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Review Article

Rootstocks for Grapevines Now and into the Future: Selection of Rootstocks Based on Drought Tolerance, Soil Nutrient Availability, and Soil pH

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Rootstocks are used in viticulture to manage plant pests and diseases, particularly phylloxera and root-knot nematodes, and to improve grape and wine production. A wide range of rootstocks are commercially available, making selecting the optimal rootstock a difficult decision. In particular, distinct rootstock genotypes may manifest varying degrees of tolerance or resistance to abiotic stress, necessitating meticulous consideration during the rootstock selection process. This article reviews characteristics of various commercial rootstocks, as well as rootstocks being developed in recent years. This review further discusses responses of rootstocks to drought, soil nutrients, and soil pH. This review mainly focuses on influence of rootstocks on physiology characteristics of grafted scions rather than berry yield and quality. The breadth of this review benefits both researchers and practitioners by providing comprehensive summery of rootstocks to inform selection and to guide future research.

1. Introduction

Rootstocks have been developed and utilised in viticulture since the late 19th century. A wide range of rootstocks have been developed through the crossbreeding of different *Vitis* species, with a particular emphasis on phylloxera-resistant American *Vitis* species. The demand for grapevine rootstocks has driven advancements in grafting and breeding technologies.

Research has revealed that rootstocks serve not only as a tool for pest and disease management but also as a crucial means to enhance grape quality by effectively managing abiotic stresses, notably drought and salinity tolerance [1–3]. Grapevine varieties used in wine production, as well as fresh and dried grapes, are predominantly of the *V. vinifera* species. Traditionally, grapevines grown on their own roots are susceptible to drought conditions and tend to accumulate salt when exposed to drought-induced saline stress [4–6]. This susceptibility can lead to reduced yields and alterations in berry biochemical composition, negatively impacting the sensory profile of wine [7].

Grafting grapevine scions onto various rootstocks (e.g., Paulsen 1103 and Ruggeri 140) can modify the root system structure [8], maximizing root surface contact with the soil and enhancing water absorption from deeper soil layers, thereby increasing drought tolerance [8]. Additionally, certain rootstocks (e.g., M4) contribute to the drought tolerance of grafted grapevines by maintaining higher stomatal conductance and photosynthesis rates, likely due to their ability to regulate abscisic acid (ABA) signalling [9]. These rootstocks are frequently employed to mitigate the impact of drought and saline stress.

Research on rootstocks has revealed that grafting scions onto rootstocks can influence nutrient uptake. The content of various nutrients in the scion, such as potassium (K), magnesium (Mg), and zinc (Zn), as well as the extent of

metal chlorosis and toxicity caused by extreme soil pH, can be affected by the choice of rootstock [10–12]. However, the regulatory effects of rootstocks on nutrient uptake depend not only on the type of rootstocks used but also on the specific type of scions grafted. In recent years, with the advancement of genomic sequencing technologies, an increasing number of studies have investigated nutrient uptake in grapevines through molecular-based research [13–15]. Consequently, a wide range of candidate genes encoding nutrient absorption and translocation have been identified, enhancing our understanding of how rootstocks contribute to nutrient uptake in grafted vines under different soil conditions. Nevertheless, as of now, the mechanisms responsible for the regulation of nutrient uptake by grapevine rootstocks remain not fully understood.

A main challenge with using rootstocks is that different rootstocks exhibit different adaptability to a given environment. This makes it difficult for grape growers to select the right rootstock for their own purpose. This article summarises the origin, characteristics, and benefits of existing and new rootstocks. Further, this article reviews pivotal characteristics inherent to divergent rootstocks affecting the selection of rootstocks in viticulture practice. These attributes encompass the drought tolerance, nutrient uptake capacity, and pH tolerance.

2. Main Parent Species for Rootstock Breeding and Existing Types of Rootstocks

2.1. Main Vitis Species for Rootstock Breeding. Nine *Vitis* species (Table 1) are commonly used for grapevine rootstock breeding, including *V. vinifera* from Eurasia and seven species from North America.

Originated in Eurasia, *V. vinifera* is the most cultivated winegrape species globally. Own-rooted *V. vinifera* have been planted for centuries, where its moderate vigour and high surviving rate in alkaline soil condition make it suitable for most grape-growing regions around the world [32, 33]. Nevertheless, its limited tolerance to phylloxera (*Daktulosphaira vitifoliae*) and a broad spectrum of nematodes, including root-knot nematodes (*Meloidogyne incognita*, *M. arenaria*, *M. hapla*, and *M. javanica*), as well as dagger nematode caused by *Xiphinema index*, has emerged as primary concerns within the field of viticulture as previously reviewed by other researchers [28]. Furthermore, the majority of *V. vinifera* varieties are susceptible to infection by grapevine fanleaf virus, a soilborne *Nepovirus* transmitted by the dagger nematode (*X. index*) that could cause fanleaf disease [34].

Common American *Vitis* species, particularly *V. rupestris*, *V. riparia*, and *V. berlandieri*, could either exhibit phylloxera resistance (preventing the formation of root gall and avoiding the development of phylloxera to the instar stage) or show relatively high tolerance to phylloxera infestation (mitigating the negative influences of infestation such as leaf yellowing, stunted growth, and reduction in fruit production). The mechanisms underlying phylloxera resistance within these species, such as the regulation of polyphenol oxidation and the formation of a corky layer surrounding phylloxera feeding sites, have been comprehensively reviewed in prior studies [35]. The limitations of these American *Vitis* species have been well reviewed previously, where both own-rooted *V. rupestris* and *V. riparia* tend to show low to moderate tolerance to calcareous soils and are prone to be influenced by lime-induced chlorosis [28]. Furthermore, *V. riparia* which originally inhabited near riverbank or areas with continual access to water exhibits low tolerance to drought [28]. That limited the application of *V. riparia* in dry climates. To cope with these issues, crossbreeding between different species of *Vitis* has been conducted. To date, numerous rootstocks with selected traits from parent species have been developed, while only a few of them have been well investigated and eventually become commercially available.

2.2. Developing Commercial Rootstocks by Crossbreeding. Crossbreeding between *Vitis* species is the predominant method to develop grapevine rootstocks. To date, a diverse array of hybrid rootstocks is used in commercial vineyards worldwide to withstand biotic and abiotic stress (Figure 1). For instance, several rootstocks that share the common parentage of *V. vinifera*, such as Fercal and Georgikon 28, exhibit and have inherited attributes of low to moderate vigour, coupled with exceptional tolerance to alkaline soils [10]. On the contrary, a wide range of *V. berlandieri* × *V. riparia* hybrid rootstocks, including Kober 5BB, SO4, and Teleki 5C, inherited moderate to high vigour but less tolerance to soil alkalinity from their *V. berlandieri* parentage [12]. Several *V. berlandieri* × *V. rupestris* hybrids, such as Paulsen 1103, Richter 99, and Ruggeri 140, also exhibit relatively high vigour with deeply developed root system, supporting them to survive extreme heat, drought, and saline stress [8, 36]. Similarly, several *V. champinii* rootstocks, such as Ramsey, have exhibited high vigour. In fact, 1-year-old Sultana vines grafted onto Ramsey have demonstrated the development of luxuriant shoots and the ability to maintain high yields even under saline stress conditions of up to 3.50 dS/m, in contrast to ungrafted Sultana vines [5]. Moreover, previous research has indicated that the adoption of Ramsey rootstocks can significantly boost the yields of grafted scions. Over a two-year observation period, it was observed that the yield of both Chardonnay and Shiraz grapes grafted onto Ramsey was approximately 50% higher compared to those grown on their own roots when the vines reached 5 years of age [37]. Another *V. champinii* rootstock, named Dog Ridge, displays remarkable vigour [38]. Dog Ridge effectively enhances the productivity of grafted scions, as demonstrated by a one-year observation showing an approximate 20% increase in the yields of Thompson Seedless, Flame Seedless, and Kishmish Chorni grapes (the age of the vines was not specified) when grafted onto Dog Ridge compared to vines grown on their own roots [39]. Oppositely, a few rootstocks, such as 101-14 Millardet et de Grasset (101-14 Mgt), 3309 Couderc (3309C), and Schwarzmann, come from crossbreeding between *V. riparia* and *V. rupestris*. These rootstocks generally exhibit low to moderate vigour and poor root development [40, 41]. Hence, they tend to be susceptible to water stress and should be used in mild climate with sufficient precipitation.

Table 1: Characteristics of the principal *Vitis* species used for rootstock breeding.

