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Review Paper

Role of Grapevine Rootstocks in Mitigating Environmental Stresses: A review

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دور أصول العنب في تخفيف الضغوط البيئية: مراجعة

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Abstract. Viticulture is one of the most important crop industries in the world and its cultivation is on the upward trend globally. Global water and soil resources continued to decline sharply and rampant extreme weather conditions are becoming a serious threat to sustainable agriculture and food security. Further, the changes in climatic conditions are increasingly becoming favorable for rearing certain harmful biotic organisms, which are hostile to sustained grape cultivation. The environmental changes have shown a projected negative impact on viticulture by increased biotic and abiotic stresses. Range of strategies can be employed to mitigate such scenarios, however, integration of rootstocks to combat such challenges is a sustainable nature. Grape rootstocks have exhibited their role in mitigating the problems raised due to a variety of environmental stresses. For example, certain Vitis species are used as rootstock against phylloxera and other harmful pests of grapes. Similarly, there are certain rootstocks developed which have their tolerance against salinity, drought, cold, and iron chlorosis. With ever-changing environmental conditions, it is not essential that one rootstock perfors better at a specific place may perform well in another place. This article reviewed several grape rootstocks which have their specific resistance or tolerance features against a variety of stresses, including pests, disease, salinity, and drought. Consistent endeavors in grapevine rootstock improvement and utilization are critical for the sustainability of the grape industry, in particular during the ever-increasing environmental stresses.

Keywords: Drought; Phyloxera; Salinity, Rootstocks; Viticulture; Stress.

المستخلص:تعتبر زراعة الكروم واحدة من أهم الصناعات المحصولية في العالم وزراعتها في الاتجاه التصاعدي على مستوى العالم. واصلت موارد المياه والتربة العالمية انخفاضها الحاد وانتشار الأحوال الجوية القاسية ، وأصبحت تشكل تهديدًا خطيرًا للزراعة المستدامة والأمن الغذائي. علاوة على ذلك ، أصبحت التغيرات في الظروف المناخية مواتية بشكل متزايد لتربية بعض الكائنات الحية الدقيقة الضارة ، المعادية لزراعة العنب المستدام. أظهرت التغيرات البيئية تأثيرًا سلبيًا متوقعًا على زراعة الكروم من خلال زيادة الضغوط الحيوية وغير الحيوية. يمكن استخدام مجموعة من الاستراتيجيات للتخفيف من مثل هذه السيناريوهات ، ومع ذلك ، فإن تكامل الجذور لمكافحة هذه التحديات هو طبيعة مستدامة. أظهرت جذور العنب دورها في التخفيف من المشاكل التي أثيرت بسبب مجموعة متنوعة من الضغوط البيئية. على سبيل المثال ، يتم استخدام بعض أنواع Vitis كجذر ضد phylloxera والآفات الضارة الأخرى للعنب. وبالمثل ، هناك بعض الجذور التي تم تطويرها والتي تتسامح ضد الملوحة والجفاف والبرد والحديد الكلور. مع الظروف البيئية المتغيرة باستمرار ، ليس من الضروري أن يعمل الجذر الأساسي بشكل أفضل في مكان معين بشكل جيد في مكان آخر. في هذه المقالة ، تم استعراض العديد من جذور العنب التي لها خصائص مقاومة أو تحمل محددة ضد مجموعة متنوعة من الضغوط ، بما في ذلك الآفات والأمراض والملوحة والجفاف. تعتبر المساعي المتناسقة في تحسين جذور العنب والاستفادة منها حاسمة لاستدامة صناعة العنب ، لا سيما خلال الضغوط البيئية المتزايدة باستمرار.

لكلمات المفتاحية: الجفاف ، phylloxera ، الملوحة ، الجذور ، زراعة الكروم ، الإجهاد

Introduction

Grape (Vitis vinifera L.) is one of the top fruit crops of the world that are grown for liquid (juice, vinegar, spirits), dry fruit (raisin) and fresh fruit consumption. At present, climate change is one of the major global concerns affecting viticulture (Sara et al., 2018) and adversely impacting grapevines growth and development, thus affecting its yield and quality (Dinis et al., 2018). The use of appropriate rootstock is a long-term strategy in changing climatic conditions (Fraga et al., 2016; Cramer et al., 2011). Hence, the grapevine rootstocks have their significant importance as they can mitigate environmental stresses by adapting to adverse soil and climate conditions. An ideal rootstock should have abilities to withstand drought, heat, salinity, cold, insect and pest resistance with the ability to adopt a wide range of soils (Ollat et al., 2015). Besides, a rootstock should have abilities of early bearing and high yield attributes, however, it is seldom that single rootstock possesses all desirable traits (Theodore and Stephen, 1997).

