vitis* spp.

We review here the literature concerning 23 species distributed from North to Central America (Figure A1 in Appendix A). Despite their poor grape quality, many of them have interesting adaptive characters, such as the susceptibility to abiotic (Table 1) and biotic (Table 2) stresses and the propagation aptitude, that could be useful in future breeding programs.

Table 1. Schematic summary of all American *Vitis* species analyzed in the work in relation to their abiotic tolerances/resistances. The absence of ticks for some of the resistances does not indicate lack of resistance but only that it has not been established in the bibliography.

Species	Tolerance or Resistance to					References
	Drought	Limestone	Salinity	Heat	Cold	
<i>Vitis berlandieri</i> Planchon	x	x	x	x	x	[54–57]
<i>V. riparia</i> Michaux					x	[54]
<i>V. rupestris</i> Scheele			x			[58]
<i>V. labrusca</i> Linnaeus	x				x	[54,56–61]
<i>V. cinerea</i> Engelmann	x					[62,63]
<i>Vitis x champinii</i> Planchon	x	x	x			[64,65]
<i>V. aestivalis</i> Michaux	x			x	x	[54,66]
<i>V. arizonica</i> Engelmann	x	x			x	[65,67,68]
<i>V. californica</i> Bentham		x				[68,69]
<i>V. rotundifolia</i> Michaux						
<i>V. vulpina</i> Linnaeus						
<i>V. mustangensis</i> Buckley	x			x		[54,70,71]
<i>V. girdiana</i> Munson	x		x	x		[69,72]
<i>V. acerifolia</i> Raf.		x				[68,69]
<i>V. palmata</i> Vahl	x				x	[70]
<i>V. shuttleworthii</i> House	x		x	x		[73,74]
<i>Vitis x doaniana</i> Munson	x		x		x	[69,70]
<i>V. monticola</i> Buckley		x		x		[68,72]
<i>V. popenoei</i> Fennel					x	[70,75]
<i>V. tiliifolia</i> Humb. & Bonpl.						

Table 1. Cont.

Species	Tolerance or Resistance to					References
	Drought	Limestone	Salinity	Heat	Cold	
<i>V. blancoi</i> Munson						
<i>V. baileyana</i> Munson		x				[70]
<i>V. nesbittiana</i> Comeaux	x			x		[76–78]

Table 2. Schematic summary of all American *Vitis* species analyzed in the work in relation to their biotic tolerances/resistances. The absence of ticks for some of the resistances does not indicate lack of resistance but only that it has not been established in the bibliography.

Species	Tolerance or Resistance to							References
	<i>Plasmopora viticola</i>	<i>Erisiphe necator</i>	<i>Botrytis cinerea</i>	<i>Gaumnardia bituella</i>	<i>Daktulosphaera vitifoliae</i>	<i>Xylella fastidiosa</i>	Nematodes	
<i>Vitis berlandieri</i>	x	x			x	x		[54,79–84]
<i>V. riparia</i>	x	x			x		x	[64,76,85–89]
<i>V. rupestris</i>	x	x		x	x			[90–94]
<i>V. labrusca</i>	x	x	x				x	[54,95–101]
<i>V. cinerea</i>	x	x			x		x	[54,102–106]
<i>Vitis x champinii</i>					x	x	x	[54,64,101]
<i>V. aestivalis</i>	x	x	x	x	x	x	x	[107–115]
<i>V. arizonica</i>		x			x	x	x	[82,116–120]
<i>V. californica</i>		x			x			[114,121–123]
<i>V. rotundifolia</i>	x	x		x	x	x	x	[54,106,124–127]
<i>V. vulpina</i>					x	x	x	[128,129]
<i>V. mustangensis</i>	x	x			x	x	x	[54,73,130–132]
<i>V. girdiana</i>					x			[70,114]
<i>V. acerifolia</i>			x	x	x			[70,133]
<i>V. palmata</i>	x				x			[70,134]
<i>V. shuttleworthii</i>	x	x		x		x	x	[128,134–139]
<i>Vitis x doaniana</i>		x					x	[139,140]
<i>V. monticola</i>			x	x				[70]
<i>V. popenoei</i>	x	x				x		[75,141]
<i>V. tiliifolia</i>	x							[134]
<i>V. blancoi</i>								
<i>V. baileyana</i>								
<i>V. nesbittiana</i>						x	x	[142,143]

2.1. *Vitis berlandieri* (= *Vitis cinerea* var. *helleri* Bailey)

2.1.1. Area of Origin

Named after the French botanist Jean-Louis Berlandier, *V. berlandieri* is native to the southern regions of the United States (Edwards Plateau area, TX, USA), southern New Mexico and northern Mexico [7,54,144–146]. In the wild, this species is predominantly found in clay, dry and calcareous soils, a geographical distribution that has significantly influenced its adaptation [54,62].

2.1.2. Susceptibility to Abiotic Stresses

The species shows a remarkable capacity for thermal adaptation, tolerating both high and cold winter temperatures [79]. The deep root system gives *V. berlandieri* a relatively high tolerance to drought [146]; however, it is very susceptible to waterlogging [54]. It is one of the species that is best adapted to calcareous soils [79], distinguishing itself from other American species, which show leaf chlorosis symptoms in lime-rich soils. Furthermore, it shows good tolerance to salinity [147].