Species	Origin	Features	References
V. acerifolia	North America	(i) Medium to high vigour (ii) Moderately tolerant to drought	[16, 17]
V. berlandieri	North America	(i) High vigour with strong roots (ii) Commonly used to breed rootstocks tolerant to drought (iii) Suitable for alkaline soil	[16, 18, 19]
V. candicans (*V. mustangensis*)	North America	(i) A candidate for breeding high vigour rootstocks (ii) Moderately tolerant to drought (iii) Resistant to root-knot nematodes *Meloidogyne incognita*	[17, 20, 21]
V. champinii	North America	(i) A natural hybridization of *V. candicans* and *V. rupestris* (ii) High vigour (iii) Very tolerant to drought (iv) Suitable for hot climate (v) Enhances potassium uptake (vi) Resistant to drought and saline (vii) Resistant to phylloxera and nematodes	[17, 22, 23]
V. labrusca	North America	(i) High vigour (ii) Suitable for both hot and cool climate with adequate precipitation (iii) Enhances the accumulation of phenolic compounds in berries and contributes to antioxidant activity (iv) Being used to develop rootstock that can improve volatile composition (especially esters) of berry (e.g., Beta, a *V. labrusca* × *V. vinifera* rootstock)	[24–27]
V. riparia	North America	(i) Low to medium vigour with less root penetration compared to *V. rupestris* (ii) Susceptible to drought (iii) Suitable for cool climate (iv) Commonly used to breed rootstocks tolerant to phylloxera (e.g., Hungarian phylloxera strain H3G)	[16, 17, 28–31]
V. rupestris	North America	(i) Originally inhabited in sand and gravel (ii) High vigour with well-developed root system (iii) Moderate to high tolerance to drought (iv) Not suitable for growing in alkaline soil	[16, 17, 28]
V. acerifolia	North America	(i) Medium to high vigour (ii) Moderately tolerant to drought	[16, 30]
V. vinifera	Eurasia	(i) Moderate vigour (ii) Resistant to alkaline soil	[28, 32, 33]

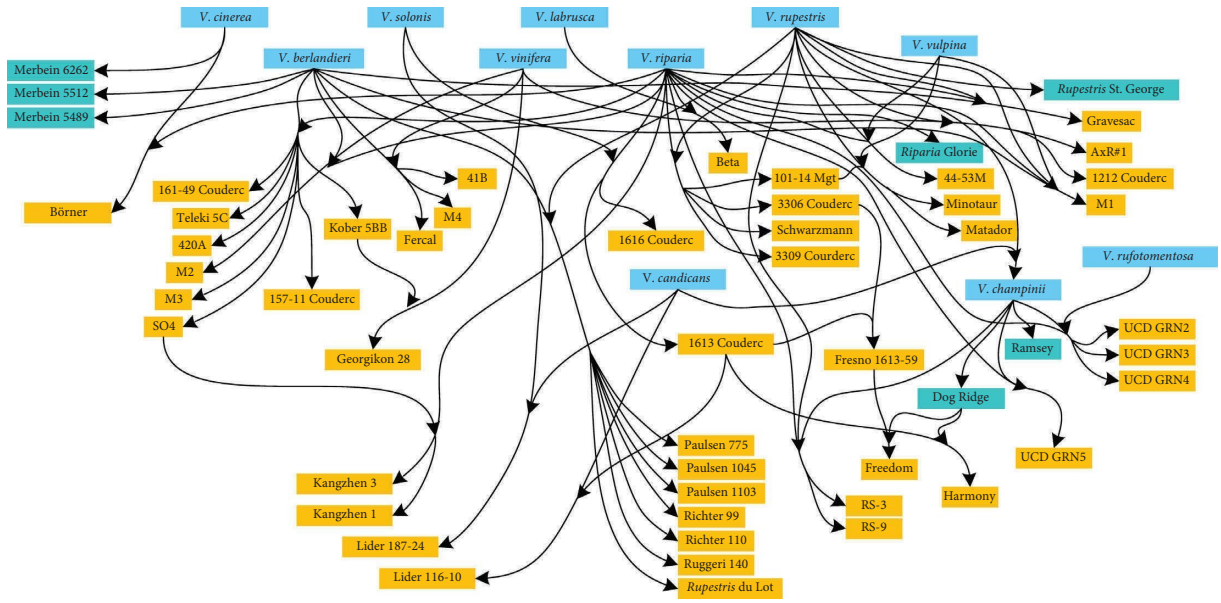

FIGURE 1: Parentage of common commercial rootstocks. Rootstocks with light blue background (■) are parent species; rootstocks with cyan background (■) are obtained from intraspecies crossbreeding; rootstocks with orange background (■) are obtained from cross-species breeding.

Overall, different genotypes of rootstocks are designed via crossbreeding, and the attributes inherent in these rootstocks are notably shaped by the genetic lineage inherited from their parent species. Various rootstocks are currently implemented in viticulture for catering to different grape varieties, climate, and soil conditions, as well as pest and pathogen defence due to their variance in vigour, phenology performance, and tolerance to abiotic and biotic stress.

2.3. New Rootstocks. Over the past 10 years, a few new rootstocks have been developed with the aim of conquering either abiotic stress or biotic stress (Table 2). Most of these rootstocks have been examined under experimental conditions and are not in widespread commercial usage.

Several rootstocks are designed for conferring pest resistance to grapevine using different parental species. For instance, one of rootstocks belonging to C series, named C20, has been proven to be resistant to common genotypes of phylloxera (G1 and G4) detected in Australia [42]. Meanwhile, it has also been reported to show resistance to root-knot nematode *M. javanica* [42]. Similarly, five GRN rootstocks developed by University of California, Davis (UCD), have been proven to possess resistance to nematode, where formation of root tip gall or existence of egg was not detected 3 months after exposure to dagger nematode (*Xiphinema index*) and root-knot nematode (*M. incognita* and *M. arenaria*) [47]. Among these rootstocks, cross-genus hybrid UCD GRN1 (*V. rupestris* × *Muscadinia rotundifolia*) stands out with additional resistance to ring nematode (*Mesocriconema xenoplax*) and citrus nematode (*Tylenchulus semipenetrans*) [47]. Several RS series rootstocks were developed by Agricultural Research Service, United States Department of Agriculture (USDA ARS), and University of California, Riverside (UCR), to prevent nematode infestation. For instance, both USDA RS-3 (*V. champinii* × (*V. riparia* × *V. rupestris*)) and USDA RS-9 (*V. champinii* × (*V. riparia* × *V. rupestris*)) rootstocks showed resistance to *M. incognita* and *M. javanica* [47, 48]. Similarly, Demko 10-17A (Edna × *V. simpsonii*) introduced by the United States Department of Agriculture (USDA) exhibited resistance to root-knot nematode (*M. arenaria*) and citrus nematode (*T. semipenetrans*) in previous studies [47, 49].

Other newly developed rootstocks are mainly designed for adapting specific type of climate and soil conditions. For example, M1, M3, and M4 rootstocks were recently developed in Italy for application in typical Mediterranean climates and they have low to moderate vigour with high tolerance to drought and heat [44, 45]. These M series rootstocks also show good nutrient uptake ability. Previous studies found that M1 exhibited high calcium and boron uptake efficiency, while M2 could increase petiole nitrogen, potassium, and magnesium content of the grafted Cabernet Sauvignon [45, 46].

These breeding efforts possess enormous potential in adapting to current challenges including spread of pests and diseases, adaptation to abiotic stress, and plantation in new grape-growing regions with problematic soil and environmental conditions. Nevertheless, with relatively young age of these rootstocks, the physiologicalcharacteristics of them have not been fully unveiled. Continuous studies are needed to further evaluate the physiology performance, influence on berry/wine quality, and durability of these newly developed rootstocks before they can be released to viticulture industry.

3. Drought Tolerance of Rootstocks

Drought has been considered as a major issue threatening the growth of grapevine. In a short term of drought, high evapotranspiration and low soil water availability can

Table 2: Newly developed rootstocks.