Before selecting and propagating a grapevine rootstock, a number of its attributes and characteristics are evaluated. Traits such as its compatibility, vigor, yield, rooting ability, and propagation technique (Pedersen, 2006), adaptation to the soil, and climate are taken into consideration (Pavloušek, 2011). Moreover, these rootstocks should have tolerance against salinity and drought with the ability to resist soil-borne pathogens. In grapes, there is the problem of graft incompatibility, which occurs over the time (Gökbayrak et al., 2007). This

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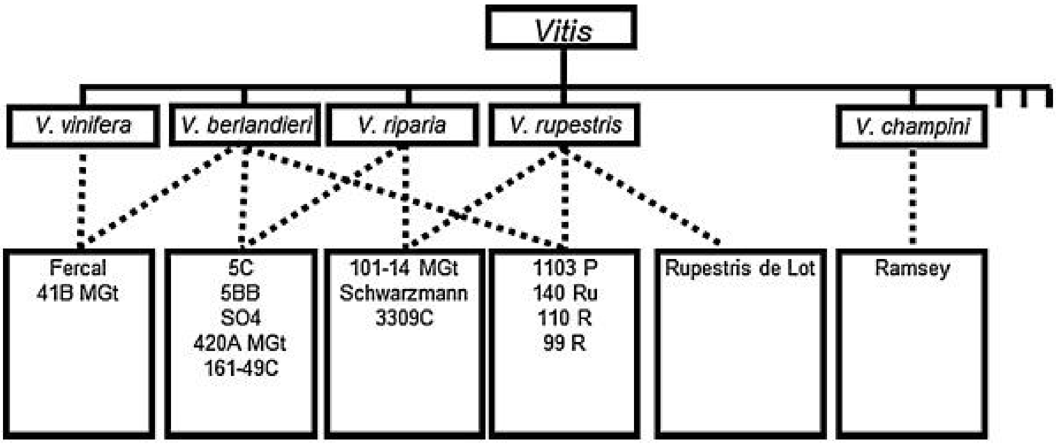

Figure 1. The genetic origin of some rootstocks used worldwide [adapted from Dry (2007)]

incompatibility results in poor vascular bundle development and causes phloem degeneration (Cookson et al., 2013). This problem resulted an uneven distribution of water and nutrients with poor plant performance (Pina et al., 2009).

In vineyards establishment, identification of the most suitable rootstock choice is one of the key factors for its success (Loreti et al., 2006). The rootstocks of grapes play a key role in dividing plant biomass between trunk, root, shoot, and fruit (Köse et al., 2014). The carbohydrates stored in canes are responsible for plant health and vigor of earlier year growth. Similarly, the carbohydrates stored in the plant roots are responsible for root and shoot development. It also increases stem growth, initiates flower bud induction, and fruit setting (Göktürk et al., 2005). Besides, rootstocks are responsible for controlling the scion flowering and fruiting. It also affects the quality of the fruit (Reddy et al., 2003). Moreover, grapes rootstocks have exhibited the ability to withstand biotic stress like phylloxera and abiotic stresses including drought, salinity and flooding (Satisha et al., 2007). At present, climate change is of great concern as erratic environmental conditions are making agriculture difficult to sustain, because of heavy rain, flood or drought, soil and water salinity, and a range of extreme weather conditions. The grapes grown under (light and water) stress conditions resulted in low yield as compared to grapes grown under ideal environments (Akram et al., 2019).

Most of the grape rootstocks are developed from North American Vitis species. Approximately 90% of grape rootstocks that exist in the world were developed from ten rootstock cultivars (Keller, 2010). The genetic origin of grape rootstock used broadly in the world is shown in (Figure 1). In viticulture, it is essential to understand the behavior of rootstocks as the success of viticulture depends upon various factors including soil, climate, biotic-abiotic factors and rootstock -scion combinations. Any change in these factors can entirely change the scenario. There are certain rootstocks in grapes that are capable of overcoming the biotic and abiotic stresses at large. Therefore, it is essential to find such rootstocks in grapes that carry the desirable traits to withstand the ever-increasing environmental stress. Thus, the objectives of this study were to review the current literature on the role of grapes rootstocks in mitigating environmental stresses in sustainable viticulture production.