2.1.3. Susceptibility to Biotic Stresses

The species is known for its resistance to phylloxera (*D. vitifoliae*) [80,81]. It also has a fair tolerance to powdery mildew (*E. necator*), downy mildew (*P. viticola*) and Pierce's disease (*X. fastidiosa*) [54,79,82,83]. In particular, the potential of *V. berlandieri* for the development of rootstocks resistant to *X. fastidiosa* has been highlighted [84].

2.1.4. Propagation Aptitude

Vitis berlandieri is unsuitable as a rootstock in its pure form due to its poor rhizogenic aptitude, which makes propagation using both cuttings and grafting difficult. This limitation has been overcome through interspecific hybridization with species characterized by a higher rooting and grafting capacity [79,145].

2.2. *Vitis riparia*

2.2.1. Area of Origin

Also referred to as 'bank grapes', *V. riparia* is a species that mainly grows along watercourses and riverbanks. However, it can grow in a wide range of environments, provided there is sufficient water availability [76]. As a result, the plant does not require a deep root system to survive and prefers deep alluvial soils [54]. *Vitis riparia* is the most widespread wild grape species in North America, with a range extending from Canada, Manitoba and Quebec to Florida and from Texas to the Colorado Rocky Mountains [54,76,148].

2.2.2. Susceptibility to Abiotic Stresses

Vitis riparia does not tolerate calcareous soils [76] and prefers sandy, moist soils [62]. Its shallow roots make it particularly susceptible to drought, a trait that is also inherited by rootstocks obtained through crossing with other species [54,64]. However, it is highly resistant to the cold, surviving average winter temperatures as low as -40 °C. Several American species are more resistant to cold than *V. vinifera*, but none of them match the cold tolerance of *V. riparia*. Furthermore, it can tolerate root flooding for several days [54].

2.2.3. Susceptibility to Biotic Stresses

In its area of origin, *V. riparia* has co-evolved with the main grapevine pathogens, powdery mildew (*E. necator*), downy mildew (*P. viticola*) and phylloxera (*D. vitifoliae*), thus developing tolerance to these diseases [85,86,121,134,149–154]. In particular, *V. riparia*, which is native to regions where phylloxera is endemic, possesses root systems that are

naturally resistant to this pest [64,76,87,88,155]. *Vitis riparia* is resistant to parasitic nematodes, confirming its suitability as a rootstock in environments prone to such parasites [89]. Despite its resistance to numerous pathogens, *V. riparia* is susceptible to Pierce's disease [54].

2.2.4. Propagation Aptitude

Vitis riparia has played a crucial role in the history of rootstocks, directly providing ready-to-use selections for vineyards where they were already adapted, without the need for further crosses or selections between seedlings [76]. Since the 1980s, breeding programs have focused on the development of cultivars, commonly known as 'northern hybrids', that are cold- and disease-resistant and suitable for growing in the cold and moist regions of the eastern and central United States [62,156–158].

2.3. *Vitis rupestris*

2.3.1. Area of Origin

By the early 1900s, the population of *V. rupestris* was distributed throughout much of the central United States [159] and may have been introduced to other geographic areas [160]. Currently, the population of *V. rupestris* is restricted to specific habitats, with a distribution primarily concentrated in the Ozark Plateau, Missouri and Arkansas, and the Ouachita Mountains, Oklahoma [6,161].

2.3.2. Susceptibility to Abiotic Stresses

Vitis rupestris is a classic chloride excluder capable of maintaining low chloride levels in the aerial organs of the plant when grown in saline soil [147,161,162]. It can grow well in soils with a very high presence of gravel [162] and is highly resistant to salinity [55]. It is considered a species with high chill requirements [163].

2.3.3. Susceptibility to Biotic Stresses

Vitis rupestris exhibits notable tolerance to biotic stresses and has become a valuable genetic resource for breeding vine varieties resistant to diseases and pests, thereby contributing significantly to modern viticulture [156,161]. *Vitis rupestris*, used both directly as a rootstock and as a parent in the development of new rootstock hybrids, has conferred durable phylloxera (*D. vitifoliae*) tolerance to grapevines for over 150 years [90]. It is also an important source of resistance to pathogens such as black rot (*G. bidwellii*) [91], powdery mildew [92,93] and downy mildew (*P. viticola*). Alleles of the resistance locus *Rpv3* (a major determinant of downy mildew resistance) were indeed associated with *V. rupestris* in more than 50% of the 233 hybrid grape cultivars examined [94].

2.3.4. Propagation Aptitude

The rooting capacity of *V. rupestris* is notably high, and it also demonstrates a strong grafting compatibility with *V. vinifera* cultivars [164]. Additionally, studies have shown that *V. rupestris* exhibits a high level of in vitro regeneration, with somatic embryos and seedlings readily produced from anther tissues [55,165].