Rootstocks	Origin	Pedigree	Features	References
C series				
C20	Australia	*V. champinii* × *V. rupestris* × *V. riparia*	(i) Moderate vigour (ii) Performs well in hot climate (iii) Resistant to phylloxera genotype G1 and G4* (iv) Resistant to root-knot nematode *M. javanica* (v) Tolerant to saline stress	[42, 43]
C113		*V. champinii* × *V. cinerea*	(i) Moderate to high vigour (ii) Good productivity (iii) Tolerant to saline stress (iv) Susceptible to phylloxera genotype G1 and G4*	
C114		*V. champinii* × *V. berlandieri*	(i) High vigour (ii) Performs well in hot and dry climate (iii) High productivity (iv) Maintains high yield under deficit irrigation (v) Resistant to phylloxera genotype G1 and G4* (vi) Resistant to root-knot nematode *M. javanica* (vii) Tolerant to saline stress	
FB01, Zamor 17, and SZF10				
FB01	Hungary	(*V. riparia* × *V. cinerea*) × (*V. vinifera* × *V. berlandieri*)	(i) High vigour (ii) Adequate phosphorus, potassium, and calcium uptake (iii) Tolerant to soil lime and acidity	[10]
Zamor 17		(*V. riparia* × *V. berlandieri*) × *V. rupestris*	(i) Low vigour (ii) Susceptible to soil lime and acidity	
SZF10		(*V. riparia* × *V. berlandieri* × *V. vinifera*) × (*V. riparia* × *V. cinerea*)	(i) Moderate vigour (ii) Moderately tolerant to soil lime and acidity (iii) Good magnesium uptake	
M series				
M1	Italy	[*V. riparia* × (*V. vulpina* × *V. rupestris*)] × *V. berlandieri*	(i) Moderate to high vigour (ii) Good phosphorus, potassium, and calcium uptake (iii) Resistant to iron chlorosis	[44–46]
M2		(*V. berlandieri* × *V. riparia*) × (*V. vinifera* × *V. berlandieri*)	(i) Good potassium and magnesium uptake ability (ii) Resistant to iron chlorosis	
M3		(*V. berlandieri* × *V. riparia*) × (*V. Berlandieri* × *V. riparia*)	(i) Low to moderate vigour (ii) Tolerant to heat and drought	
M4		(*V. vinifera* × *V. berlandieri*) × *V. berlandieri*	(i) Resistant to drought (ii) Resistant to soil salinity	

Table 2: Continued.

Rootstocks	Origin	Pedigree	Features	References
UCD GRN series				
UCD GRN1	United States	*V. rupestris* × *Muscadinia rotundifolia*	(i) Resistant to root-knot nematode (*M. incognita* and *M. arenaria*), dagger nematode (*X. index*), ring nematode (*M. xenoplax*), and citrus nematode (*T. semipenetrans*)	[47]
UCD GRN2		*V. rufotomentosa* × *V. champinii* × *V. riparia*		
UCD GRN3		*V. rufotomentosa* × *V. champinii* × *V. riparia*	(i) Resistant to root-knot nematode (*M. incognita* and *M. arenaria*) and dagger nematode (*Xiphinema index*)	
UCD GRN4		*V. rufotomentosa* × *V. champinii* × *V. riparia*		
UCD GRN5		*V. champinii* × *V. riparia*		
RS series				
RS-3	United States	*V. champinii* × (*V. riparia* × *V. rupestris*)	(i) Moderate to high vigour (ii) Resistant to root-knot nematode (*M. incognita* and *M. javanica*)	[47, 48]
RS-9			(iii) Low vigour (iv) Resistant to root-knot nematode (*M. incognita*, *M. javanica*, and *M. arenaria*)	
USDA rootstock				
Demko 10-17A	United States	Edna (America × Malaga) × *V. simpsonii*	(i) Resistant to root-knot nematode (*M. incognita*, *M. javanica*, and *M. arenaria*), citrus nematode (*T. semipenetrans*), and root lesion nematode (*Pratylenchus vulnus*)	[47, 49]

*Definition of *D. vitifoliae* genotypes based on the pattern of DNA fragment sizes at 4 specific microsatellite loci identified by a previous study [50].

significantly alter plant physiology, nutrition, and metabolism [51]. For example, the cell metabolism of the plant will be affected, leading to elevated reactive oxygen species (ROS) production, which causes oxidative damage of lipids, proteins, and nucleic acids [52]. In a long term of drought, consistently low water availability in soil will affect the efficiency of leaching salt from soil and lead to increased saline stress. Grapevine leaves are unable to maintain high osmotic potential when exposed to extreme saline stress induced by drought, resulting in reduction in leaf water content and increase in the production of active O_2 species (AOS) including superoxide, hydrogen peroxides, and hydroxyl radicals [53, 54]. This can further influence leaf cell function of grapevine, resulting in decreased cell division and attenuated cell expansion and eventually declined plant growth [55, 56]. Plants have developed an osmotic adjustment system to maintain water absorption from soil to root in response to water deficiency, through the accumulation of organic osmolytes such as sugars and quaternary ammonium compounds [54]. This activity is regulated by several endogenous hormones, such as ABA and methyl jasmonate [57]. Own-rooted *V. vinifera* grapevines (e.g., Cabernet Sauvignon) regulated ABA synthesis and signalling differently compared to vines grafted to rootstocks [9].

Adaption of rootstock has become common to alleviate the issues of drought in vineyards, and different rootstocks have different capacities in drought tolerance (Table 3). For example, several rootstocks including Ramsey, Richter 110, and Ruggeri 140 are drought tolerant, while rootstocks such as 101-14 Mgt and Schwarzmann are highly susceptible to drought [58, 59].

The drought tolerance capacity of rootstocks can be attributed to the root depth and architecture. For example, *V. vinifera* Merlot grafted to both Ramsey and Richter 110 could develop roots sharply angled to soil surface (>30° at each root intersection) under drought condition (completely nonirrigated for 1 week) [58]. This allows increased contact between root tissues and soil and therefore improves water absorption ability [58]. Similarly, the vertically developed root structure of Paulsen 1103 and Ruggeri 140 has been previously observed. Grafting both Nerello Mascalese and Nero d'Avola scions onto these rootstocks significantly increases the number of roots and total root mass in midlevel and deep soil layers (61–100 cm) compared to ungrafted vines [8]. The vertically distributed root system of Paulsen 1103 and Ruggeri 140 facilitates the grafted vine's ability to access water and nutrient resources from deeper soil layers, thereby enhancing its tolerance to water deficiency [8, 66]. Another drought-resistant rootstock, SO4, exhibits alterations in its root architecture in response to salinity. A previous study documented a mortality of thick roots (diameter >1 mm) induced by 30 mM NaCl in ungrafted SO4 vines. This resulted in a significantly increased proportion of thin roots (diameter <1 mm) compared to ungrafted Paulsen 1103 and Richter 110 [67]. Consequently, this led to a larger surface area of the root system, optimizing root-soil contact and benefiting the plant's ability to cope with salt stress by enhancing the absorption of water and nutrients [67, 68]. Additionally, an increase in specific root area (the ratio of root surface area to root dry mass) has been identified as a response of the root system to drought. Specific root area was determined by root length, the density of root tissue, and the diameter of the root cross section, where thin roots combined with low tissue density could typically result in high specific root area [67]. SO4 rootstock demonstrates an increase in specific root area when exposed to 30 mM NaCl, primarily due to a significant reduction in both root diameter and tissue density [67], where the increase in specific root area of SO4 in response to saline stress could limit the metabolic activity required for the formation and maintenance of root system, allowing efficient root development with defined metabolic cost [69].

The mechanism of rootstock tolerating drought is also closely related to plant hormones. Previous studies suggested that ABA biosynthesis can be a critical drought tolerance biomarker in grapevines. Increased transcript levels of ABA-related genes such as *Nine-Cis-Epoxycarotenoid Dioxygenase 3* (*NCED3*) and *NCED5* in the roots of ungrafted Ramsey after two weeks of water stress (50% relative soil water content at field capacity) have been observed previously [61], which contribute to drought tolerance of grapevines by maintaining higher stomatal conductance and photosynthesis rate [70]. Meanwhile, ABA perception is mediated by soluble ABA receptors named pyrabactin resistance/pyrabactin resistance-like/regulatory components of ABA receptors (PYR/PYL/RCAR), which are ABA-binding proteins. The structure of PYR/PYL/RCAR protein will change slightly after binding with ABA, which further provides a platform for ABA to interact with the ABA signalling proteins, such as ABI1 and ABI2 [71]. Relative expression of *RCAR* genes including *RCAR1*, *RCAR3*, and *RCAR6* was considerably higher in the roots of ungrafted drought-tolerant Ramsey rootstocks compared to that of drought-susceptible rootstock Riparia Gloire after being exposed to drought environment (50% relative soil water content at field capacity) for two weeks [61]. A similar result was reported in another study investigating the drought tolerance of grafted Cabernet Sauvignon [9], where twelve days of water deficiency by progressively reducing the water supply down to 30% of soil field capacity resulted in significantly increased expression of *VviNCED3*, as well as two protein phosphatase 2C genes (*VviPP2C4* and *VviPP2C9*) responsible for ABA signalling in the roots of Cabernet Sauvignon grafted to 101-14 Mgt, M4, and autografted Cabernet Sauvignon. Notably, in the same study, scion grafted to drought tolerance rootstock M4, which maintained high leaf water potential and stomatal conductance, showed less ABA-related gene expression compared to autografted Cabernet Sauvignon [9]. That is likely because M4 rootstock could satisfy the water demand of the grafted scion even under water deficiency condition, thus requiring less extent of ABA-mediated responses. Apart from ABA, certain cytokinins such as zeatin riboside and isopentenyladenosine also contribute to moisture absorption of grapevine in drought condition, as these phytohormones could stimulate xylem fibre differentiation and increase hydraulic conductivity [72]. A previous study reported high shoot tip zeatin riboside concentration in Cabernet

Table 3: Drought tolerance of different rootstocks.