Response of Grape Rootstocks to Biotic Stresses

Phylloxera

The "phylloxera" species is one of the most destructive pests of grapes. It consists of several species. In the 1880s, its first species (Phylloxera vitifoliae Fitch.) appeared and it was a root parasite (Coombe, 1999). It severely affected the grapes growing areas. Then in 1930, grapes first rootstock was developed to tolerate the attack of "phylloxera", which in the 19th century destroyed several European vineyards (Granett at al., 2001). The use of rootstock in viticulture was initiated due to this pest. To cope with phylloxera, the grapes rootstock from North American Vitis species were selected and European varieties were grafted (Vrsic et al., 2016). Later grape hybrids were used to solve this problem. But the phylloxera species (Daktulosphaira vitifoliae Fitch) became a dynamic and more aggressive strain, which destroyed several vineyards of Europe. American rootstocks showed their resistance against this pest.

After the 1990s, the European rootstocks were replanted again and were grafted on "Borner" rootstock (Becker, 1989). This rootstock has shown strong resistance against phylloxera and since it is used commercially (Blank et al., 2009). This rootstock was a hybrid

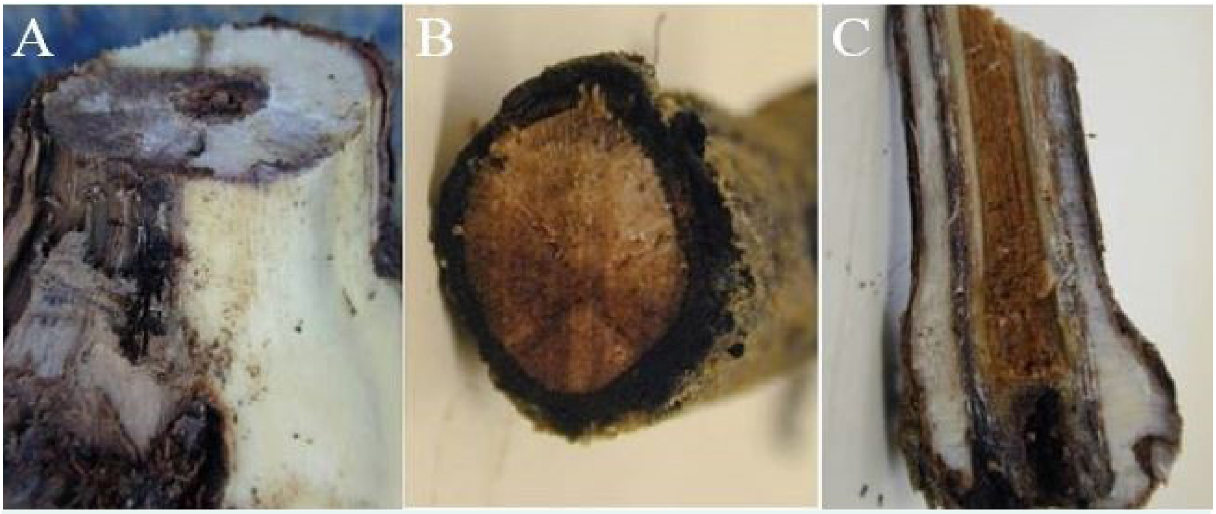

Figure 2. The cross-section of rootstock infected by black foot disease (A), cross-section of the root (B) and longitudinal-section of a young grapevine infected with Cylindrocarpon spp. (C) [adapted with the permission from Halleen et al. (2007)].

that was obtained by the crossing of two grape species "Vitis riparia 183 Gm × Vitis. cinerea Arnold" (Ambrosi et al., 1994). At present, several rootstocks are being developed in Europe, which showe their resistance against phylloxera (Arrigo and Arnold, 2007). The highest resistance against phylloxera has been observed in American species, but its mechanism of resistance is still not clear. The American species that showed resistance against phylloxera includes: Vitis Rupestris, Vitis riparia and Vitis berlandieri. Most of the grapevine rootstocks are developed from these species show a very less genetic variability among them. Serra et al. (2013) reported that about 90% of grape genotypes are grafted on ten rootstocks, which shows that the grapes are at huge risk and these rootstocks can lose their significance with time being due to less genetic diversity. For example, A × R1 Californian rootstock which was the combination of Vitis vinifera ×Vitis rupestris has lost its root system significance and it is further not effective (Corso and Bonghi, 2014). Until now, the most resistant hybrids against phylloxera developed from Vitis Rupestris, Vitis riparia and Vitis berlandieri species are 101-14, 196.17 Castel and Schwarzmann (Grant and Matthews, 1996). Similarly, another grapevine rootstock SO4 (Selection Oppenheim 4) showed its highest resistance against phyloxera (Schmid et. al., 1998). However, there is always a great need to develop more rootstock against this pest.