2.4. *Vitis labrusca*

2.4.1. Area of Origin

Vitis labrusca, also known as the "northern fox grape", is a vigorous climbing plant native to the eastern United States. Its distribution extends from Georgia to southeastern Canada, with Indiana marking the western boundary [54]. As a North American native species, it exhibits excellent adaptability to its natural environment [60]. This vine thrives in climates characterized by mild to high temperatures in spring, hot summers, and abundant rainfall throughout the year, averaging around 1700 mm annually [95].

2.4.2. Susceptibility to Abiotic Stresses

Vitis labrusca demonstrates remarkable cold resistance, as shown in several studies [54,56–60], and moderate drought tolerance [61]. The species is also adapted to acidic soils, which are preferred for cultivation [54,166,167], and, thus, it shows poor tolerance to calcareous soils. In terms of iron uptake efficiency, *V. labrusca* is similar to *V. riparia* and *V. rotundifolia*, being inefficient. This is due to its limited ability to release protons (H^+) into the soil to enhance iron solubility. However, under iron deficiency, the plant can produce organic acids to alleviate this stress [168].

2.4.3. Susceptibility to Biotic Stresses

Vitis labrusca is distinguished by its high resistance to various pathogens and pests. It is highly resistant to the fungus *B. cinerea* [96], downy mildew (*P. viticola*) [95,97–99,169–171], and powdery mildew (*E. necator*) [54,97–100,172,173]. Additionally, it shows significant resistance to the dagger nematode (*Xiphinema index*) [101]. However, it is susceptible to Pierce's disease [54]. A distinctive feature of *V. labrusca* is the presence of leaf trichomes and the constitutive and inducible expression of genes involved in the biosynthesis of terpenes, flavonoids, and phenylpropanoids. This makes it less palatable to *Popillia japonica* (Japanese beetle) compared to *V. vinifera* [60]. Furthermore, the genetic composition of *V. labrusca* provides an additional advantage in resisting herbivorous insects, demonstrating a better adaptation compared to other grapevine species [54].

2.4.4. Propagation Aptitude

Vitis labrusca has hermaphroditic flowers [167] and is known for the high rooting capacity of its cuttings, making it an ideal species for rapid and efficient propagation [174]. Native to North America, it has been utilized in breeding programs since the 1980s to create hybrids with enhanced resistance to abiotic and biotic stresses [60]. These so-called “northern hybrids” result from crosses between *V. vinifera* and wild species such as *V. labrusca*, which has contributed to improved resistance to both abiotic and biotic stresses [62,157].

2.5. *Vitis cinerea* (= *Vitis simpsonii* Munson)

2.5.1. Area of Origin

Vitis cinerea, commonly known as “possum grape,” “sweet grape,” or “pigeon grape,” is a native species primarily distributed in the southeastern United States, extending as far west as Texas. Its geographical range is concentrated along the banks of the Mississippi and Missouri rivers, where it thrives in humid environments, particularly woodlands located near watercourses [54].

2.5.2. Susceptibility to Abiotic Stresses

Vitis cinerea prefers relatively acidic soils [54], is drought-tolerant [62,63] and is particularly well adapted to warm-humid climatic conditions [175].

2.5.3. Susceptibility to Biotic Stresses

Vitis cinerea is resistant to powdery mildew (*E. necator*) [54,102] and, due to its co-evolution with the pathogen, shows complete resistance to downy mildew (*P. viticola*), like many other North American *Vitis* species, including *V. rotundifolia* and *V. riparia* [54,103]. It also possesses a high level of resistance to the nematode *Meloidogyne javanica* [104] and total resistance to phylloxera (*D. vitifoliae*) [105,106].

2.5.4. Propagation Aptitude

Vitis cinerea represents a genetic resource of considerable interest for rootstock selection, not only for its ability to confer complete resistance to phylloxera but also for its potential to

improve scion performance. This positive effect is especially evident in shallow soils, soils with high gravel content and dry conditions [176,177]. The adaptation to warm-humid climatic conditions of this species seems to be passed on to its progeny in crosses [175].

2.6. *Vitis X champinii*

2.6.1. Area of Origin

Vitis champinii is considered a natural hybrid between *V. mustangensis* and *V. rupestris*. It is native to some arid and low-rainfall regions of west-central Texas and northern Mexico, where the ranges of these two species overlap [64,65].

2.6.2. Susceptibility to Abiotic Stresses

Vitis champinii is known for its high drought tolerance [65]. Under moderate water deficit conditions, this species maintains higher stomatal conductance and photosynthesis rates than other *Vitis* species [178,179]. In addition, one study showed that *V. champinii* develops a larger canopy and a more extensive root system than other species in the genus [180]. It is also particularly tolerant to calcareous and saline soils [64].

2.6.3. Susceptibility to Biotic Stresses

Vitis champinii is resistant to phylloxera and has strong resistance to nematodes [54,64]. In particular, it is resistant to the nematode *X. index* [101] and contains a xylem sap phytochemical that hinders the development of mature biofilms by *X. fastidiosa*, significantly inhibiting colony growth compared to susceptible cultivars [181]. Although *V. champinii* does not possess the *PdR1* locus associated with resistance to *X. fastidiosa*, it has defense mechanisms that affect both the vector insect and the bacterium, including the presence of leaf trichomes [182].