Susceptible to drought	Moderately tolerant to drought	Very tolerant to drought
101-14 Millardet et de Grasset [58–60], Schwarzmann [59], Riparia Gloire [58, 60, 61]	Kober 5BB [59, 60], SO4 [60], Richter 99 [60], 3309 Couderc [60], 420A [60], Fercal [11, 60], 41B Millardet et de Grasset [60], St. George [60, 62], Merbein 5489 [63, 64], Merbein 5512 [63, 64], Merbein 6262 [63, 64], Dog ridge [64]	Ruggeri 140 [59, 60, 62, 64], Paulsen 1103 [11, 59, 60, 64, 65], Ramsey [58, 59, 61, 62, 64, 65], Lider 116-40 [59], Lider 187-24 [59], Richter 110 [58, 60], 44-53M [60]

Data retrieved from previous research on grafted grapevines.

Sauvignon grafted to Ruggeri 140 compared to that grafted to 101-14 Mgt and Malegue 44-53 (44-53M) under both drought (completely nonirrigated for 1 week) and adequate water supply conditions (regular irrigation to maintain the soil close to 100% field capacity), which explained the relatively higher drought tolerance of Ruggeri 140 [73].

4. Soil Nutrient Availability and Rootstock Selection

Soil nutrients are important for grapevine health. They are involved in the balance of plant cell osmotic pressure, support of energy, formation of proteins, activation of enzymes, and formation of cell structure [74, 75]. Different rootstocks exhibit variation in nutrient uptake capacity and regulate the balance of nutrients in grapevine [10]. In this section, effect of grafting scions to different rootstocks in response to nutrient deficiency/toxicity will be reviewed.

4.1. Potassium. Potassium (K) is responsible for enzyme activation and stomatal activity in plants. It can bind pyruvate kinase for catalysis, thus converting phosphoenolpyruvate (PEP) and adenosine diphosphate (ADP) to pyruvate and ATP in the glycolytic pathway [76]. Similarly, potassium ions act as catalytic metal ions of asparaginase, an important enzyme responsible for nitrogen transport and storage [74]. Therefore, inadequate potassium in grapevines could suppress protein biosynthesis even with sufficient nitrate supply, which may further affect cell division and elongation [77]. The role of potassium in regulating stomatal activity is well studied, where potassium ion flows in or out of guard cells surrounding the stomata in response to water supply. This changes the morphology of guard cells, which control the open and closure of stomata [78, 79]. In the case of potassium deficiency, the potassium ion efflux in guard cells would reduce and potassium ion-related stomatal activity would be attenuated considerably. This results in delayed response to water deficiency, unnecessary loss of water vapor, and increased consumption of D-glucose via photosynthesis processes [78]. Potassium deficiency is a common issue for grapevines, especially during anthesis and veraison [80]. The main reason of this is the low availability of potassium in soil. Over 98% of potassium in soil is nonexchangeable potassium or soil mineral such as feldspar and mica, which cannot be utilised by plants directly [79]. Only 1-2% of potassium in the soil is biologically available, which can be acquired by plant roots through diffusion or via specific high-affinity K^+ transporters/K^+ uptake permeases/K^+ transporters (HAK/KUP/KT) [81, 82]. Nevertheless, in certain regions, such as Sunraysia and Riverland in Australia, excessive potassium uptake has been witnessed due to high soil potassium content, which leads to increased berry pH (>3.8) and could negatively affect wine quality [83].

Adaption of selected rootstocks can manage potassium uptake (Table 4). Certain rootstocks, such as Dog Ridge, Freedom, St. George, and Harmony, have outstanding potassium uptake capacity. Previous study showed that Cabernet Sauvignon grafted onto these rootstocks had significantly higher concentrations of petiole potassium compared to that grafted to Paulsen 1103 and 101-14 Mgt [84]. Another rootstock, named Freedom, is the offspring of two open-pollinated parents Fresno 1613-59 and Dog Ridge [106]. Its good potassium uptake capacity is likely due to the high genetic similarity to Dog Ridge, where their commonly shared parent species *V. champinii* rootstocks is known for enhancing potassium uptake [22]. St. George and Harmony have also exhibited good potassium absorbing and transporting abilities. Shiraz vines grafted onto both of these rootstocks exhibited consistently high petiole potassium content over five consecutive growing seasons when compared to ungrafted Shiraz vines [97]. On the contrary, for regions suffering from excessive soil potassium, a few rootstocks including Merbein 5489 and Merbein 5512 can be used to reduce absorption of potassium, predominately due to their low vigour and limited root development [107]. Both rootstocks have been proven effective to reduce potassium accumulation in the petioles of Cabernet Sauvignon scion and to increase berry acidity compared to ungrafted vines [94]. Controversial roles of the SO4 rootstock in managing grapevine potassium uptake have been reported. While grafting Shiraz onto SO4 resulted in a reduction in petiole potassium content [97], a higher potassium concentration was observed in both young (10 apical leaves) and mature leaves of *V. vinifera* L. cv. Negrette grafted onto SO4 rootstocks compared to those grafted onto 101-14 Mgt and 3309C [108]. These findings suggest that the influence of rootstocks on modifying nutrient uptake can occasionally be specific to certain scion varieties.

Grapevines can regulate potassium uptake through the modulation of K^+ transporter/high-affinity K^+/K^+ uptake (HAK/KUP/KT) family [109–111]. Two potassium transporters belonging to the KUP/KT/HAK family, namely, *VvKUP1* and *VvKUP2*, were previously isolated from *V. vinifera* berries [111]. Their expression in the green cane, seeds, flowers, and berries of Shiraz supported the accumulation of potassium in the berries [111]. Similarly, another study on table grapes suggested that the expression of *VvKUP1* and *VvKUP2* in both the roots and shoots of Chawga (*V. vinifera* L.) significantly increased in response to 50 mM NaCl, resulting in a rapid increase in potassium accumulation in the roots and shoots two weeks after exposure to saline stress [109]. It should be noted that different rootstocks may exhibit variations in the transcriptional abundance of the KUP/KT/HAK family genes. Thus, comparing the expression of *VvKUP1* and *VvKUP2* in various rootstocks should be considered for future studies.

4.2. Sodium. Sodium ions (Na^+) engage in the photosynthesis of C_4 plants by promoting the conversion of pyruvate into phosphoenolpyruvate, and this mechanism is not observed in C_3 plants including grapevines [112]. Sodium ions can act as osmolyte together with potassium ions in grapevines. Sodium ions maintain extracellular osmotic pressure, while potassium ions accumulate in the vacuole of plant cells to balance the intracellular osmotic pressure

Table 4: Extreme soil pH tolerance and micronutrient absorption capacity of different rootstocks.

Rootstocks	Soil acidity tolerance	Soil lime tolerance	Soil micronutrient absorption ability							Reference
			N	Ca	K	Na	P	Mg	Zn	
101-14 Millardet et de Grasset										[3, 45, 84–88]
1212 Couderc										[3, 86]
1616 Couderc										[89]
3309 Couderc										[84]
41 B Millardet et de Grasset										[84, 88, 90, 91]
420A										[84, 92, 93]
44-53 M										[84]
Börner										[94]
Dog ridge										[84]
Fercal										[10, 12, 95, 96]
Freedom										[84, 97]
Georgikon 28										[10]
Gravesac										[84, 98]
Harmony										[97]
Kober 5BB										[10, 12, 98, 99]
Merbein 5489										[94]
Merbein 5512										[94]
Paulsen 775										[100, 101]
Paulsen 1103										[3, 5, 45, 67, 84, 86, 87, 90, 92–94, 97, 98, 102–104]
Ramsey										[3, 5, 86, 97, 105]
Richter 99										[97]
Richter 110										[67, 84, 85, 90, 94, 98]
Riparia Gloire										[84, 88, 102]
Ruggeri 140										[86, 90, 94, 97, 105]
Schwarzmann										[3, 86]
St. George										[3, 84, 86, 97]
SO_4										[12, 67, 84, 85, 88, 92, 97, 99, 104]
Teleki 5C										[12, 99]

Data retrieved from previous research on grafted grapevines. Different colours stand for different levels of ability: (■) low; (■) medium; (■) high; (■) very high; (□) data not available.

