Effect of Rootstocks on Grapevines

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Grafting vines as a means of propagation was known as early as the 2nd century B.C. (Cato in his treatise *De agri cultua*.). The use of rootstocks in *Vitis*, however, was not extensively used until 1880 because it was the only effective method to combat the devastating root louse phylloxera, *Phylloxera vitifoliae* (Fitch), (Coombe, 1999). In California, grape growers have been using rootstocks for over 100 years (Foott et al., 1989). Much of the world's viticulture is based primarily on grafting, where the scion is a cultivar of *Vitis vinifera* and the rootstock is either a North American *Vitis* species or an interspecific *Vitis* hybrid (Weaver, 1976). The major reason to use rootstocks is in their resistance to some severe biotic problems such as phylloxera and nematodes. Reynolds and Wardle (2001) outlined seven major criteria for choosing rootstocks in the order of importance as phylloxera resistance, nematode resistance, adaptability to high pH soils, adaptability to saline soils, adaptability to low pH soils, adaptability to wet or poorly drained soils and adaptability to drought. Numerous reports have also proved that rootstocks affect vine growth, yield, fruit quality and wine quality. These effects take place in a more or less indirect manner and are consequences of interactions between environmental factors and the physiology of the scion and rootstock cultivars employed.

Effect of Rootstocks on Tolerance or Resistance to Pests/Pathogens

Resistance of Rootstocks to *Phylloxera*

Grape phylloxera historically has been among the worst threats to modern viticulture because of its ability to destroy vineyards by attacking vine roots. It was first found in California in 1873, about ten years after its detection in Europe. Between 1885 and 1900, a significant effort to develop rootstock cultivars was made after the discovery by European investigators of the resistance of native American *Vitis* species to the insect (Lider et al., 1995). These phylloxera resistant species include *V. riparia*, *V. berlandieri*, and *V. rupestris*. Subsequently, some rootstock cultivars with phylloxera resistance were produced by grape breeders (see appendix of this review). Harmon (1949) compared 13 selected rootstocks grafted with ten *V. vinifera* grape cultivars (including 'Zinfandel' and 'Gewurztraminer') in Oakville, California and found that the five highest ranking rootstocks were '*Rupestris* St. George', 'Dog Ridge', 'Constantia', '*Mourvedre* x *Rupestris* No. 1202', and '*Monticola* x *Rupestris*'. Harmon and Snyder (1952) also compared some selected rootstocks in the Napa Valley and found that 'St. George' was the one most resistant to phylloxera. Representative rootstocks with resistance to phylloxera are '*Riparia* Gloire', '1104-14 Mgt', 'SO4' (Selection Oppenheim 4), 'K5BB' (Kober 5BB), and 'St. George' (Harmon and Snyder, 1952; Lider et al. 1995; Mullins et al. 1992; Pearson and Goheen, 1988; Schmid et al., 1998; Shaulis and Steel, 1969; Snyder and Harmon, 1956).

Resistance of Rootstocks to Root Nematodes

Root nematodes (*Meloidogyne spp*.) are another severe pest problem in *Vitis*. Nematode resistant *Vitis* species include *V. champini*, *V. cinerea, and V. longii* (Mullins et al., 1992.). Magoon and Magness (1937) tested 42 rootstocks in South Mississippi and found only 6 of them exhibited resistance to root nematodes, namely, 'Barnes' (*V. champini*), 'Joly' (*V. champini*), '*Monticola* x *Rupestris*', 'Ramsey' (*V rupestris* x *V. candicans),* '*Riparia* x *berlandieri* 161-49', and '*Rupestris* St. George'. Some other rootstocks considered to be resistant to nematodes are 'Ramsey', 'Dog Ridge', 'Harmony', '1613 C' and 'SO4' (Cirami et al., 1984; Harmon, 1949; Harmon and Snyder, 1952&1956; McCarthy and Cirami, 1990; Mullins et al. 1992; Pearson and Goheen, 1988; Wachtel, 1986).

Resistance of Rootstocks to Pierce's Disease

Pierce's Disease is a fatal grape vascular disease in North and Central America viticulture regions that have mild winters (Mullins et al., 1992). It is caused by a Gram-negative bacterium, *Xylella fastidiosa*. *V. rupestris, V. berlandieri, V. aestivalis, V. champini* and *V. rotundifolia* x *V. bourquiniana* are resistant. Rootstock cultivars 'Barnes', 'Dog Ridge', and 'B-45' were reported to be the most resistant (Loomis, 1965; Pearson and Goheen, 1988).