2.6.4. Propagation Aptitude

Vitis champinii is known for its low rooting and grafting ability, often proving difficult to propagate [64,183]. However, the late selection of cuttings has been identified as a promising practice to increase propagation success [184]. Despite these limitations, *V. champinii* is widely used as a rootstock in vineyards and selection programs, especially in areas with high nematode concentrations or saline soils, such as the Central Valley of California and some regions of Australia [64].

2.7. *Vitis aestivalis* (= *Vitis rufotomentosa* Small)

2.7.1. Area of Origin

Vitis aestivalis is native to eastern North America and grows in dry upland areas and ravines. Its distribution extends from southern Ontario to Florida, east to Maine, and west to Oklahoma and Texas [185]. This species evolved by adapting to the sandy habitats of the Appalachian Mountains, a naturally inhospitable environment for the development of the phylloxera root form [54,79].

2.7.2. Susceptibility to Abiotic Stresses

Vitis aestivalis demonstrates remarkable adaptability to temperature extremes, showing less susceptibility to the adverse effects of high root temperatures compared to European *Vitis* species [186]. Additionally, it exhibits exceptional cold tolerance, withstanding temperatures as low as $-30\text{ }^{\circ}\text{C}$. This cold resistance is notable, even though no specific genes directly associated with this trait have been identified [54,66]. Furthermore, it shows high drought resistance and adapts well to wet and rainy summers, hence the name ‘summer grape’ [54].

2.7.3. Susceptibility to Biotic Stresses

Vitis aestivalis is highly resistant to economically important diseases such as black rot, and downy mildew [107–109] and to powdery mildew, but this resistance can be overcome by virulent isolates of the pathogen, suggesting a specific interaction between races of the fungus and resistance genes [110]. A *V. aestivalis* hybrid called ‘Norton’ also shows tolerance to Pierce’s disease [111,112]. It is resistant to phylloxera [111,113,114] and to *B. cinerea* bunch rot [109,111]. In addition, accessions of *V. aestivalis* resistant to root-knot nematodes have been identified [115].

2.7.4. Propagation Aptitude

It is a species that has difficulty propagating through dormant cuttings, with rooting rates ranging between 9.4% and 22.0% [187,188]. The propagation of *V. aestivalis* achieved a 40.9% success rate under background heat and rooting hormone treatments, with cuttings treated with indole-3-butyric acid (IBA) showing up to four times greater rooting success than untreated ones [189,190].

2.8. *Vitis arizonica*

2.8.1. Area of Origin

Vitis arizonica, also known as “Canyon grape,” is a species native to the extreme west of Texas and endemic to the American Southwest [191,192]. This region is characterized by an arid climate and a considerable variety of ecological conditions, to which the species has successfully adapted [72].

2.8.2. Susceptibility to Abiotic Stresses

Vitis arizonica exhibits high cold resistance [67]. Furthermore, this species is tolerant to lime-induced chlorosis, a condition that occurs when it is grown in calcareous soils. This tolerance, shared with other species such as *V. californica*, *V. longii*, and *V. monticola*, suggests the presence of a common protective mechanism that allows these species to mitigate stress from high soil alkalinity [68]. *Vitis arizonica* shows moderate vulnerability to xylem embolism caused by drought, but is able to repair it rapidly after irrigation, restoring water transport. This adaptation, supported by increased root pressure under water stress, allows the plant to quickly recover transpiration rates and effectively cope with drought conditions [65]. The ability of *V. arizonica* to tolerate lime-induced chlorosis and recover from drought-induced embolism suggests that it possesses adaptive traits that could be valuable for grapevine rootstock breeding programs aimed at improving tolerance to stresses in calcareous soils and drought-prone environments [65,68].

2.8.3. Susceptibility to Biotic Stresses

Vitis arizonica exhibits high resistance to infection by *X. fastidiosa* [116]. This resistance is attributed to a single dominant locus, named *PdR1*, which has been genetically and physically mapped [193–196]. Native grape phylloxera strains that form leaf galls on *V. arizonica* in Arizona and New Mexico have not been found on the roots, suggesting a possible intrinsic resistance of *V. arizonica* to root infestations, as well as the inability of the parasite to induce root galls [82,117]. Additionally, *V. arizonica* has been identified as resistant to *X. index* [118], powdery mildew (*E. necator*) [119,120] and highly resistant to anthracnose [197].

2.8.4. Propagation Aptitude

Vitis arizonica demonstrates excellent rooting ability when propagated from cuttings. In vitro studies have shown a success rate greater than 73% for *V. arizonica* cuttings, indicating effective propagation through this method [198]. Furthermore, stem cuttings,

particularly those from semi-hardwood, exhibited the highest rooting success compared to softwood or hardwood cuttings [199].

2.9. *Vitis californica*

2.9.1. Area of Origin

Vitis californica, commonly known as the California wild grape, is a species endemic to the northern Central Valley, in California [200]. It is found from the Tehachapi Mountains in the south to southern Oregon and is common in the Central Valley, extending up to about 1000 m in the Coastal Range, Sierra Nevada, Cascade, and Klamath Mountains [200].