[113]. However, when the concentration of potassium ions is low, sodium ions could flow into cell vacuoles and substitute potassium ions to balance intracellular osmotic pressure and thus maintain the basic physiological functions of plants under potassium deficiency [114]. The most commonly found problem with sodium in vineyard is high sodium stress. High sodium stress could exacerbate potassium homeostasis disorders in plants, where sodium ions could affect the affinity of potassium ion transporters. This could further alter potassium-related physiological activities discussed in previous section [115].

Rootstocks could be used to address the challenges of soil salinity (Table 4). Some commercial rootstocks can tolerate sodium stress by limiting the uptake of sodium from the soil as well as restraining the transport of sodium to the leaves. For example, the concentration of sodium ions in trunk wood was significantly lower in Shiraz scions grafted onto Ruggeri 140 and 101-14 Mgt in comparison to ungrafted vines [3]. In the same study, grafting both Chardonnay and Shiraz to Ramsey and Ruggeri 140 considerably alleviated the loss of yield caused by salinity compared to that on ungrafted vines, suggesting their higher salt tolerance [3].

Briefly, the mechanisms of salinity tolerance in plants encompass tissue tolerance (the ability of plants to withstand high salt ion concentrations within the plant), osmotic tolerance (the capacity of plant roots to endure osmotic stress induced by soil salinity), and ion exclusion achieved through the regulation of membrane proteins with ion transport activity [116]. Notably, significant research efforts have been dedicated to investigating the molecular regulation associated with ion exclusion. For example, the role of *HKT* genes in managing salt tolerance has been widely studied in various plants such as cucumber and seepweeds [117, 118]. HKT family genes including *VvHKT1*, *VvHKT2*, *VvHKT3*, *VvHKT4*, and *VvHKT5* have also been identified in grapevine [13, 14]. Higher expression of the *VvHKT1* and *VvHKT2* in A15 and A17 rootstocks leads to increased sodium retention in the root zone and lower sodium concentrations in petioles and blades compared to that of SO4 [13]. C-repeat binding factor/dehydration responsive element binding protein 1 (CBF/DREB1) genes also play important roles in salt stress management. Overexpression of *VrCBF1* and *VrCBF4* isolated from *V. riparia* can increase the survivability of *A. thaliana* Col-0 exposed to drought-

induced saline stress [119]. This may explain why Cabernet Sauvignon grafted to several descendants of *V. riparia*, including Börner and Freedom, exhibited enhanced Na^+ exclusion ability and lower sodium content in the petiole [84]. However, to further understand the mechanism of salinity tolerance by grafted rootstocks, the expression of *VrCBF1* and *VrCBF4* in scion leaves under saline stress needs to be compared among different rootstocks. Grapevine Na^+/H^+ exchanger (NHX) family is also involved in salt tolerance, where upregulated expression of *VvNHX1* and *VvNHX2* in the leaves of ungrafted Cabernet Sauvignon 200 mM NaCl condition was observed [120]. Among NHX family, *VvNHX1* is a cation-proton antiporter localised in vacuolar membranes of berry and plays an important role in inducing tonoplast internalisation of sodium, which could reduce the damage caused by excess sodium ion to organelles and cellular metabolism [121, 122]. To date, the investigation on *VvNHX* family genes was mainly focused on ungrafted grapevines, whereas future studies can compare the expression of these genes in different grafted rootstocks and examine their effects in managing ion transport activity to better understand their role in salinity tolerance.

4.3. Chloride. In addition to sodium, chloride is a major mineral contributing to soil salinity. Chloride-induced salinity can lead to reduction in stomatal conductance and photosynthesis of grapevine along with increased shoot chloride content and leaf burn [123, 124]. A few rootstocks can be used to mitigate chloride-induced saline stress. Previous study showed that *Rupestris* St. George is effective in reducing chloride absorption, where chloride concentrations in laminae of Shiraz and Chardonnay grafted to *Rupestris* St. George were consistently lower compared to vines grown on own roots over 7 years of observation [125]. Ruggeri 140 and M4 are also tolerant to saline stress [2, 7, 124]. The physiological performance of these rootstocks, including leaf area index, leaf expansion rate, leaf water potential, net CO_2 assimilation, and stomatal conductance, was less influenced by saline stress compared to other rootstocks, such as 101-14 Mgt and Merbein 6262 [7, 124].

The mechanisms of rootstocks tolerating chloride-induced salinity have not been fully understood, but a few genes differently expressed under saline stress have been identified in grapevine [2]. Higher expression of *VvNAXT1* that encodes nitrate excretion transporter in grapevine was found in the roots of Ruggeri 140 compared to K51-40 (a rootstock with high chloride concentration in shoot), and its expression was further upregulated in Ruggeri 140 when rooted leaves (established from cuttings and maintained in a glasshouse for 3 weeks to develop roots) were cultured in 50 mM chloride ions for 4 days [2]. Similarly, the abundance of *VvSLAH3*,a gene encoding plasma membrane-localised Slow Anion Channel 1 protein, was also higher in the roots of Ruggeri 140 compared to K51-40 [2]. A previous study on *Arabidopsis* suggested that the coexpression of SLAH1 and SLAH3 in xylem-pole pericycle cells played a regulatory role in facilitating $NO3^-$ translocation to the shoot in response to high Cl^- stress [126]. Eight *NPF* genes exhibited significant differential expression between Ruggeri 140 and K51-40, whereas whether these genes contribute to the Cl^- tolerance of Ruggeri 140 remains unclear [2]. Therefore, further investigation is required to elucidate the roles of these genes in regulating saline tolerance in grapevines and provide insight into breeding saline-tolerant rootstocks.

4.4. Phosphorus. Phosphorus is an essential macronutrient for plants including grapevines. The roles of phosphorus in constituting plant cell membrane, nucleic acids, and various energy-supportive compounds, such as adenosine triphosphate, have been well reviewed previously [127, 128]. Despite the high phosphorus content in soil, the bioavailable inorganic phosphate (PO_4^{3-}, HPO_4^{2-}, and $H_2PO_4^-$) only presents in a small proportion. The predominate organic phosphorus source in soil, inositol hexaphosphate, cannot be utilised by grapevines unless it is converted to immobile forms such as $H_2PO_4^-$ and HPO_4^{2-} [129]. In addition, inorganic phosphate can form ion pairs or complex species with calcium or magnesium, making it more difficult for roots to absorb [130].

Some rootstocks can be used to mitigate phosphorus deficiency (Table 4). High concentrations of inorganic phosphorus could usually be detected in the petioles of Flame Seedless, Thompson Seedless, Superior Seedless, and Red Globe grafted to Ramsey compared to same scions grafted to nine other studied rootstocks, including Freedom, Harmony, St. George, SO4, 1613C, Paulsen 1103, Richter 99, Richter 110, and Ruggeri 140 [131]. Likewise, Richter 110 and 41B Millardet et de Grasset (41B) can also tolerate phosphorus deficiency, where higher petiole phosphorus concentrations have been observed in Cabernet Sauvignon grafted to these rootstocks compared to other rootstocks such as Millardet et de Grasset 420A (420A) and 44-53M [84]. Both Richter 110 and 41B share the same parent species *V. berlandieri* from which they may inherit the trait [84].

Excessive phosphorus content in soils can be another problem affecting the growth of plants [132]. The ideal soil phosphorus ion concentration for growth of majority high phosphorus demanding plants is 5 to 60 μM, where excessive phosphorus may lead to zinc and iron deficiencies, which can subsequently affect protein synthesis and result in iron deficiency-induced leaf chlorosis [29, 133]. Rootstock can be used to limit phosphorus uptake from soil (Table 4). Freedom is one of the best rootstocks to limit phosphorus uptake. The petiole phosphorus concentration of Flame Seedless and Thompson Seedless vines grafted to Freedom was significantly lower than same scions grafted to 3309C, Richter 99, and SO4 [131]. Similarly, Riparia Gloire, 44-53M, and 420A can limit phosphorus uptake by grapevine, and the petiole phosphorus contents of Cabernet Sauvignon grafted to these rootstocks were significantly lower compared to those grafted to Richter 110 and Dog Ridge [134].