Black Foot Disease

In 1961, black foot disease was recorded for the first time in France (Maluta and Larignon, 1991). After that, this disease was observed in the vineyards of Tasmania (Sweetingham, 1983), Portugal (Rego et al., 2000) and the USA (Gugino and Travis, 2003). The causal organism isolated for this disease was Cylindrocarpon species, which was a soil-borne pathogen (Francois et al., 2006) and this affects the roots of grapes (Brayford et al., 2004). In the black foot, several species of Cylindrocarpon are involved, namely C. destructans, C. obtusisporum, C. macrodidymum and C. fasciculare. But the most destructive one was the C. destructans (Halleen et al., 2004). Recently this disease is also reported with fungal species of genera "Dactylonectria" and "Neonectria" (Lombard et al., 2013). It is called "black foot" as it causes brown to black streaks or black discoloration at the main base of the rootstock. The damage caused by this disease on grapevine rootstock is presented in Figure 2.

This disease causes contraction in root biomass with deep necrotic lesions on root hairs (Agustí-Brisach and Armengol, 2013). It also affects plants aerial parts by weakening vegetation, bud breaking, uneven wood maturity and interveinal chlorosis (Larignon, 2004). This disease is most common around the coastal area where it is known as "aka young vine decline". It affects the roots of mature and young vines (Bleach et al., 2007). This disease can be controlled by planting the resistant rootstock against this disease or by controlling the disease management practices at the nursery level. In grapes rootstock, the least susceptible rootstock reported against this disease was 101-14 while the most susceptible rootstock to this disease was Riparia Gloire (Brown et al., 2013). The other resistant rootstocks reported against this disease are 'O39-16' and 'Freedom', which were taken from the species Vitis riparia (Gubler et al., 2004). While in the coastal areas, the rootstock A X R1 (Aramon Rupestris Ganzin No. 1) showed the highest resistance against this disease as compared to 140R and 039-16 (Battany, 2015).

Petri Disease

Petri disease is the most destructive disease of newly established vineyards, especially which have less than ten years' lifespan. This disease is reported by several countries around the world (Chicau et al., 2000; Crous

Table 1. Grapevine rootstocks tolerance reported to different biotic stresses (Phylloxera, Black foot disease, Petri disease, Crown gall and Nematodes)

Rootstocks	Phylloxera	Black foot disease	Petri disease	Crown Gall	Nematodes	References
196.17 Castel	High	-	-	-	-	Corso and Bonghi (2014)
Schwarzmann	High	Low	High	-	Medium	Corso and Bonghi (2014); Eskalen et al. (2001)
101-14*	High	-	-	-	-	Brown et al. (2013)
A X R1**	Low	High	High	-	-	Battany(2015); Eskalen et al. (2001)
Riparia Gloire	Medium	High	Medium	High	-	Corso and Bonghi (2014); Ferreira et al. (2018)
Freedom	Medium	High	-	Low	High	Corso and Bonghi (2014)
1103 Paulsen	Medium	Low	Medium	-	Medium m	Corso and Bonghi (2014); Ferreira et al. (2018)
O39-16	High	High	-	-	Low	Gubler et al. (2004)
Ramsey	High	-	-	High	High	Davut et al. (2018)
110-R	-	-	High	High	-	Davut et al. (2018); Eskalen et al. (2001)
SO4***	High	-	Low	Low	Medium	Schmid et al. (1998); Ferreira et al. (2018)
Kober 5 BB	Medium	-	-	High	Medium	Demir et al. (1998)

Full name of rootstocks: 101-14 (101-14 Millardet et de Grasset); A X R1** (Aramon Rupestris Ganzin No. 1); SO4*** (Selection Oppenheim 4)

and Gams, 2000). This disease is also called young vine decline or black goo decline (Gubler et al., 2004). It is a fungal disease and is mostly associated with P. Phaeoacremonium spp. (Gramaje and Armengol, 2011), and with other fungi Cephalosporium and Acremonium (Larignon, 2012). This disease shows both external and internal symptoms. The affected plant has undersized trees, having less vegetation and chlorotic leaves with necrotic borders. While internally, it causes brown necrosis and results in the formation of phenolic compounds, gums and tyloses around the xylem tissues (Gramaje and Armengol, 2011). The sap flux appears during necrosis and it is known as "black goo" (Larignon, 2012). The pathogens associated with this disease are soil-borne pathogens, and it is directly affecting the roots of the plant.