Resistance of Rootstocks to Crown Gall

Crown gall of grapevines is a tumor inducing disease caused by *Agrobacterium tumefaciencs* (Smith and Townsend) Conn and *A. vitis*. It is widespread and economically important in vineyards and nurseries. Inoculating stem tissue of greenhouse rootstocks '5C' (Teleki 5C), 'SO4', 'K5BB', '8B' (Teleki 8B) and '125AA' with *A. tumefaciens*, Goodman et al. (1993) found that '5C' was suscepable, while 'K5BB' was resistant to this disease. They suggested that '5C' is an inordinately sensitive host to *A. tumefaciens* and its use in replanting vineyard sites where spring frosts are likely is hazardous because crown gall is exacerbated by damage caused by winter or spring cold. Sule and Burr (1998) conducted research involving a crown gall-susceptible *V. vinifera* cultivar 'Kiralyeanyka' and grafted it to '5C' (susceptible) and 'Gloire '(resistant) rootstocks. They found that only 13% of the originally planted vines on '5C', but 82% on 'Gloire' were still alive by the end of the sixth year after inoculation, indicating the relative resistance of *V. riparia* to crown gall (Gao et al., 1993; Sule, 1999).

Resistance to Other Diseases

Grapevines are subject to several other diseases. Some of the major diseases and rootstock species with resistance are listed in Table 1.

Effect of Rootstocks on Tolerance of Abiotic Stress

Grapevines are subjected to various abiotic stresses. Tolerance of rootstocks to lime soil, salinity, drought, flood, and low temperarues has been reported.

Tolerance of Rootstocks to Lime Induced Chlorosis

Lime induced chlorosis is due to it's the high pH of the soil. The chlorosis may be caused by a low iron translocation to leaves (Bavaresco et al., 1992). Bavaresco et al. (1993) reported the effect of rootstocks on the occurrence of lime-induced chlorosis of potted *V. vinifera* 'Pinot Blanc', a susceptible cultivar to lime-induced chlorosis. They found that the iron-efficient rootstock '140 Ruggeri' (*V. berlandieri* x *V. rupestris*) did not induce chlorosis when growing on calcareous soil, while the iron-inefficient rootstock '101-14' (*V. riparia* x *V. rupestris*) did. They suggested that the resistant rootstocks have a "strategy" to overcome chlorosis with higher root iron uptake and greater reducing capacity (Bavarresco et al. 1991). Later, Bavaresco and Lovisolo (2000) confirmed that the chlorosis in 'Pinot Blanc' was reduced when grafted to rootstocks 'SO4' and '3309C', which was thought to be related to different hydraulic conductivities between the rootstock and the own-rooted vines. For example, the own-rooted 'SO4' showed the highest specific conductivity, associated with the highest rate of shoot growth and leaf chlorophyll content. Species reported to be tolerant to growing on lime soil are *V. berlandieri* and *V. cinerea*; some representative rootstocks include '41 B', '333 EM' and 'Fercal' (Kocsis et al., 1998; Mullins et al., 1992; Zimmermann and Zimmermann, 1973).

Table 1. Grape diseases and resistant *Vitis* species.

Disease	Resistant *Vitis sp.*	References
Downy mildew *(Plasmopara viticola)*	*V. cinerea, V. riparia, V. rupestris, V. berlandieri, V.vulpina ,V. aestivalis*	Brown et al., 1999a b; Staudt and Kassemeyer, 1995.
Powdery mildew *(Uncinula necator)*	*V. cinerea, V. rupestris, V. riparia, V. berlandieri, V. aestivalis*	Staudt, 1997; Alleweldt and Possingham, 1988.
Grapevine leaf roll virus (GLRV)	*V. cinerea*, *V. riparia*	Liu and Kong, 1998.
Fusariosis *(Fusarium oxysporum f.sp. herbomontis)*	*V. vulpina* *(V. riparia, sensitive)*	Andrade et al., 1993.
Botrytis bunch rot (*Botrytis cinerea)*	*V. riparia* x *V. berlandieri*	Cristinzio et al., 2001.
Black rot *(Guignardia bidwelii)*	*V. rupestris, V. riparia, V. berlandieri*	Pearson and Goheen, 1988

Tolerance of Rootstocks to Low Soil pH

Although grapevines can grow in soils with a wide range of pH (4.5-6.5), very acid soils present a problem. Based on vine growth, Himelrick (1991) found different responses of *Vitis* species or cultivars to low soil pH. The cultivars most tolerant to strong acid soils were *V. labrusca* cv. 'Concord' and 'Catawba', along with rootstock 'SO4' and '3309C', and the hybrid cultivar 'Seyval'; *V. vinifera* 'White Riesling' and 'Chardonnay' were the most intolerant. The use of acid-tolerant rootstocks, such as 'SO4' and '3309C', was highly recommended.