2.9.2. Susceptibility to Abiotic Stresses

Vitis californica is categorized as a species tolerant to lime-induced chlorosis [69] when grown in calcareous soil [68]. The leaf movement of *V. californica* allows the plant to balance light absorption with the risk of thermal stress, helping to protect its photosynthetic components. This adaptive strategy prevents excessive temperatures that could reduce photosynthetic capacity and ensures optimal performance even under high-radiation and -temperature conditions [201].

2.9.3. Susceptibility to Biotic Stresses

Vitis californica did not show sufficient resistance to phylloxera, so it is not suitable for use in rootstocks [114,122,123]. *Vitis californica* does not exhibit significant resistance to powdery mildew [121]. Some *V. californica* plants were found to be highly susceptible to nematode attack (*M. incognita*) and had no relevant natural defenses [202].

2.9.4. Propagation Aptitude

Some studies state that it is possible to easily propagate *V. californica* [203].

2.10. *Vitis rotundifolia* (= *Muscadinia rotundifolia*)

2.10.1. Area of Origin

Vitis rotundifolia, commonly known as ‘Muscadine’, is a species of *Vitis* primarily associated with the southeastern United States [204]. Its natural distribution range extends from Delaware to central Florida and along the Gulf of Mexico to the eastern part of Texas [205–208]. The species also extends north along the Mississippi River to Missouri and reaches areas near the Appalachian Mountains from both the east and west [208].

2.10.2. Susceptibility to Abiotic Stresses

Vitis rotundifolia is particularly sensitive to winter freeze and lime-induced chlorosis [54]. This species prefers deep, well-drained soils and thrives in humid, shaded environments, conditions that support optimal vegetative growth [70].

2.10.3. Susceptibility to Biotic Stresses

The species *V. rotundifolia* has coevolved with the native grapevine diseases and pests of North America, developing resistance or tolerance, although variable, to numerous pathogens and pests. It is particularly resistant to downy mildew (*P. viticola*) [124,125], powdery mildew (*E. necator*) [125–127], and phylloxera (*D. vitifoliae*) [125,176]. Additionally, *V. rotundifolia* exhibits resistance to black rot, the bacterium causing Pierce’s disease, and the dagger nematode *X. index*, which transmits the grapevine fanleaf virus [54].

2.10.4. Propagation Aptitude

Vitis rotundifolia exhibits three distinct floral types: perfect hermaphrodite, staminate (male), and imperfect hermaphrodite (female) [125]. It has a chromosome set of $2n = 40$,

unlike *V. vinifera* where $2n = 38$ [209,210]. For this reason, it is generally incompatible with *Vitis* species in both flowering and grafting, but it can produce fertile hybrids with *V. rupestris*, a characteristic that enables its use in modern rootstock breeding programs [54]. This ability to generate fertile hybrids allows for the incorporation of desirable traits, such as disease resistance, into rootstock varieties, making *V. rotundifolia* an important resource for improving the resilience and productivity of grapevine cultivation.

2.11. *Vitis vulpina* (= *Vitis cordifolia* Michaux)

2.11.1. Area of Origin

Vitis vulpina is also called the 'winter grape'. Its habitat extends from Pennsylvania to Florida [211]. This species name has unfortunately been misinterpreted by many taxonomists and viticulturists over the years, but some investigations indicate that *V. vulpina* is a synonym of *V. cordifolia* [128,212], according to the International Standards of Botanical Nomenclature. Furthermore, *Vitis illex* is another minor variant of *V. vulpina* and is therefore treated as a synonym [128,159].

2.11.2. Susceptibility to Abiotic Stresses

Vitis vulpina has shown a lower response to sprouting than other species and is considered a high-chilling species, requiring more than 1000 chilling hours [163,213].

2.11.3. Susceptibility to Biotic stresses

Resistance to root-knot nematode (*Meloidogyne* spp.) has been reported in grape rootstocks with *V. vulpina* in their parentage [129]. It has been used in the past in France for breeding phylloxera-resistant rootstocks [128]. Furthermore, it may have some resistance to Pierce's disease [128].

2.11.4. Propagation Aptitude

Vitis vulpina stands out for its high competitive ability, adapting well to gaps in shrubland contexts, where it maximizes light availability and exhibits a higher propagation density compared to other *Vitis* species in undisturbed areas [214].

2.12. *Vitis mustangensis* (= *Vitis candicans* Engelmann)

2.12.1. Area of Origin

Vitis mustangensis (syn. *V. candicans*), commonly known as the 'Mustang grape', is a species native to the southern United States, particularly Texas, and northern Mexico [54,70,73,215,216]. It predominantly thrives in floodplains, on the slopes and summits of calcareous and chalk hills in southwestern Texas, as well as in the wooded ravines of the Texas black prairies. It prefers limestone-rich soils, although it grows vigorously in almost any soil type [70].

2.12.2. Susceptibility to Abiotic Stresses

Vitis mustangensis exhibits significant tolerance to drought and extreme heat but shows limited or no resistance to low temperatures [54,70,71]. However, it is vulnerable to chlorosis, a condition that frequently occurs in calcareous soils [73].