The incidence of this disease varies with rootstocks susceptibility. The rootstock "Freedom", "1103" and "SO4" are highly susceptible to this disease while the rootstocks "Salt Creek", "St George", "Harmony", "110R", "3309C", "Schwarzman" and "A X R1" and proved least susceptible to Petri disease (Eskalen et al., 2001). In another finding, the rootstock "Golia" showed its highest resistance against Petri disease. While the rootstocks "SO4", "Riparia Glorie" and "1103" were moderately tolerant, whereas the rootstock "IAC 572" was highly susceptible to this disease (Ferreira et al., 2018).

Crown gall

Crown gall is one of the most destructive diseases of grapes and it limits the grape production worldwide (Burr et al., 1997). The causal organism of this disease is bacteria "Agrobacterium vitis". This pathogen affects the main trunk and canes of the grapevine. This pathogen induces small galls on the infected part of the vine. The incidence of the disease started with the mechanical or with the frost injury at the sites. After the injury, small galls start to form on the infected parts. With disease severity, the galls start to enlarge. In most destructive cases, the pathogen disturbs the graft union, internal disturbance of the plant systematic system, or even death is seen in grape growing regions.

The disease incidence is normally reduced by good cultural practices along with effective bio-control and using tolerant rootstock. In grapes, Vitis raparia is considered as a tolerant species against this disease (Süle and Burr, 1998). Other rootstocks (i.e. Ramsey, 110-R and 1613-C) are tolerant against this disease (Davut et al., 2018). The incidence and variability of the disease vary with the climate of a region and rootstocks used. For example, "Chardonnay" and "Riesling" showed resistance in Chile, while these two genotypes were found susceptible in different regions of the USA (Burr et al., 1997). Similarly, the rootstock "Ramsay" was found highly resistant to this disease in Turkey, while it was found susceptible in South Africa (Davut et al., 2018). In another finding, the rootstocks "Kober 5 BB" and "Ramsey" were found moderately tolerant to crown gall disease (Demir et al., 1998).

Nematodes

In grapevine, root-knot nematode is another common destructive pest. In America, this pest reduces 20% of the total yields of grapevines and these nematodes are becoming a serious problem of Australian viticulture (Nicol et al., 1999). There are several common nematode species available in vineyards, such as Meloidogyne incognita, M. arenaria, Pratylenchus vulnus and M. javanica (Mckenry and Safdar, 2006). All nematodes species can penetrate deeply into the root of a plant for taking their nutrients. There are two types of nematodes, endoparasitic and ectoparasitic. Some species are endoparasitic nematodes entered into the root of the plant and consume nutrients from the root, while the ectoparasitic nematodes live outside the plant root and consume nutrients from outer tissues of the roots.

In grapes, the most common and destructive root-knot nematodes belong to the genus Meloidogyne. These nematodes are sedentary endoparasites, which hatch eggs at the second stage of juvenility and then migrate from soil towards the root of grapevine roots. After penetration in the roots, they form giant cells where it completes its next juvenile stages. A single gall or giant cell can consist of one to several females which can lay up to 1500 gelatinous matrix eggs (Brown et al., 1993). The best way to control nematodes is the use of resistant rootstock. In Australia, Ramsey rootstock is specifically used to control Meloidogyne species nematodes, while the rootstocks, V. champini, V. longii and V. cinerea have their resistance against root-knot other nematodes species (Nicol et al., 1999). Normally a single rootstock has resistance against single species, but now several developed rootstocks show their resistance against more than one nematode. Recently developed rootstocks RS-3, RS-9, USDA 6-19B, USDA 10-17A and USDA 10-23 Band have their resistance against more than one nematode species (Anwar and McKenry, 2006; Gu and Ramming, 2005). Recently, five grape rootstocks UCD GRN1, UCD GRN2, UCD GRN3, UCD GRN4 and UCD GRN5 are developed, which show their resistance against Paratylenchus hamatus, Mesocriconema xenoplax, Tylenchulus semipenetrans and Pratylenchus vulnus nematodes (Ferris et al., 2012). The specific rootstocks have their specific tolerance against each biotic stress (phylloxera, black foot disease, Petri disease, crown gall and nematodes) and these are shown in Table 1.