Tolerance of Rootstocks to Salinity

V. champini and *V. vinifera* are considered to be tolerant to salinity (Leon et al. 1969). When 'Cardinal' and 'Thompson Seedless' were grafted to rootstock 'Dog Ridge', '1163-3', and 'Salt Creek', the accumulated chloride contents in leaves were only $^1/_3$, $^1/_{10}$, and $^1/_{16}$ of those of the own-rooted vines, respectively (Leon et al. 1969). Grown at high salinity conditions, 'Shiraz' grape had higher wine K^+, pH and color hue on 'Ramsey', '1103 Paulsen' and '140 Ru' than on their own roots (Walker et al., 2000). Under a relatively high saline soil condition in South Africa, different rootstocks showed different symptoms of stress; rootstocks '101-14 Mgt' and '143-B Mgt' were recommended for salinity tolerance (Southey and Jooste, 1992). More recently, rootstock effects on salt tolerance of 'Sultana' were reported by Walker et al. (2002); the best performing rootstocks were 'Ramsey', '1103P' and 'R2', which could impart most vigor to the scions. Salinity tolerance may be influenced by the different root distribution of rootstocks (Southey, 1992) and may involve the contribution of chloride-exclusion on promising rootstocks (Walker et al., 2002).

Tolerance of Rootstocks to Drought

Rootstocks from *V. berlandieri* x *V. rupestris* were considered to be drought tolerant (Ezzahouani and Williams, 1995). Hybrids of *V. berlandieri* x *V. riparia* were reported to be more tolerant to drought by Kocsis et al. (1998) while reported to be less tolerant to drought by Carbonneau (1985) and Shaulis and Steel (1969). It was pointed out that the drought resistance classification of rootstocks might vary from country to country (Ezzahouani and Williams, 1995). In countries where water is a limiting factor to grapevine productivity, e.g. Morocco, using drought resistant rootstocks '110R', '140Ru' and '1103P' should be beneficial (Ezzahouani and Williams, 1995).

Tolerance of Rootstocks to Poor Drainage

Soil drainage is an important aspect for site selection of grapevines. *V. cinerea* was considered to be flood tolerant (Pongraz, 1983). In a study done by Striegler et al. (1993), rootstock cultivars 'St. George', '3309C', 'Seyval', '*Riparia* Gloire', 'K5BB' and 'Cynthiana' and scion 'Seyval', a flood susceptible cultivar, were evaluated. Results demonstrated that flooding tolerance was increased slightly by grafting on rootstock '3309C'. The rate of shoot elongation was considered the most sensitive index of flood tolerance.

Tolerance of Rootstocks to Cold Temperatures

There have been only a few studies related to rootstock effects on scion cold hardiness. Miller et al. (1988a) found differences of cane and bud hardiness of rootstock 'K5BB', '3309C' and 'SO4'. Rootstock '3309C' had the most cold hardy canes and buds; its acclimation in fall was faster and deacclimation in spring was slower than 'K5BB' and 'SO4'. They also found that rootstock cultivars affect cold hardiness of scions grafted to them (Miller et al., 1988b). For example, grafted 'White Riesling' was significantly hardier than the own-rooted vines. Different rootstocks had a differential influence on cold hardiness of scion cultivars, the observed differences in the LT_{50} values (the low temperature lethal to 50% of primary buds death) ranged from 0.5˚C to 3.0˚C in cane hardiness; 'White Riesling' grafted to '3309C' had significantly fewer shootless nodes and grafted ‘White Riesling’ on ‘K5BB’ had hardier buds in most cases. They proposed that ‘3309C’ would be the cold hardiest. Using ‘Seyval’ as scions (grafted to ‘K5BB’, ‘3309C’ and ‘Seyval’) plus own-rooted ‘Seyval’ as a control, Striegler and Howell (1991) found that the rootstock did not affect the distribution of hardy canes within the canopy; ‘Seyval’ grafted on ‘3309C’ appeared to be the most cold hardy. Palliotti et al. (1991) investigated the rootstock effects on frost sensitivity of grapevines ‘Cabernet Sauvignon’ and ‘Chardonnay’, there was less damage of scions on ‘K5BB’ and ‘1103P’ than on ‘SO4’ and ‘420A’. The development of replacement buds after cold damage was greater in ‘Cabernet Sauvignon’ on ‘1103P’ than in ‘Chardonnay’ on ‘K5BB’.

Effect of Rootstocks on Vine Growth and Production

Effect of rootstocks on scion yield and vigor has been well documented; most results showed that rootstock significantly affects scion vigor and yields. Vaile (1937) found that rootstocks could exert a definite influence on the behavior of scion cultivars, as shown by increased vine vigor and yields. Snyder and Harmon (1948) found that vigorous rootstocks produced the most wood and produced it faster in the first season of growth. Cultivars on weaker stocks produced less wood but held up fairly well in fruit production. They suggested that yields were possibly negative-correlated to vine vigor, which was also demonstrated by Wolf and Pool (1988) and Parejo et al. (1995). In a test of 14 grape rootstocks and 12 scion varieties, Loomis (1952) found that some of the rootstocks improved yields, vigor, and longevity on nearly all scion varieties compared to grown on their own roots; rootstock ‘Dog Ridge’ was noticeable for its yield increase. Hedberg (1980) found that yields of all grafted cultivars were much higher than those of the own-rooted vines, especially on ‘Ramsey’ and ‘Dog Ridge’ rootstocks. Ferree et al. (1996) reported increased yield of grafted ‘Cabernet Franc’and ‘White Riesling’ than the own-rooted vines. Wunderer et al. (1999) reported that ‘Gruner Veltliner’ grape had a higher wood productivity when grafted on all three rootstocks tested (‘SO4’, ‘K5BB’ and ‘5C’) than that of the own rooted vines.