The mechanism for rootstocks to regulate phosphorus content is complicated and not fully understood. In general, phosphorus uptake not only is determined by the rootstocks

used but also depends on the scions grafted. A recent study compared the phosphorus uptake ability of different scion-rootstock combinations under low or high phosphorus supply [15]. This study highlighted that the scion could exert long-distance regulation of rootstock responses to low phosphorus condition, including the expression of Inorganic Phosphate Transporter 1 genes (*PHT1*) and Purple Acid Phosphatase genes (*PAP*). Inorganic Phosphate Transporter 1 family proteins are responsible for the uptake of inorganic phosphorus in roots, while acid phosphatases are responsible for catalysing the hydrolysis of organic phosphorus to inorganic phosphorus in soil [135]. Under high nitrogen condition, transcription of *PHT1.3b* and *PHT1.4d* was affected by both scion and rootstock, while *PHT1.4a* was only affected by scion [15]. Furthermore, significant elevated transcription of *PHT1* genes (*PHT1.3a-b, PHT1.4a-d*) was observed in all scion-rootstock combinations under low phosphorus supply compared to that under high phosphorus condition. Similar to *PHT1* genes, the transcript abundance of *PAP* genes was higher under low nitrogen supply than that in high nitrogen condition. Elevated transcription of *PAP10* was observed in scion/rootstock combinations of Paulsen 1103 grafted to Paulsen 1103 and Pinot Noir grafted to Paulsen 1103 than that with Paulsen 1103 and Pinot Noir scions grafted to Pinot Noir rootstock under low nitrogen supply, while the abundance of *PAP12* transcripts was higher in both scions grafted to Pinot Noir rootstock than those grafted to Paulsen 1103 under high nitrogen supply [15]. This suggested that the genetic variation in shoot-borne signals can regulate root response to different phosphorus supply conditions and the impacts of rootstocks on phosphorus uptake should not be studied alone [15]. Instead, both scion-root interaction and the level of nitrogen supply should be taken into consideration. In addition, grapevine rootstocks could influence rhizosphere microbes. For example, a previous study unfolded that Paulsen 1103 could significantly increase the relative abundance of Pseudomonadaceae compared to other rootstocks, including Kober 5BB, 161-49 Couderc, and Ruggeri 140 [136]. Inoculation with several strains belonging to Pseudomonadaceae, especially *Pseudomonas putida* RC06 and *Pseudomonas putida* FA19d, to rhizosphere soil could result in an increased content of phosphorus in the leaves of grafted vines [137]. In summary, rootstocks can be used to overcome both phosphorus deficiency and phosphorus toxicity. Further research on the molecular mechanisms is required to better explain how grapevine rootstocks regulate phosphorus uptake and translocation.

4.5. Magnesium. Magnesium is an essential component of chlorophyll and as such contributes to photosynthetic CO_2 assimilation. In the photosynthesis process, magnesium binds to both catalytic chaperone Rubisco activase and the side chain of carbamylated Rubisco, promoting CO_2 assimilation [138]. Reduced CO_2 assimilation in grapevines caused by a lack of magnesium stimulates ROS generation in cells, increases oxidative stress, and causes severe cell damage [139, 140]. Therefore, it is essential to ensure adequate magnesium uptake to maintain the health of grapevines.

Different rootstocks have altered magnesium uptake capacities (Table 4). A previous study found that Richter 110 could reduce magnesium uptake of the grafted vines, where both Xinomavro and Chardonnay grafted to Richter 110 showed considerably low magnesium content in leaf compared to same grapevine scions grafted to 41B, Paulsen 1103, and Ruggeri 140 [90]. Likewise, Freedom, Ramsey, and SO4 also have a tendency to restrict magnesium uptake in grapevines. In a 5-year observational study, Shiraz vines grafted onto these rootstocks exhibited significantly lower petiole magnesium content compared to ungrafted vines [97]. Paulsen 1103, 3309C, and Ruggeri 140 exhibit good magnesium absorption ability and tolerate low magnesium concentrations in the soil [90, 108, 141]. These rootstocks respond quickly to increased oxidative stress induced by magnesium insufficiency and produce higher concentrations of carotenoids and certain anthocyanins such as pelargonidin (3-O-(6-O-malonyl)-β-D-glucoside) compared to SO4 rootstock [141]. In addition, stronger tolerance of Paulsen 1103 to magnesium deficiency-induced ROS is also supported by the higher abundance of molybdenum cofactor (Moco) in roots, where several Moco-dependent enzymes including sulfite oxidase, sulfite reductase, and xanthine dehydrogenase are capable of sulfite [142] and hydrogen peroxide [143] detoxification. Paulsen 1103 attenuates magnesium deficiency-induced oxidative stress by downregulation of a Respiratory burst oxidase protein D (*RBOH D*) transcript in roots, which is involved in reactive oxygen intermediate production in grapevine [141, 144]. Another mechanism influencing magnesium uptake is the *MRS2/MGT* gene family which encodes transporters in grapevine roots [141]. Expression of both *AtMRS2-4*/*AtMGT6* and *AtMRS2-7*/*AtMGT7* was responsible for Mg^{2+} uptake under a magnesium deficiency environment in *Arabidopsis* [145, 146] and a similar mechanism may be present in grapevines, which needs to be further validated.

4.6. Zinc. Zinc is recognised as a crucial micronutrient for grapevines, as it facilitates the formation of auxin, which, in turn, supports the development and elongation of shoots and internodes [147, 148]. Additionally, zinc binds with a wide range of proteins to regulate the immune responses of plants [149]. For example, a zinc finger protein needs at least one zinc ion to stabilise the secondary and tertiary molecular structure [150].

Zinc deficiency may affect the grapevine structure, development, and disease resistance. Zinc toxicity is another relevant situation. Soil zinc concentration above 80 mg/kg can cause problems, where high level of zinc content in the shoot may inhibit electron transfer in photosynthesis and reduce the biosynthesis of chlorophyll and eventually result in decreased leaf area and pruning mass of grapevines [92, 93]. The phenomenon of zinc toxicity has gained increased attention in recent years, and its influence may be more severe than zinc deficiency, especially in vineyards using zinc-based fungicides [151].

A few studies have compared zinc uptake ability of grapevine rootstocks (Table 4). Rootstocks SO4 and 420A showed superior capacity of zinc uptake in low zinc soils (20–40 mg/kg), and zinc concentrations in the roots and shoots of these rootstocks were significantly higher compared to Paulsen 1103 [93]. The canopy size and dry weight of scions grafted to SO4 and 420A rootstocks were approximately 1-2 times higher than those grafted to Paulsen 1103 and IAC313 rootstocks in low zinc soil [151]. Paulsen 1103 is a good candidate for high zinc conditions; for example, high soil zinc content (80–160 mg/kg soil) had limited influence on the mass of root and scion of own-rooted Paulsen 1103 [151]. The variance of zinc tolerance among different rootstocks is not fully understood but could possibly be related to the expression of zinc-regulated transporter/iron-regulated transporter protein (ZIP) gene family responsible for regulating zinc uptake, transportation, and homeostasis in grapevine [152]. A previous study noticed that upregulated expression of *VvZIP2*, *VvZIP6*, *VvZIP7*, and *VvZIP13* could be observed in the leaf of "Merlot" (*V. vinifera* L.) at both 4 and 10 days after treated by zinc spray (2880 mg/L). This supported zinc translocation within entire plant and prevented excessive zinc accumulation in plant [153]. Noticeably, in the same study, zinc stress-induced expression of *VvNRAMP3* has also been observed [153]. NRAMP is a multimetal transporter located in the vacuolar membrane. It is involved in zinc detoxification, despite its mechanism remaining unclear [154]. Expression of zinc uptake-related genes in grapevine can also be affected by ABA, where elevated expression of *VvZIP2*, *VvZIP6*, and *VvZIP7* in the roots of "Merlot" was induced by application of 10 μM ABA to rhizosphere soil [153]. However, whether ABA accumulation can directly affect zinc uptake and translocation remains uncertain due to the controversial role of in ABA in regulating plant growth and shaping root structure [155, 156].

To better examine the role of ABA in zinc uptake by grapevine rootstocks, future studies are recommended to evaluate the zinc status in different organs of grafted grapevines in response to the exogenous application of ABA. Furthermore, whether different grapevine rootstocks could express genes related to ABA biosynthesis and ABA perception differently under zinc deficiency environments remains a promising area to explore further upon if the mechanisms of ABA regulating zinc uptake are fully understood.

4.7. Nitrogen. Nitrogen is essential for grapevines and is needed for the biosynthesis of proteins, chlorophyll, phytohormones, and nucleic acids [157]. Uptake of nitrogen from soil is strongly correlated to its content in the soil, where insufficient yeast assimilable nitrogen (YAN) (<150 mg/L) caused by nitrogen deficiency in soil would hinder the initiation of yeast fermentation winemaking [43]. Oppositely, excessive YAN in berries can lead to residual nitrogen during primary fermentation, which encourages microbial instability that speeds up yeast fermentation and increases the risk of microorganism spoilage [158, 159]. Furthermore, high YAN may result in formation of undesirable haze and thiols in the wine [160].