Response of Grapes Rootstocks to Abiotic Stresses

Salinity

Salts are present in the form of minerals and these are required for the growth of plants. These salts are readily available in soil and water. Every plant species has its specific potential to tolerate salt. The capacity of a plant to withstand or endure excessive salt in its root zone is called "Salt tolerance" (Adnan, 2004). Deficiency or toxicity of minerals, both are harmful to plants. The excessive salts present in the soil are called "salinity". Saline soils contain excessive amounts of salts (Na^+ and Cl^-) present in the soil that are harmful to grape growth and yield (Corso and Bonghi, 2014). In grapes, high salinity level causes disturbance in water and minerals uptake (Ismail et al., 2012). Grape genotypes are moderately tolerant of saline conditions however prolonged exposure to salt stress especially the chloride ions are highly damaging. These ions disturb the CO_2 assimilation and show effects on the stomatal conductance of grapes by its osmotic pressure (Cramer et al., 2007). Grapes growing in semi-arid irrigated areas are highly affected by this problem. The saline area of the world is increasing day by day and around 40% of world arable land is under saline conditions (Nabati et al., 1994).

Several factors are affecting soil salinity. It includes water or irrigation systems, the climate of a particular area, soil of grapes cultivated area and the genotypes, especially the rootstock–scion combination used for commercial cultivation. It is also reported that grapes rootstocks are more affected by Cl^- ions as compared to Na^+ (Cramer et al., 2007). The grapes rootstocks have great variability in taking up of these ions and their accumulation concentration varies with the selected rootstocks (Fisarakis et al., 2001). The wild species grapes (i.e. Vitis rupestris) have the maximum strength to exclude Cl- ions. Similarly, the grapevine's other rootstocks Vitis cinerea and Vitis champini tolerate saline conditions. For the good production of grapes, the combination of scion and rootstock is very essential. Vitis berlandieri had great strength to withstand salt but when vinifera scion was used. It reduces the strength of Na^+ and Cl^- expulsion. For example, a hybrid 41B which was the combination of Vitis berlandieri × Vitis vinifera lost its ability to exclude ions. Other reported grapes rootstocks (Ramsey and two hybrids, 1103 Paulsen and R2) showed a positive response towards salinity and increased the weight and bunches number (Walker et al., 2002). While Southey and Jooste (1992) recommended 101-14 Mgt and 143-B Mgt rootstocks against salinity. In a comparison of 101.14 and M4 as commercial rootstocks, M4 showed greater capacity to tolerate saline and drought stress by maintaining the physiological processes and photosynthetic activity (Meggio et al., 2014). Scion/rootstock grafting interaction showed that a sensitive variety (i.e. Syrah) grafted onto a moderately tolerant rootstock (i.e. 1103P) resulted in enhanced tolerance levels against salt stress as compared to a moderately tolerant variety (i.e. Muscat d'Italie), which was grafted on a sensitive rootstock (SO4) (Hanana et al., 2015).

Drought Stress

Climate change is one of the major threats and an increase in temperature on the landmass is causing the problems of drought and water scarcity. Among abiotic factors, drought is one of the main factors that directly affect the yield and productivity of a crop (Tsago et al., 2014). Based on climate models and weather predictions, it is assumed that there is an increase in arid land in the future (Dai, 2013). The solution to this problem is to use such genotypes that are greatly water efficient. This is one of the breeding key strategies for the improvement of genotypes (Marguerit et al., 2012).

In grapes, there are certain rootstocks, which use water more efficiently. Hence, the rootstock can play an effective role in drought by improving water efficiency. The efficacy of rootstock depends upon several factors, such as scion, vigor, stomatal conductance, aquaporin proteins and their combinations. In water stress conditions, stomatal conductance plays an effective role in water regulation and first organelles to respond to drought (Damour et al., 2010). Moreover, during stress conditions, a plant releases an abscisic acid hormone, which accumulates in grape leaves and this retards the plant cellular growth (Serra et al., 2013). This hormone is immediately released by the plant when it is in stress and the accumulation of abscisic acid in leaves causes closure of stomata. It is also observed that in water stress conditions, there is a production of aquaporin genes, which controls the water use efficiency of plants and these genes are more in drought-tolerant rootstocks.

Considering drought conditions, the rootstocks are divided into two categories: (i) the rootstocks having higher vigor and drought tolerance mechanism, (ii) rootstocks having least vigor and drought tolerance. The rootstocks exhibit higher vigor; they develop rapid roots growth in a later season, especially during wet conditions while rootstocks having less tolerance and develop roots in the early growing season without prevailing any wet conditions (Serra, 2013). In grapes rootstocks, it is essential to find both drought tolerance mechanisms to cope with water-scarce conditions. Plants may suffer metabolic changes due to exposure of abiotic stresses and these result in the decline of quality and productivity of grapevine. Rootstock integration approach can be used to mitigate such harmful impacts due to their abilities to enhance the drought tolerance mechanism during the scion. Under deficit water regimes, the grafter grapes rootstocks (i.e. Mgt 101-14 and 1103 Paulsen) showed significant alterations in grape technological maturity. The primary metabolism was not noticed in the rootstocks, while the accumulation of phenolic compounds in berries (e. g. anthocyanins) was very distinct. Plants under water stress and normal water regimes showed a significant difference in the gene and miRNA expressions. Results conferred that the rootstocks can modulate water stress effects on grapes through regulating the secondary metabolism (Zombardo et al. 2020).