Effect of rootstocks on scion vigor and yield is specific to scion/rootstock combinations. Rootstock ‘AxR No. 1’ had the best yield for ‘Cabernet Sauvignon’ and ‘Chardonnay’, while ‘1202C’ imposed best vigor (Foott et al., 1989). In a trial of soilless culture, Fardossi et al. (1995) found that shoot growth of ‘Gruner Veltliner’ was slower on ‘5C’ and ‘Fercal’, but more rapid on ‘1103P’, ‘725P’ and ‘125AA’; ripening occurred earlier on ‘1103P’, ‘G1’ and ‘*Riparia* Sirbu’ than on other rootstocks. Colldecarrera et al. (1997) reported that rootstocks ‘110 R’, ‘SO4’ and ‘140 Ruggeri’ had the most vigorous scions while ‘110 R’ and ‘140 Ruggeri’ had the most productive scions. Ezzahouani and Larry (1997) found that the scion cultivar ‘Italia’ was most vigorous on rootstocks ‘101-14’ and ‘*Rupestris* de Lot’, and had highest yields on ‘140 R’ and ‘1103 P’. Lovicu et al. (1999) also found differences among rootstocks; yields of ‘Chardonnay’and ‘Tocai’ were highest on ‘420A’, followed by those on ‘*Rupestris* de Lot’.

There also have been reports about negative or indifferent effects of rootstocks on scion vigor and yields. ‘Chardonnay’ vines on rootstocks ‘5C’, ‘K5BB’, ‘G13’, ‘Teleki 8B’, ‘SO4’, ‘1103 P’ and ‘41 B’ had no significant effect on yields when compared to yields from the own-rooted vines (Boselli et al., 1992). The size of ‘Chardonnay’ vines was even reduced by rootstock ‘K5BB’ and ‘1103P’ (Ferroni and Scalabrelli, 1995).

There were no significant differences between the own-rooted or grafted 'Gewürztraminer' regarding yield, fruit composition and pruning weight (Reynolds and Wardle, 1995). Novello et al. (1996) showed that 'Erbaluce' grape had higher vigor when grown on its own roots than on rootstocks '101-14', '420 A', '*Rupestris* du Lot', 'K5BB' or 'SO4'. Sommer et al. (2001) found that grafted 'Sultana' vines were always less fruitful than the own-rooted vines. In an experiment involving nine wine grape cultivars ('Chardonnay', 'Gewürztraminer', 'Ortega', 'Riesling', 'DeChaunac', 'Marechal Foch', 'Okanagan Riesling', 'Seyval blanc', and 'Verdelet') and four rootstock cultivars ('3309C', 'K5BB', '5C', and 'SO4'), Reynolds and Wardle (2001) found that yield per vine, clusters per vine, cluster weight and berry weight were not affected by rootstocks. They suggested that rootstocks might not provide any significant advantage over own-rooted vines under conditions in arid parts of the Pacific northwestern U.S. and British Columbia.

Effect of Rootstocks on Fruit and Wine Qualities

Quality of fruit and wines is closely linked. Grape quality factors, which eventually affect wine quality, include soluble solids (˚Brix), organic acids, pH, phenolics and anthocyanin, monoterpenes, other components (for example, proline, arginine and other amino acids), and asynchronous berry development (Jackson and Lombard, 1993). Rootstocks usually affect these factors in an indirect manner.

Hale and Brien (1978) investigated the influence of the rootstock 'Salt Creek' (*V. Champini*) on composition and quality of 'Shiraz' grapes and wine for the first time. Their results were that grafted 'Shiraz' had berries with lower soluble solids, but had higher pH, titratable acidity, malate and potassium. Wines made from grafted vines were less dense, had a duller hue than from the own-rooted vines, and had lower values for total phenolics, anthocyanins and ionized anthocyanins. Wine tasters could tell the difference between wines made from grafted or own-rooted vines. Wine quality decreased after grafting. Grafting 'Shiraz' to rootstocks 'Ramsey', 'Dog Ridge', 'Harmony', 'Schwarzmann' and '1613', Cirami et al. (1984) found the fruit juice of their own-rooted vines had lower pH than of grafted vines; wine made from this juice had higher color density and ionized anthocyanins, and the lowest wine color hue. Higher wine K^+, pH and color hue of grafted 'Shiraz' than of the own-rooted were also found by Walker et al. (1998 &2000).