2.12.3. Susceptibility to Biotic Stresses

Vitis mustangensis shows significant resistance to numerous pathogens. It is particularly resistant to phylloxera, powdery mildew, and downy mildew. Furthermore, it appears to be capable of transferring resistance to Pierce's disease to varieties grafted onto it [54,73,217]. It is also resistant to the fungal disease caused by *Phymatotrichopsis omnivora*, the causal agent of the common root rot found in Texas, Mexico, and the southwestern United States [217].

Additionally, it has been identified as a source of resistance against the nematode *M. incognita* [130].

2.12.4. Propagation Aptitude

Rootstocks containing *V. mustangensis* may encounter some rooting difficulties depending on the associated parent [73]. Its root penetration ability is deeper than that of any other species [70]. It is very difficult to propagate by cutting and although interspecific hybridization in *Vitis* can sometimes be limited by cross-incompatibility this species shows high pollen fertility and good compatibility with other species, allowing the effective transmission of its characteristics through hybridization [70]. Other southern species, such as *V. champinii* and *V. longii*, are probably natural hybrids of *V. mustangensis*, *V. rupestris*, and other native species [90], which are known to be highly resistant to nematodes [54].

2.13. *Vitis girdiana*

2.13.1. Area of Origin

Vitis girdiana is a species endemic to Southern California [70,200]. It is found in or near springs and creeks from Baja California to the Tehachapi Mountains and from coastal areas to the desert regions of California and southern Nevada [200].

2.13.2. Susceptibility to Abiotic Stresses

Vitis girdiana has good tolerance to salt and drought [69]. This species has a highly developed palisade layer in its leaves, which are also thicker compared to other wild species of the genus *Vitis*. This makes it particularly suitable for xeric habitats [72]. Reflective leaf pubescence, as observed in the characteristically gray leaves of *V. girdiana*, could be adaptive under xeric conditions and could work in reducing leaf temperature and water loss [72].

2.13.3. Susceptibility to Biotic Stresses

Vitis girdiana did not show sufficient resistance to phylloxera [70,114].

2.14. *Vitis acerifolia* (= *Vitis longii* Prince)

2.14.1. Area of Origin

Vitis acerifolia has several synonyms including *V. longii* and *V. solonis*. It is a vigorous, small-seeded vine native to the United States on the banks of the Red River, north of Denison, Texas [70,133]. It was validly described under the name of *V. longii* [218,219].

2.14.2. Susceptibility to Abiotic Stresses

It is categorized as a tolerant species to lime-induced chlorosis [69] when grown in calcareous soil [68]. This species shows strong adaptation to calcareous soils, where it tolerates drought exceptionally well. In contrast, its performance declines markedly on deep sandy upland soils during prolonged droughts, as observed in parts of Texas [70,133].

2.14.3. Susceptibility to Biotic Stresses

Vitis acerifolia exhibits high resistance to phylloxera (*D. vitifoliae*) [70,133]. During wet seasons, young leaves of the species from the Texas Panhandle region are vulnerable to attacks by gray mold (*B. cinerea*) and anthracnose (*Elsinoë ampelina*), although the 'Microsperma' variety is not affected. In contrast, the species is minimally impacted by black rot (*G. bidwellii*), with only slight damage observed [70].

2.14.4. Propagation Aptitude

Its roots are thin, highly branched, very fibrous and deeply penetrating [70]. Its flowers show high fruit set, with abundant and viable pollen. Germination and inflorescence are

among the earliest, while defoliation is late [70]. It grows easily from cuttings. The pollen of staminate plants is highly prolific and exhibits high fertility, exerting a significant influence on trait expression in interspecific crosses. Due to its great vigor, its resistance and the ease of growth from cuttings, this species offers great incentives for hybridization [70].

2.15. *Vitis palmata* (= *Vitis rubra* Michaux)

2.15.1. Area of Origin

Also known as the ‘Cat Bird Grape’, *V. palmata* (syn. *Vitis rubra*) discovered by Michaux, it is native to the Illinois region near Chicago and near the Illinois River, a tributary of the Mississippi [70,220].

2.15.2. Susceptibility to Abiotic Stresses

Vitis palmata has a very compact leaf mesophyll to optimize gas exchange and water management [72]. Moderately branched and climbing, it can grow in shallow soils [70], and it is resistant to cold and drought when it is well-rooted. It prefers argillaceous, alluvial, moist bottomlands [70].

2.15.3. Susceptibility to Biotic Stresses

It is resistant to phylloxera and is free from all major diseases [70] and it is considered resistant to downy mildew [134].

2.15.4. Propagation Aptitude

Its roots are rather thick, abundant, hard and penetrating. Germination and inflorescence are very late, and in the first years of growth, it is structurally [54].

2.16. *Vitis shuttleworthii* (= *Vitis coriacea* Planchon)

2.16.1. Area of Origin

Vitis shuttleworthii is a species native to the southeast United States [135,221].

2.16.2. Susceptibility to Abiotic Stresses

It is well suited for cultivation in tropical and subtropical regions thanks to its adaptation to environmental stresses such as soil salinity [73,74].