Several grapevine rootstocks showed their variability in drought tolerance. In grapes, the highest drought tolerance was shown by V. champinii species (Padgett-Johnson et al., 2003). Early 1935, two rootstocks 'Riparia' and '101-14Mgt' were commonly used against drought (Dry and Coombe, 2005). After another rootstock "Ramsey" of V. champinii became very famous and was widely used in Australian vineyards due to its highest drought tolerance (Walker and Clingeleffer, 2009). The other grapevine rootstocks (i.e. Kober 5BB, 140 Ruggeri, Lider 116-60, 1103 Paulsen and Richter 110) showed their tolerance towards drought (Flexas et al., 2009). M4 rootstock planted at water-deficient and salt stress soil showed its tolerance towards salt stress and water stress. It also maintains its photosynthetic activity. In another finding, the rootstock '110R' showed the highest drought tolerance while '101-14Mgt' showed the medium tolerance, whereas 'Riparia' showed the least tolerance to drought (Ollat et al., 2015). Similar results were reported by Pouget and Delas (1989) and it showed that 'Riparia' and '101-14Mgt' were low in drought tolerance as compared to '110R'.

In other studies, it was reported that the level of aquaporin genes was different in grapes roots and leaves. The concentration of this gene was less in leaves where it reduced the transpiration rate, while its concentration was more in roots and it promotes roots elongation for water uptake (Galmés et al., 2007). In a hot and dry climate, rootstocks having vigor extends greater as compared to less vigorous rootstocks. Similarly, the grapevines grafted on 1103P rootstock showed a deep root system for water uptake during water stress as compared to 101-14 rootstock and it showed less depth during summer (Alsina et al., 2011). In grapes, certain hybrid rootstocks were developed with the combination of grapes xerophylic species V. rupestris. It was observed that the combination of V. berlandieri × V. rupestris was highly drought-tolerant (Tramontini et al., 2013). Similarly, the scions grafted on drought-tolerant rootstocks showed good evaporation, transpiration, carbon assimilation and water conductance (Alsina et al., 2011).

Low Temperature Stress

Low temperature is one of the major environmental constraints affecting grape production. Most cultivars growing in different geographical parts of the world belonging to European origin showed poor cold resistance (Yu et al., 2017). Low temperature disturbs the physiological and biological function of plants. In extreme cases, low temperature causes problems like crown gall or in severe situations, it may kill the whole grapevine. In grape genotypes, there is a minute difference in temperature of 1 to 2°C for cold tolerance, but this small difference is essential for vine survival. Because each genotype has a certain capacity to tolerate freezing temperature, especially in dormant seasons. In low temperatures, grapes cane showed cytoplasmic desiccation, bud freezing, and primordial death, especially in late winter (Anne, 2004).

The grapes rootstocks have their direct effect on freezing tolerance and scion biochemistry, whereas it

Table 2. Grapevine rootstocks tolerance reported to different Abiotic stresses (Salinity, Drought, Iron chlorosis, Low-temperature stress)

Rootstocks	Salinity	Drought	Iron chlorosis	Low temperature	References
196.17 Castel	High	High	-	-	Corso and Bonghi (2014)
Schwarzmann	Medium	Medium	-	-	Corso and Bonghi (2014)
101-14*	Low	Medium	Low	-	Alsina et al. (2011)
Riparia Gloire	Medium	Low	-	Low	Corso and Bonghi (2014); Ollat et al. (2015)
101-14Mgt	High	Medium	Low	-	Ollat et al. (2015); Southey and Jooste (1992)
Freedom	Low	Medium	Low	Medium	Gubler et al. (2004)
110R	-	High	-	-	Ollat et al. (2015)
1103 Paulsen	High	High	-	Medium	Corso and Bonghi (2014)
O39-16	High	-	-	-	Corso and Bonghi (2014)
Ramsey	High	Medium	Medium	-	Flexas et al. (2009)
3309C	-	-	High	High	Hoover et al. (2002)
SO4**	-	-	Medium	Low	Bavaresco and Lovisolo (2000)
Kober 5 BB	Low	Medium	-	High	Flexas et al. (2009)