Fruit and wine quality of 'Cabernet Sauvignon' and 'Chardonnay' were affected by rootstocks. Wines of grafted 'Cabernet Sauvignon' and 'Chardonnay' contained significantly less tartaric and more malic acid than of the own-rooted (Walker et al., 1998). Boselli et al. (1992) grafted 'Chardonnay' to seven rootstocks and found that rootstocks 'SO4' and 'K5BB' produced fruit with the highest juice K^+ content and pH while '1103P' and '5C' made the lowest. Huang and Ough (1989) showed that amino acid content of 'Chardonnay' juice was higher for vines on the most vigorous rootstocks although amino acid content of 'Cabernet Sauvignon' was less influenced by rootstocks. Using 19 rootstocks and four scion cultivars of 'Riesling', 'Ruby Cabernet', 'Shiraz' and 'Chardonnay', Ruhl et al. (1988) showed that own-rooted 'Riesling', 'Ruby Cabernet' and 'Shiraz' had low to medium juice pH while the own-rooted 'Chardonnay' had higher juice pH; rootstocks 'Harmony', 'Dog Ridge', 'Freedom' and '*Rupestris* du Lot' generally caused a high juice pH, whereas ‘140R’, ‘1202’, ‘5A’, ‘SO4’ and ‘101-14’ had low pH. The profiles of free amino acids were affected by rootstocks (Treeby et al., 1998); free assimilable amino-N was lowest in ‘Chardonnay’ grapes on ‘140 Ruggeri’ and ‘101-14’ rootstocks, and was highest on the own-rooted or on ‘Schwarzmann’ and ‘K51-40’ rootstocks.

Rootstocks also influence fruit and wine quality of other grape cultivars. Kubota et al. (1993) grafted ‘Fujiminori’ (*Vitis vinifera* x *V. labruscana*) on 7 different rootstocks (‘3309C’, ‘3306’, ‘101-14’, ‘5C’, ‘8B’, ‘SO4’ and ‘420A’) and found that glucose and fructose contents in the pulp were higher in berries grafted on ‘3309C’, ‘3306’ and ‘8B’ although the predominant sugars in berry pulp and skin were glucose and fructose, irrespective of rootstocks; the highest level of skin anthocyanin was observed in berries from vines grafted on ‘3306’. Kaserer et al. (1997) tested the effects of rootstocks ‘K5BB’, ‘5C’, ‘SO4’, ‘41B’, ‘Fercal’, ‘EM333’, and ‘Ruggeri 140’ on ‘Gruener Veltliner’ and found that the accumulation and concentration of sugars, the decrease in titratable acidity, the ratio of malic and tartaric acids, the K^+ concentration in berry juice, and the wine quality were all affected by rootstocks. He concluded that rootstock ‘SO4’ was the best for all sites tested. In order to study the lack of acidity in wines made of *V. vinifera* cv. Negrette, a problem partially due to high potassium content, Garcia et al. (2001a&b) grafted ‘Negrette’ onto rootstocks ‘101-14 Mgt’, ‘3309C’ and ‘SO4’ and grew them in a nutrient solution; they concluded that ‘3309C’ was the most appropriate rootstock with less potassium absorption than other rootstocks. The ‘Negrette/3309C’ combination produced wines with the highest total acidity and tartaric acid content.

Effect of Rootstocks on Vine Phenology

Bud break is affected by rootstocks. Prakash and Reddy (1990) reported the effect of different rootstocks (‘St. George’, ‘Gulabi’, ‘Teleki 5A’, ‘1616’, ‘1613’ and ‘Dog Ridge’) on budbreak of grapevine ‘Anab-e-Shahi’. They found that the overall duration of budbreak was not significantly affected by rootstock although the number of days required for budbreak was shorter with ‘Gulabi’ and longer with ‘Dog Ridge’. Tangolar and Ergenoglu (1989) found that budbreak time was not significantly affected by rootstock although it tended to be earlier on ‘420A’ and ‘*Rupestris* du Lot’.

Time of fruit bearing can be affected by rootstock. Using the scion cultivar ‘Erbaluce’ and rootstocks ‘101-14’, ‘420 A’, ‘*Rupestris* du Lot’, ‘K5BB’, and “SO4’, Novello et al. (1996) found ‘420A’ the most efficient rootstock in stimulating fruit bearing, i.e. the rootstock inducing greatest precocity. Fardossi et al. (1995) grafted grape ‘Gruner Veltliner’ on ten rootstocks and found that the ripening occurred earlier on ‘1103P’, ‘G1’ and ‘*Riparia* Sirbu’ than on the other seven rootstocks.