Grapevines can utilise nitrate and ammonium as nitrogen sources and convert these inorganic nitrogen forms into glutamine [161]. Plants actively uptake nitrate through a proton/nitrate-coupled mechanism primarily mediated by low-affinity transport systems and high-affinity transport systems [102]. Both of these systems can be induced in grapevines within 24 hours in response to increased nitrate availability [162].

Rootstocks, on the other hand, can modify nitrate uptake by either enhancing the kinetics or regulating the intensity of the high-affinity transport system induction response [157, 163]. These effects can be particularly pronounced in Pinot Noir grafted onto Riparia Gloire. In this case, the expression of two genes that regulate the high-affinity nitrate transporter, named *VitviNRT2.4A* and *VitviNRT3*, in root tips significantly increased in response to 0.5 mM Ca $(NO_3)_2$ after 10 days of nitrogen starvation, in comparison to the same scion grafted onto Paulsen 1103 [102]. Similarly, an increase in the expression of *VitviNRT2.4A*, *VitviNRT3*, and another gene named *VitviNAXT*, which encodes nitrate excretion transporter1, was also observed in the roots of Chardonnay and Sauvignon Blanc grafted onto Kober 5BB [157] and Corvina grafted onto SO4 [162] during their recovery from nitrogen deficiency. The responsiveness of rootstocks to nitrogen availability may also be influenced by the accumulation of free amino acids in root tips [102]. Free amino acids accumulated within 24 hours after nitrate induction in Pinot Noir scion grafted to Riparia Gloire, leading to elevated expression of *VitviGS2*, an ortholog encoding Glutamine synthetase in root tips, thus enhancing nitrogen assimilation [102]. Likewise, previous research on ungrafted M4 rootstock revealed that the abundance of several proteins involved in the biosynthesis of methionine, isoleucine, and serine increased significantly in roots in response to 10 mM NO^{3-} for 30 hours [164]. That further supports the role of free amino acid accumulation in managing nitrogen uptake and may explain why several nitrogen uptake supporting rootstocks, such as SO4 [165] and Riparia Gloire [166], have higher expression of genes encoding nitrate reductase, nitrite reductase, and glutamine synthetase isoform 1. On the contrary, 420A has been proven effective to reduce nitrogen uptake of the grafted Cabernet Sauvignon scion, suggesting a proper candidate for vineyards with high soil organic nitrogen content [160].

4.8. Other Nutrients. In addition to the nutrients above, other macro- and micronutrients such as boron, calcium, and selenium can influence the growth of grapevines.

Boron is an essential nutrient responsible for forming borate-diol ester bonds that link two rhamnogalacturonan II (RGII) chains, a plant cell wall pectic polysaccharide [167]. Specifically, in grapevines, boron is associated with grapevine flowering, fruit ripening, and fruit yield [168]. A deficiency in boron may lead to impaired pollen tube growth

and, ultimately, the development of shot berries (seedless and small in size) [169]. Effective boron absorption abilities are evident in several rootstocks, including 101-14 Mgt, Paulsen 1103, Richter 99, Ruggeri 140, and Schwarzmann [170, 171]. These rootstocks could be used to alleviate the symptoms of boron deficiency, likely due to the expression of NIP5;1, a boric acid channel, and BOR1, a boric acid/borate exporter that localises to the plasma membrane in these rootstocks [172, 173], and further investigation is required to validate this hypothesis. On the contrary, boron toxicity, which frequently occurs in sedimentary soils, is another issue affecting grapevine physiology. Excessive boron uptake could result in the accumulation of boron in grapevine leaves, inducing oxidative stress and lipid peroxidation, which would, eventually, cause membrane damage [174]. A previous study investigated the response of grafted grapevines to boron toxicity, where *V. vinifera* L. cv. Kalecik Karasi grafted to Kober 5BB showed increased superoxide dismutase (SOD) and catalase activities in leaves in response to 30 mg/kg soil boron content [174]. This indicated that grafted grapevine could display a defensive mechanism to protect plant cell against boron toxicity-induced oxidative stress. However, such a mechanism could be affected by the variety of scion grafted. For instance, Merlot grafted to Paulsen 1103 exhibited more severe leaf burns, higher boron accumulation in leaf, and significantly lower SOD activity in leaf compared to Sangiovese grafted to same rootstock when treated by 30 mg/kg boron in the soil, suggesting its poor tolerance to boron stress [175]. Limited studies compared the antioxidant activities of different grapevine rootstocks against boron toxicity, which can be considered in future studies.

The nutritional role of soil calcium for grapevine health remains controversial. Calcium can regulate chloroplast stroma function and thylakoid assembly in grapevines, and calcium enrichment could inhibit plant absorption of magnesium and potassium [176, 177]. Different genotypes of rootstocks can confer different effects in calcium absorption and translocation to grapevine. For example, increased calcium content in shoots and leaves was observed in Merlot grafted to rootstock 101-14 Mgt [171]. Similarly, a higher calcium content in the leaves of both Xinomavro and Chardonnay grafted onto Paulsen 1103, in comparison to scions grafted onto 41B and Ruggeri 140, was previously observed [90]. Nevertheless, the mechanism influencing calcium uptake by different grapevine rootstocks remains unclear.

Selenium is a micronutrient contributing to drought tolerance of grapevine. For example, foliar application of 5–10 mg/L selenium could increase the accumulation of osmolytes in the leaves of *V. vinifera* L. cv. Sultana and upregulate antioxidant activity in grapevine leaves under saline stress [178]. Previous study suggested that grapevine cultivar "Chambourcin" grafted to 3309C had slightly higher selenium concentration in leaves compared to vines grafted to Paulsen 1103, SO4, and ungrafted grapevines [179]. One of the possible mechanisms by which grafted rootstocks affect selenium status is the regulation of salicylic acid synthesis and accumulation in plants. The role of salicylic acid in managing selenium uptake and translocation in grapevine has been examined previously, where selenium contents in the roots, stems, leaves, and shoots of seedless "Summer Black" grapes increased significantly after spraying salicylic acid to the leaves at 200 mg/L [180]. Another study noticed that grafting Cabernet Sauvignon to different rootstocks, including Riparia Gloire de Montpellier and Paulsen 1103, could result in different expression of three genes responsible for the synthesis and degradation of salicylic acid in shoot apex zones [181]. Nevertheless, limited research compared salicylic acid content level among different grafted rootstocks. Future study can investigate this topic to reveal the relationship between selenium uptake and endogenous hormone production by grafted rootstocks. However, one of the challenges future studies on phytochemistry may face is distinguishing the direct influence of rootstocks on root-derived salicylic acid, which affects the absorption of nutrients by root systems, from the indirect influence of shoot-derived hormones that affect the nutrient status in plants.

5. Soil pH and Rootstock Selection

Soil pH can affect the growth of grapevine by influencing the availability of nutrients and thus modifying their uptake efficiency. Soil pH may also influence the rhizosphere microbiome community and therefore have other effects on the health of grapevines. Generally, the optimum soil pH for grapevine is between 6.0 and 7.0, while acidic and alkaline soil may have different impacts on plant growth.

5.1. Acidic Soil. The accessibility of several nutrients varies with soil pH. When soil pH is lower than 5.5, the ability of roots to take up phosphorus, potassium, and magnesium reduces dramatically [182]. In contrast, the availability of aluminium increases at low soil pH, where excess protons (H^+) release Al^{3+} from $AlOH^{2+}$, $Al(OH)_2^+$, $Al(OH)_3$, and $Al(OH)_4^-$ [183]. Excessive uptake of aluminium at low soil pH is associated with inhibition of intercellular transport of micronutrient ions and attenuated elongation of roots and is therefore toxic for plants [184, 185]. The availability of manganese also increases in acidic soil, and the efficiency of roots in uptake of manganese maximised at around pH 4.5 [186]. Excessive manganese can become toxic due to the accumulation of manganese oxides, oxidised phenolic compounds, and ROS in cell walls, which cause damage to chlorophyll [187, 188], whereas prolonged exposure to manganese toxicity can result in the chlorosis and necrosis of leaves [188].

Rootstocks perform differently in responding to excessive soil acidity (Table 4). Several rootstocks, such as Fercal and Gravesac, have previously demonstrated exceptional tolerance to soil acidity (pH 4.9) [10]. In comparison to Kober 5BB, these own-rooted Fercal and Gravesac maintained relatively higher shoot and leaf mass after being planted in acidic soil for 3 months [10], likely inheriting the trait from their parent species, *V. berlandieri*.