2.16.3. Susceptibility to Biotic Stresses

This species has been useful in developing rootstock cultivars with resistance to Pierce’s disease and nematodes [128]. In particular, it is considered one of the most resistant to Pierce’s disease and has long been used to develop grape varieties resistant to severely infected areas [135–137]. This species also shows resistance to downy mildew [134,138], black rot [135] and anthracnose [138]. Most accessions of *V. shuttleworthii* can be characterized as moderately resistant to powdery mildew [139]. The grapes of this vine exhibit resistance to *Colletotrichum acutatum* [222].

2.17. *Vitis X doaniana*

2.17.1. Area of Origin

Vitis doaniana (Doan’s Grape) is a hybrid grape resulting from the natural hybridization of *V. mustangensis* with *V. acerifolia*. Its native range includes Oklahoma, Colorado, Texas and New Mexico [70,216].

2.17.2. Susceptibility to Abiotic Stresses

Vitis doaniana exhibits good tolerance to salt and drought, with excellent chloride exclusion, and demonstrates great hardiness in enduring cold and drought, making it one of the best species for dry climates [69,70].

2.17.3. Susceptibility to Biotic Stresses

Some accessions of *V. doaniana* are considered moderately resistant to powdery mildew [139]. In some experiments on grapevine resistance to nematodes it was found that *V. doaniana* may have intrinsic resistance to damage caused by nematodes, making it one of the most promising varieties [140].

2.18. *Vitis monticola*

2.18.1. Area of Origin

Vitis monticola is a vine species endemic to the Edwards Plateau of central Texas [70,221].

2.18.2. Susceptibility to Abiotic Stresses

It is classified as a tolerant species to lime-induced chlorosis when grown in calcareous soils [68]. It can grow in shallow soil [70], and it is considered a xeric species due to its sclerophytic leaves [223], which have smaller but more numerous vascular bundles than those of mesophytic species. In addition, reflective leaf pubescence aids heat dissipation and reduces water loss [72].

2.18.3. Susceptibility to Biotic Stresses

This vine is highly disease-resistant and therefore always appears healthy. Its foliage resists gray mold (*B. cinerea*) well and the fruit is free from black rot [70].

2.18.4. Propagation Aptitude

The cuttings root with some difficulty, but a little more easily than those of *V. berlandieri*. Hybrids containing this *Vitis* species are excellent for grafting because of their vigor and strength [70].

2.19. *Vitis popenoei* (*Muscadinia* subgenus)

2.19.1. Area of Origin

Vitis popenoei is a relatively unknown species. It is native to Central America, with its distribution range extending from eastern Maryland to Texas and southward to the Gulf Coast [54]. It is adapted to specific climatic conditions, with a distribution range that extends several hundred kilometers further south than that of the other two known species of the subgenus *Muscadinia*, *V. rotundifolia* and *V. munsoniana* [224].

2.19.2. Susceptibility to Abiotic Stresses

Vitis popenoei grows in environments characterized by humid climate [225]. However, the primary limitation to its geographic distribution is its sensitivity to cold. Regions where minimum winter temperatures consistently drop to -18°C are considered unsuitable for its cultivation [75].

2.19.3. Susceptibility to Biotic Stresses

Vitis popenoei shows natural resistance to Pierce's disease (*X. fastidiosa*) [141]. Like other species belonging to the *Muscadinia* subgenus, such as *V. rotundifolia* and *V. munsoniana*, it is also resistant to many other pathogens, including grapevine downy mildew (*P. viticola*) and powdery mildew (*E. necator*) [75].

2.20. *Vitis tiliifolia*

2.20.1. Area of Origin

The wild grapevine *V. tiliifolia* is widely distributed in the southern regions of Mexico and the Antilles, with its range extending to Colombia [226,227].

2.20.2. Susceptibility to Biotic Stresses

Vitis tiliifolia exhibits moderate resistance to *P. viticola*, the causal agent of downy mildew [134].

2.21. *Vitis blancoi*

2.21.1. Area of Origin

Vitis blancoi grows along waterways in the Sierra Madre mountains in the state of Jalisco, near the city of Guadalajara, and also near Montemorelos, Nuevo Leon state, in Mexico [70].

2.21.2. Susceptibility to Abiotic Stresses

It appears to be very susceptible to spring frosts because just 8–10 degrees of frost are enough to destroy the vitality of the vine above the ground [70].

2.21.3. Propagation Aptitude

This vine is easily propagated and grows by cuttings [70].

2.22. *Vitis baileyana*

2.22.1. Area of Origin

This species, also known as the ‘Wild ‘Grape Possum,’ has been observed along the Kanawha River near Kanawha Falls, as well as in the North Carolina area [70].

2.22.2. Susceptibility to Abiotic Stresses

Vitis baileyana grows well along mountain streams at altitudes up to 900 m (about 3000 feet). It grows well on calcareous clay soils [70].

2.22.3. Susceptibility to Biotic Stresses

Some specimens of *V. baileyana* were observed with the presence of phylloxera galls on the leaves, but in general, they were in good health [70].