Interactions between Rootstocks and Scions

The way rootstocks interact with scions is still unclear. The primary change after grafting is the direct replacement of the root system. Root anatomy and morphology, development and distribution may be different among rootstock species (Richards, 1983). The replaced roots will directly affect water and mineral absorption, which eventually affect growth of the shoot system and modify vine physiology.

Root Systems of Rootstocks

Functions of grapevine roots include anchorage, storage of reserves, uptake and translocation of water and minerals, and supply of growth substances (Richards, 1983). Most grapevine roots occur in the top 100 cm of soil although individual roots might penetrate to a depth of 600 cm or even more. The fine roots, which comprise the majority of absorptive roots, are found in the top 10-60 cm (Richards, 1983). The main framework roots (6-100mm in diameter) are usually found at a depth of 30-35cm from the surface. Permanent roots (2-6mm in diameter) arise from the main framework, grow more horizontally and are usually found within the top 20-50 cm layer (Mullins et al., 1992). The anatomy and morphology, development and distribution of root systems may be different on rootstock species, which largely depend on genetic properties. For instance, the main roots of *V. rupestris* form narrow angles with the vertical axis and can penetrate deeply, while those of *V. riparia* form wide angles and remain relatively shallow (Perold, 1927). One unique characteristic of grape roots is that the commencement of spring root growth is after budbreak. This may affect shoot growth by absorbing water and nutrients, and the supply of root synthesized plant hormones, e.g. cytokinins and gibberellins (Richards, 1983).

Root study is difficult because roots cannot be readily viewed in soil or separated from it (Richards, 1983). Study of grape roots, however, has received a moderate degree of attention throughout the past century, beginning with Colby's (1922) "Preliminary Report of the Root Systems of Grape Varieties", in which he found that "feeding roots" were found "from a depth of six inches" and that "it was often necessary to use a pick" (to examine the roots) "from four feet down". Wiggans (1926) reported roots at a depth of 30 feet on grapes grown on a loess soil. Later, Doll (1955) studied six-year-old 'Concord' grape roots on a loess soil and found "very extensive" root development, reaching 14.5 feet in depth and over 24 feet in horizontal spread.

Research on root distribution of grape rootstocks is relatively scarce. Harmon and Snyder (1934) studied root distribution on grafted vines that averaged about 25 years old, growing on sandy loam soil with depths to hardpan ranging from 32 to 88 inches (average 55 inches). Total root weights varied from about 4,000g to over 18,000g. The differences appeared to be loosely correlated with the rootstock and to a lesser degree, with the +scion. Williams and Smith (1991) studied the root distribution of grafted 'Cabernet Sauvignon' on rootstocks 'Aramon Rupestris Ganzin No. 1' (AxR 1), 'St. George' and '5C', and found large differences in the number of roots counted among the rootstocks, with 'AxR 1' having the lowest number and 'St. George' having the greatest number per soil wall profile. There were no apparent differences in the distribution of roots of any dimension within the soil among the rootstocks. Later, using the same materials, Morano and Kliewer (1994) studied the root distributions in detail. They found that there was a significant difference among rootstocks for both total root numbers and the class of smallest root size. In their study, 'St. George' had a different root distribution pattern from either '110R' or 'AxR 1'. It also had the largest root numbers. In addition, there was a significant rootstock-soil depth interaction for the roots with diameter classes of 2mm-5mm and 5mm-12mm, indicating the influence of soil characteristics on root distribution. Grant and Matthews (1996) studied the effect of rootstocks on characteristics of 'Chenin blanc'. The only difference they found between the two rootstocks was the root area ratio (root surface area/plant dry weight); 'Freedom' had a greater ratio than 'St. George'. Besides the above findings, there have been reports about differences of root density (Daulta and Chauhan, 1980), and distribution (Harmon and Snyder, 1934; Perry and Lyda, 1983) among grapevine species or cultivars.

Mineral Uptake of Rootstocks

There have been many reports concerning mineral uptake and its distribution in grapevines. Cook and Lider (1964) reported that rootstocks had no effects on foliage Ca^{2+} and Mg^{2+}; but contents of nitrate, K^{+}, and total P were higher in petioles on 'St. George' than on '99-R'. Tangolar and Ergenoglu (1989) grafted 'Gruner Veltliner' onto 10 rootstocks and concluded that leaf N and Fe levels were similar for scions on all rootstocks. The leaf K^{+} was highest on '*Rupestris* du Lot' and '110 R', leaf P was highest on '110 R', leaf Ca^{2+} was highest on '420A', and Mg^{2+}, Mn^{2+} and Zn^{2+} were highest on '41A'. Fardossi et al. (1995) used the same scion and rootstocks and confirmed that leaf mineral concentrations could be influenced by rootstock, but the changes were in the normal range. They also tested 'Neuburger' grape on 12 different rootstocks to determine the micro- and macronutrients in leaf blades and found that vines on the Euro-American hybrid rootstocks '26G' and '333 EM' showed the lowest K^{+} but the highest Ca^{2+} concentrations (Fardossi et al., 1992). There were considerable differences among the rootstocks tested for K^{+} and Ca^{2+} concentrations. Brancadoro and Valenti (1995) grafted 'Croatina' onto 20 different rootstocks and found that K^{+} content of must and leaves was affected significantly by rootstocks. They suggested that K^{+} deficiency should be improved by choosing an appropriate rootstock. Ruhl (1991) also suggested that K^{+} accumulation in scions is affected by rootstock genotypes.