Full name of rootstocks: 101-14 (101-14 Millardet et de Grasset); SO4** (Selection Oppenheim 4)

has an indirect effect on vine size (Striegler and Howell, 1991). The grapevine rootstocks are made up of genus 'Vitis' having several species. Each species has its specific cold tolerance. In laboratory conditions, V. rotundifolia tolerated -20 to -23°C, whereas in field conditions it can tolerate up to -13°C freeze (Clark and Watson, 1998). In grapes, Couderc 3309 (C3309), Kober 5BB (5BB) and Selection Oppenheimer No. 4 (SO4, V. spp.) are widely used rootstocks of cold regions as they can tolerate the low temperature. However, the performance of scion grafted on these rootstocks varies with the individual rootstock (Anne, 2004). In field conditions, the rootstock "C3309" acclimated more rapidly as compared to others, while rootstock "5BB" was least acclimatized rootstock (Miller et al., 1988). Similarly, another rootstock used in Eastern US is 3309 Couderc (C-3309). It is the combination of V. riparia and V. rupestris. It is a cold-hardy rootstock having tolerance against phylloxera and acidic soils as well (Hoover et al., 2002). The temperate region fruit rootstocks must contain the character of winter or cold hardiness (Nimbolkar et al., 2016).

Iron Chlorosis

The calcareous soils usually have iron (Fe) deficiency, leading to grapevines grown on calcareous soils having iron chlorosis. The grapevines are also sensitive to the calcareous soils, especially when these are rich in bicarbonates compounds. In grapevines, iron chlorosis causes stunted growth of the vine with low yield. Further, it also affects plant longevity and productivity (Covarrubias and Rombolà, 2013). During iron chlorosis, the production of Fe-reductase enzyme increases in grapevines and the plant excretes organic compounds and protons in its roots, thus resulted in increased Fe solubility and lowered pH. This condition of the plant is known as a strategy I (Jiménez et al., 2007).

In response to iron chlorosis (calcareous soils), grape rootstock (140 Ruggeri) is proved more efficient as it has not shown signs of iron deficiency. The high tolerance against iron deficiency was observed in this rootstock due to Fe (III)-reductase activity in its root. Moreover, this rootstock releases toxic phenolic compounds to the soil when planted in calcareous soils (Ksouri et al., 2006). The Fercal rootstock in France and 140 Ru (Vitis berlandieri × Vitis rupestris) rootstock in Italy, showed its highest tolerance against lime chlorosis (Fregoni and Bavaresco, 1986). The scion and rootstock combination is also necessary when planted at calcareous soils. The grape rootstocks 3309C showed a positive response when Pinot blanc cultivar was grafted on it (Bavaresco and Lovisolo, 2000). Similarly, the rootstock SO4 showed its medium tolerance against iron chlorosis (Bavaresco and Lovisolo, 2000).

Nowadays, mostly hybrid rootstocks are used against chlorosis. The hybrids showed the highest tolerance against chlorosis when a combination of Vitis riparia, Vitis cinerea and Vitis berlandieri were used. The hybrid rootstocks developed from the combination of Vitis rupestris and Vitis amurensis showed medium tolerance towards chlorosis. For example, the hybrid (Binova × Börner) showed its medium resistance towards lime chlorosis, whereas the rootstock hybrid developed with the combination of Teleki 5C × Börner and [Binova × (Binova × Teleki 5C) × Börner] showed their highest tolerance towards lime chlorosis (Pavlousek, 2009). The specific rootstocks have their specific tolerance against each abiotic stress (salinity, drought, iron chlorosis, and low-temperature stress) as shown in Table 2.

Conclusion

Globally, climate change is one of the major threats to sustainable grape production since it has shown to have a profound impact on the proliferation of several biotic and abiotic environmental stresses. Rootstocks have demonstrated the abilities to mitigate such stresses through their peculiar evolving plant traits. Several grape rootstocks are developed from Vitis and each species of Vitis has its specific characteristic and tolerance mechanism against specific ranges of stress. Grape rootstock responses to biotic and abiotic limiting factors are multifaceted which involves several ecological, physiological, molecular and genomic mechanisms. Many of these mechanisms have been discussed earlier where several plant traits related to such mechanisms and genomic areas have previously been recognized at the scion and rootstock levels. However, a better understanding of the specific role of alleles in these areas can benefit from manipulating the plant materials to handle the increased risk of biotic or abiotic stresses. In this article, several grapevine rootstocks with their specific resistance or tolerance features against a variety of stresses, including pests, disease, salinity and drought were reviewed. Prolongation of grapevine rootstock improvement through conventional and molecular breeding, extensive evaluation and crop management research is critical for the sustainability of the grape industry as new biotic and abiotic stress factors continued to emerge.

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