2.23. *Vitis nesbittiana*

2.23.1. Area of Origin

Vitis nesbittiana is a species native to central Mexico, discovered in 1987 by Comeaux, and found in tropical rainforests near Jalapa, Veracruz, at elevations between 1700 and 2120 m [228].

2.23.2. Susceptibility to Abiotic Stresses

Vitis nesbittiana being native to mountainous areas, it can be used as a rootstock for its ability to develop in tropical climates [76–78].

2.23.3. Susceptibility to Biotic Stresses

In some experiments, some resistance to Pierce’s disease has been observed [142]. In addition, some resistance to root-knot nematodes (*Meloidogyne* spp.) was also observed in seedlings hybridized with *V. nesbittiana* in other experiments [143].

3. Conclusions

The development of hybrid varieties, thanks to their tolerance to diseases and insects, could be the most promising tool for low-input, low-cost and time-saving viticulture [132,229], especially in the context of global climate change, which has significant implications for food security and agricultural sustainability, affecting crop growth and overall productivity [230–233]. All around the world, *Vitis* germplasm repositories represent a valuable resource for discovering and introducing new sources of resistance [169]. Compared to domesticated cultivars, wild crop relatives exhibit greater resilience to the impacts of global climate change and possess a stronger capacity to adapt to challenging environmental conditions [234]. Wild species within the *Vitis* genus represent valuable genetic resources for breeding programs, offering traits such as resistance to both biotic and abiotic stresses [235–238]. It is well known how interspecific gene flow has contributed to the origin of crop plants, to the restoration of crop diversity after domestication or genetic erosion and to the adaptation to challenging environments [239]. Plant protection treatments can be reduced by up to 75% without compromising grape health [240]. In recent years, due to the increasingly evident effects of global climate change, the importance of developing new grapevine genotypes capable of effectively adapting to abiotic stresses has grown. Many of the current programs aim to ensure sustainable viticulture through genetic improvement and the introduction of resistance-related genes present in wild grapevine species, obtained through interspecific crosses [241]. The responses of vines to extreme temperatures, drought, heavy metals, and other environmental stresses are the focus of numerous scientific studies, with a clear goal: to create new hybrids that are more resilient and better suited to the challenges of climate change [22]. Our analysis of the scientific literature highlights that within the genetic pool of American *Vitis* species, there are highly valuable traits of resistance to both biotic and abiotic stresses, which could play a pivotal role in modern grapevine breeding programs. A central step in these programs has always been the selection of suitable parents for resistance transfer. For this reason, considering the resistance or susceptibility traits of each American wild species is of fundamental importance.

Among the species considered, *V. aestivalis* emerges as one of the most promising for resistance to multiple biotic stresses, including *P. viticola*, *E. necator*, *B. cinerea*, *G. bidwellii*, *D. vitifoliae*, *X. fastidiosa*, and nematodes. Similarly, *V. rotundifolia* shows a broad spectrum of resistance to most of these pathogens, with the exception of *B. cinerea*. Other species such as *V. berlandieri*, *V. riparia*, *V. rupestris*, *V. labrusca*, *V. cinerea*, and *V. shuttleworthii* also exhibit interesting resistance patterns, particularly against downy and powdery mildew, which remain major diseases in viticulture. In addition, specific resistance genes such as *PdR1* in *V. arizonica* highlight the importance of focusing on single loci, even when the overall resistance of the species is not extended to other factors.

With regard to abiotic stresses, the potential of wild species is strongly linked to their geographical origin and environmental adaptation. *Vitis berlandieri* is particularly valuable for its tolerance to drought and low temperatures, while *V. aestivalis*, *V. mustangensis*, *V. girdiana*, and *V. shuttleworthii* show high levels of adaptation to heat and water scarcity, making them especially relevant for breeding programs in warm and arid viticultural regions.

Overall, the integration of these wild species into modern breeding strategies will enable the development of new grapevine cultivars capable of withstanding both biotic and abiotic pressures, ensuring sustainable viticulture in the face of global climate change. However, a recurrent limitation concerns the accessibility of genetic material for breeding. Although ex situ germplasm collections represent an important reservoir of diversity, their establishment and maintenance are costly and often limited in scope. Even more critical are the barriers related to the exchange of plant material (cuttings, seeds, pollen), which are increasingly subject to phytosanitary regulations and quarantine requirements. While such

measures are justified to prevent the spread of pests and diseases, they significantly slow down the circulation of genetic resources and consequently delay breeding progress.

In addition, further challenges arise in the process of transferring resistance. On the one hand, the traceability of resistance genes is often problematic since the loci responsible are not always known or may fail to be effectively transmitted to progenies. On the other hand, many resistance traits do not depend on a single gene but result from complex interactions among multiple genes and physiological mechanisms. As a consequence, it is possible that a plant carrying a known resistance gene does not actually express effective resistance under natural conditions. For this reason, it is essential to complement genetic approaches with direct inoculation tests with pathogens and physiological evaluations on candidate plants, in order to validate resistance traits before their integration into breeding programs.

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Appendix A



Figure A1. Geographic distribution of American *Vitis* species. The map shows the main regions of origin of wild grapevine (Google Earth, 2025).

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