The differences in nutrient uptake and distribution may be explained in different ways. First, rootstocks may have different absorption capability or tendency for some specific minerals. For example, Bavaresco et al. (1991) pointed out that rootstocks with lime resistance have a 'strategy' to overcome chlorosis with high root iron uptake and reducing capacity. Grant and Matthews (1996) thought that different rootstocks might have different ability to absorb phosphorus. Ruhl (2000) also found a high K^{+} absorbing mechanism on some rootstocks, which would affect pH of fruit and wines. Second, translocation and distribution of nutrients may differ among rootstocks. Bavaresco and Lovisolo (2000) confirmed that the chlorosis should be attributed to the different hydraulic conductivities between the rootstocks and the own-rooted vines for iron. Giorgessi et al. (1997) found differences in number and size of the xylem vessels between rootstocks and own-rooted vines. Third, hormone synthesis of rootstock roots and their translocation may be different. Skene and Antcliff (1972) found different levels of cytokinins in bleeding sap of rootstocks. For instance, rootstock '1613' contained less cytokinins in the sap, both on a concentration basis and in terms of the total amount passing to the shoot each day. Fourth, some nutrients might be assimilated mostly by roots, thus reducing the amount translocated to the shoots. Keller et al. (2001) discovered that over 85% of nitrogen was assimilated by way of vine root metabolism.

Rootstock Affects Scion Physiology

Rootstocks affect photosynthesis and dry matter partitioning of scion cultivars, which influence vegetative growth and yield. During (1994) studied rootstock effects on scion photosynthesis and found that the rootstock effect on gas exchange is scion-specific, for example, ‘Riesling’ grafted to ‘K5BB’ had significantly higher rates of daily maximum photosynthesis than the own-rooted vines. Carboxylation efficiency is distinctively higher in all grafted varieties. The rates of photosynthesis and stomatal conductance are also influenced by rootstock genotype (and age). In some cases, grafting increased the rate of photosynthesis more than could be attributed to changes of stomatal conductance. He suggested that grafting vines to appropriate rootstock cultivars that favor the increase of carboxylation efficiency of scion leaves may help to improve drought resistance, by raising water use efficiency. Bica et al. (2000) found that the effect of rootstocks was significant on leaf area, chlorophyll content, stomatal conductance and quantum yield. ‘Chardonnay’ vines grafted on ‘SO4’ showed lower photosynthesis, quantum yield, stomatal conductance and chlorophyll content than on ‘1103P’. ‘Pinot noir’ plants grafted on ‘SO4’ and ‘1103P’ showed similar rates of assimilation. ‘K5BB’ rootstock improved leaf area, stomatal conductance and transpiration in comparison with ‘SO4’.

Koblet et al. (1996) demonstrated that rootstocks had a marked effect on net assimilation rates on ‘Pinot noir’. The highest photosynthetic rates were found on ‘K5BB’ and the lowest on ‘SO4’ if the vines were unfertilized. However, ‘SO4’ could give the highest photosynthetic rates in the fertilized vines, so the effect might not be due to rootstocks themselves. They suggested that choosing of rootstocks should be based on soil fertility to avoid unnecessary fertilization. Photosynthetic rates varied differently for *V. vinifera* ‘Muller Thurgau’ on different rootstocks (Candolfi-Vasconcelos et al., 1997). Among rootstocks ‘K5BB’, ‘SO4’, ‘8B’, ‘5C’, ‘3309C’ and ‘Ruggeri 140’, ‘K5BB’ and ‘SO4’ had the highest and ‘Rugeri 140’ had the lowest photosynthesis rate. Their work (Candolfi-Vasconcelos et al. 1994) on ‘Pinot noir’ showed that vines on ‘101-14 Mgt’ had higher CO_2 assimilation, transpiration rates, and higher water use efficiency than on ‘3309C’. Johnson et al. (2000) found that under non-irrigated conditions, rootstock *V. riparia* can modify gas exchange behavior of scions even though vine water status was not altered. This could explain the effect of rootstocks on drought resistance, which agreed with During’s suggestions (During, 1994). Incono et al. (1998) found that the drought resistant rootstock was not always transferred to scions; only hybrid rootstock ‘H1’ and ‘H8’ transmitted the resistance to ‘Muller Thurgau’ grape. Incono and Peterlunger (2000) also found that scion-rootstock combinations that showed high ABA flux and low net photosynthesis under well-watered conditions were those classified in the drought tolerant groups. Recently, Keller et al. (2001) found that chlorophyll content (which influences photosynthesis) was highest for vines grafted on ‘K5BB’ and lowest for ‘3309C’. Differences due to rootstocks were mostly unaffected by soil nitrogen level except for vines grafted on ‘SO4’.