Research on the mechanism of grapevine rootstocks tolerating low pH condition is limited. It is possible that the NHX antiporter plays an important role. Six NHX antiporters genes have been identified in grapevine (*VvNHX1–6*), where *VvNHX1* is the dominant one and responsible for the homeostasis of monovalent cations, pH regulation, and salt tolerance [121] but has not been extensively characterised. NHX antiporters have been better studied in other plants. In rice for example, *HtNHX1* and *HtNHX2* overexpression line showed higher growth rate compared to wild type under two stress conditions: 100 μM $AlCl_3$ for 3 days, or soil acidity (pH 4.5) for 30 days, suggesting that expression of both *HtNHX1* and *HtNHX2* could enhance rice tolerance to acid soil and subsequent Al^{3+} stress induced by low soil pH [189]. *HtNHX1*, in particular, located in plant cell tonoplast, is more capable of driving cytosolic K^+ to flow into cell vacuoles, where K^+ could exchange excessive H^+ and alleviate damage caused by extreme acidity. On the other hand, *HtNHX2* is mainly located in cell endosome, which can promote luminal pH homeostasis of the endomembrane system. This further results in stimulated secretion of the membrane and cell wall material to the cell surface and apoplast, thus increasing tolerance of plants to acidic soil-induced Al^{3+} stress [189, 190]. Expression of *HtNHX1* in rice can also stimulate citrate secretion of roots under stress of 100 μM $AlCl_3$ for 1 day [189], where secretion of citrate and other organic acids for chelating Al^{3+} in rhizosphere zone is a major mechanism of Al^{3+} detoxification [191, 192]. With the presence of similar antiporter in grapevine roots, similar mechanisms may exist. Due to the limited understanding of *VvNHX* family genes in different genotypes of grapevine rootstocks, further investigation is recommended to compare the expression of *VvNHX* family genes in various rootstocks in response to extreme soil acidity. This will help better understand the mechanisms by which *VvNHX* family genes are involved in the tolerance of low soil pH environments by rootstocks.

5.2. Alkaline Soil. High pH of soil (above 7.5) is mainly caused by high lime (calcium carbonate) content and can result in oxidation of Fe^{2+} ions, thus lowering availability of iron [193]. Lack of iron in grapevines can lead to leaf chlorosis as well as poor canopy structure [194].

A few rootstocks can tolerate alkaline soils (Table 4). For instance, rootstocks Fercal and Georgikon 28 maintain high shoot, leaf, and root biomass when exposed to an alkaline soil environment (pH 8.49) for 3 months [10]. Fercal is a good candidate suitable for divergent extreme soil pH conditions, at both low and high pH. A previous study on Pinot Gris suggested that vines grafted onto Fercal exhibited an increase in stomatal conductance in response to high pH conditions (pH 9), along with enhanced plant water-use efficiency compared to the same scion grafted onto Paulsen 1103. This response appears to represent a specific strategy employed by the rootstock to promote nutrient mass-flow, consequently augmenting mineral acquisition capacity [11]. Furthermore, the observed increase in root mass in Pinot Gris grafted onto Fercal under pH 9 conditions suggests a mechanism contributing to improved nutrient uptake capacity and enhanced root exploration in alkaline soil conditions [11]. The mechanism of Fercal rootstock tolerating high pH calcareous soil has also been explained in another previous study, where own-rooted Fercal maintained high iron and chlorophyll contents in grapevine leaves, under the iron deficiency (9 mg/L iron chelates) and heavy bicarbonate (840 mg/L $NaHCO_3$) compared to Richter 99 and 1613C [195]. This suggested the role of Fercal in alleviating bicarbonate-induced iron deficiency under high pH calcareous soil condition [195]. In the same study, the researchers mentioned that the tolerance to bicarbonate-induced iron deficiency may be physiologically related to iron uptake strategy I, where the plasma membrane H^+-ATPase from plant roots caused acidification of the rhizosphere, which increased the solubility of Fe^{3+} and promoted the uptake of iron by roots [195]. Similarly, Teleki 5C and Paulsen1103 were also reported to tolerate alkaline soil and have been applied in Czech Republic to overcome chlorosis induced by calcareous soils [12]. Both rootstocks share a proportion of *V. berlandieri* pedigree, where *V. berlandieri* is known as a key species for the breeding of soil lime-tolerant rootstocks [196].

Soil lime-induced iron deficiency can stimulate phosphoenolpyruvate carboxylase (PEPC) activity in soil lime-tolerant rootstock [197]. PEPC is involved in the tricarboxylic acid cycle in roots and can facilitate the production of various organic acids such as citric and malic acids [198, 199]. Secretion of organic acids from root to soil may adjust soil pH and increase iron availability, which has been considered as a common way to achieve alkaline soil tolerance [198]. Two genes encoding PEPC named *PEPC3-1* and *PEPC3-2* and 2 PEPC kinases genes named *PEPCK1-1* and *PEPC1-2* have been identified from grapevines. Significant increased expression of these genes was observed in rootstock A15 (*V. amurensis* × *V. berlandieri* × *V. riparia*) when exposed to $NaHCO_3$-induced alkalinity, resulting in stimulated biosynthesis of oxaloacetate and its downstream products, oxalate and malate [200]. A similar mechanism was also noticed in soil lime-tolerant rootstock Ruggeri 140, where microcuttings (a stem cutting technique which uses cuttings from the juvenile mother plants) of Ruggeri 140 showed significantly higher H^+ extrusion from the roots and root H^+ release activity compared to Ramsey, along with enhanced root ferric chelate reductase activity under iron-deficient condition [105]. Conversely, iron deficiency caused a significant decrease in phosphoenolpyruvate carboxylase (PEPC) and malate dehydrogenase activity in own-rooted 101-14 Mgt, a typical soil lime-susceptible rootstock [85]. Rootstocks can also modify root exudates in response to lime-induced iron deficiency. In the case of microcuttings of Ruggeri 140, several primary metabolites in root exudates, especially L-glutamate and maltose/sucrose, significantly reduced after being exposed to iron deficiency for 3 hours [105]. This reduction in root exudates at the rhizosphere supports the reabsorption of amino acids and other components by rootstocks, along with the release of antimicrobial metabolites. These actions reduce microbial competition for the iron mobilised by root activities

[105, 201]. Iron deficiency can also lead to a decrease in the concentrations of salicylic acid, p-coumaric acid, caffeic acid ethyl ester, caffeic acid 4-O-glucoside, apigenin 6-C-glucoside, isoxanthohumol, and wighteone in root exudates from Ruggeri 140 [105]. However, the roles of these compounds in regulating soil alkaline stress remain unclear, and genes responsible for their biosynthesis and metabolism in grapevine roots have not been well-reported previously. Future studies are required to compare the composition of root exudates from different rootstocks in response to soil lime-induced iron deficiency and to investigate the mechanisms by which these compounds contribute to soil lime tolerance in grapevine rootstocks.

6. Conclusion

Rootstocks have been used in almost all grape-growing countries due to their advantages in managing abiotic and biotic stress and improving berry production and quality. Commercial rootstocks are obtained from crossbreeding between *Vitis* species, and many rootstocks share similar genetic background and therefore characteristics. Considerations related to the management of abiotic stress factors play an important role in the selection of rootstocks for viticultural production. In particular, the disparate capacities of rootstocks in mitigating water stress necessitate thoughtful decision making in accordance with the specific conditions prevailing in the vineyard. Moreover, meticulous attention to the soil profile within the vineyard, encompassing parameters such as soil pH and nutrient availability, is critical for rootstock selection.

There are clear research gaps in the following areas: (1) new rootstocks should be developed to address emerging challenges, such as new phylloxera genotypes, and their performance should be evaluated; (2) the mechanism of how rootstocks manage biotic and abiotic stress at molecular level is not well explored; (3) the role of hormones secreted by rootstocks in managing stress and nutrient uptake should be investigated; (4) the effects of rootstocks in managing berry/wine composition need to be further reviewed; and (5) future studies should focus on the interaction between rootstocks and soil microbiome and investigate how they can contribute to the growth of grapevines.

Data Availability

No data were used to support this study.

Additional Points

Highlights. (i) The review summarises characteristics of main grapevine rootstocks. (ii) This review evaluates tolerance of different grapevine rootstocks to water stress. (iii) This review compares nutrient uptake capacity of different grapevine rootstocks. (iv) This review discusses the tolerance of rootstocks to soil acidity and soil lime.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

Authors' Contributions

Yipeng Chen was responsible for methodology, formal analysis, investigation, visualization, and original draft preparation. Yanan Fei was responsible for methodology, formal analysis, investigation, and original draft preparation. Kate Howell, Deli Chen, and Peter Clingeleffer were responsible for conceptualization, methodology, supervision, and review and editing. Pangzhen Zhang was responsible for conceptualization, methodology, supervision, review and editing, and project administration.

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