In addition to the effect of rootstocks on photosynthesis, transpiration and water use efficiency, partitioning of dry matter might also be affected by rootstocks. Williams and Smith (1991) found no differences in dry matter partitioning on ‘Cabernet Sauvignon’ grafted to ‘AxR 1’, ‘St. George’, and ‘5C’. Tardaguila et al. (1995), however, found that the dry weight partitioning of ‘Cabernet Sauvignon’ is different on rootstocks; rootstock ‘101-14’ favored dry weight accumulation in canes while ‘41B’ favored accumulation in clusters.

Conclusions

The above review described the complicated influences of rootstocks on scions besides the resistance to phylloxera. The rootstock influence may affect scion vigor, yields, and fruit and wine qualities. These influences may be either positive or negative. Striegler and Howell (1991) tried to explain this effect by dividing the effect of rootstock into direct effect and indirect effect (their original purpose was to explain the effects of rootstock on scion cold hardiness). The direct effect is caused by the function of root systems and the indirect effect is due to the vine size modification. Considering the fact that different rootstocks may have varied root distribution patterns, root dry weight and root numbers (Morano and Kliewer, 1994; Williams and Smith, 1991), they may have some direct influences on scion cultivars, e.g. mineral uptake. The indirect influences, however, are rootstock-scion specific and require further investigation.

Research on grape rootstocks still appears to be superficial although it has been ongoing for years. We know, for example, rootstocks may be able to affect budbreak, but we don't know the exactly mechanism. Assuming that the budbreak is the results of hormone interactions, can rootstocks affect the budbreak of scions via the alteration of plant hormone content? We may also find it interesting to study the characteristics of rootstocks themselves (for example, water use efficiency and photosynthesis) and to compare those with grafted scions, i.e., taking both own-rooted scions and rootstocks as controls.

Based on this review, some conclusion can be drawn:

1. Besides the original purpose of using its resistance to phylloxera, *Vitis* rootstocks influence vegetative growth, yields, and fruit and wine quality. These influences may be either positive or negative and affect scion cultivars *via* physiological processes.

2. Effects of rootstock are comprehensive. There may be primary (direct) and secondary (indirect) effects.

3. Different rootstocks may have different effects on the same scion and *vice versa*.

4. Selection of rootstocks must be done carefully for 'new' environments, for example in Nebraska.

5. Research on rootstock effects on grape scions is still superficial. More research needs to be done in the field of rootstock/scion relationships.

Appendix: Some Internationally Important Rootstocks

Name Abbreviation	Full Name	Heritage	Alias
A x R 1	Aramon Rupestris Ganzin No. 1’	*V. vinifera* x *V. rupestris*	ARG1
Dog Ridge	Dog Ridge	*V. champini*	
Fercal	Fercal	*V. berlandieri* x 333EM	
Harmony	Harmony	*V. champini* x 1613C	
Gloire	*Riparia* Gloire (de Montpellier)	*V. riparia*	
St. George	*Rupestris* St. George	*V. rupestris*	*Rupestris* du Lot
Schwarzmann	Schwarzmann	*V. riparia* x *V. rupestris*	
SO4	Selection Oppenheim de Teleki No. 4	*V. berlandieri* x *V. riparia*	
K5BB	Kober 5BB	*V. berlandieri* x *V. riparia*	Teleki 5BB
5C	Teleki 5C	*V. berlandieri* x *V. riparia*	
41B	41B	*V. vinifera* x *V. berlandieri*	
99 Richter	99 Richter	*V. berlandieri* x *V. rupestris*	
101-14	101-14 Millardet et de Grasset	*V. riparia* x *V. rupestris*	
110	110 R	*V. berlandieri* x *V. rupestris*	
140	140 Ruggeri	*V. berlandieri* x *V. rupestris*	
161-49	161-49 Couderc	*V. riparia* x *V. berlandieri*	
333 EM	333 EM	*V. vinifera* x *V. berlandieri*	
420A	420 A Millardet et de Grasset	*V. berlandieri* x *V. riparia*	
1103	1103 Paulsen	*V. berlandieri* x *V. rupestris*	1103P
1613	1613 Couderc	*V. riparia* x *V. rupestris* x *V. vinifera* x *V. candicans* x *V. labruska*	1613C
1616	1616 Couderc	*V. riparia* x *V. rupestris* x *V. candicans*	1616C
3309	3309 Couderc	*V. riparia* x *V. rupestris*	3309C
Ramsey	Ramsey	*V. rupestris* x *V. candicans*	

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