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Tolerance to Lime - Induced Chlorosis and Drought in Grapevine Rootstocks

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Additional information is available at the end of the chapter

1. Introduction

Many woody crop plants such as grapevine are traditionally grown with scion varieties grafted onto rootstocks. The selection of an appropriate rootstock provides a powerful tool to manage the growth and fruiting of the scion (Jones, 2012). In the grapevine propagation, the use of rootstocks is not a new matter. The evidence of the use of rootstocks can be found out even in works written by the Roman author Columella who occupied himself with agriculture and viticulture. However, the use of rootstocks obtained a new dimension after the phylloxera calamity, which destroyed European vineyards in the second half of the 19th century.

Rootstocks were introduced to Europe after the phylloxera invasion, a pest which rapidly spread through vineyards and destroyed large areas of sensitive cultivars. At present, grafting European varieties on pathogen-resistant rootstock is a normal procedure and many rootstock varieties have been developed by plant breeders (Arrigo & Arnold, 2007).

When choosing a suitable rootstock it is important to select one with a good tolerance to phylloxera and well as being to the specific climatic conditions and soil characteristics of individual vineyard sites. The rootstock connects the grafted plants with soil and influences mutual relationships. The root system of the rootstock enables the uptake of water and nutrients from soil. The rootstock also shows a marked effect on the growth intensity of grafted plants. When selecting a suitable rootstock, it is important to consider characteristics and parameters of the site. The most important of them are the following: depth of the soil horizon, water-holding capacity of soil, slope and exposure of the site, and climatic conditions. The architecture of the root system of the plant is also very important for its resistance/tolerance to drought. In the case of grapevine, selection and use of a suitable rootstock may help to solve problems of plant protection and of overcoming extreme soil conditions. Adaptability of plants

to environmental conditions, e.g. their tolerance to lime, low soil pH, soil humidity, salts etc., is very important.

Nowadays, grapevine plants are more and more influenced by various kinds of environmental stress. The most important kinds of abiotic stress are the following: extreme temperatures or too high (or too low) irradiation, water logging, drought, lack of minerals in soil (their deficiency) and too high salinity of soil (Koyro et al., 2012). Stress can be defined as an environmental factor that shows a negative effect on the living organism (Levitt, 1980).

This review tries to summarise data about the adaptation of rootstocks to soil (pedological) conditions, viz. their resistance to lime-induced chlorosis and drought. Regarding the global warming, these properties of rootstocks are very important also under conditions of the Central European viticulture.

2. Root system of grapevine plants

The most important functions of the grapevine root system involve anchoring of plants in soil, storage of reserve substances, uptake and conduction of water and dissolved nutrients within the plant and synthesis of growth hormones. The root system consisted not only of older, lignified roots but also of a great number of new ones that are used above all for the uptake of nutrients. Regarding their diameter, roots can be divided into two groups. Thick roots (with the diameter above 2 mm) represent a great proportion of root biomass. They create the "architecture" of the root system, enable the transport of water and nutrients and fulfil the function of a reserve organ. Fine roots (with the diameter below 2 mm) enable above all the uptake of water and nutrients. These are above all root hairs that develop on thicker roots. Root tips consist of root caps and apical meristem. This apical meristem assures growth and development of roots. Root growth takes place in the elongation zone which is approximately two milimeter long. Root tips are also the place of synthesis of plant hormones (gibberelins and cytokinines). These growth hormones are transported via conductive tissues into the aboveground parts of the plant and participate in processes controlling the balance between roots and tops, initiation of flowering, and growth and development of berries. Cell division (and, thus, the growth of roots) is controlled by auxins that are transported from tops of annual shoots into roots via phloem. The elongation growth is influenced by gibberellins that are synthesised in roots. Root hairs are localised behind the elongation zone of roots and assure the uptake of water and nutrients. It is capable to release organic compounds into the soil and to participate in propagation and development of microflora existing in the root zone (Pavloušek, 2011a).

The distribution of roots in soil is influenced by soil and environmental factors, e.g. temperature, degree of aeration, texture, availability of water and nutrients, pH value and frequency and depth of tillage operations (Richards, 1983, Morlat & Jaquet, 1993).

The root system of grapevine plants is mostly created by the root system of rootstocks. The root system of grapevine rootstocks enables the uptake of water and nutrients from greater

soil depths. Distribution of root systems of individual rootstocks enables to identify their uptake capacity for nutrients. This means that different rootstocks have a different capacity to uptake individual nutrients from soil (Somkuwar et al., 2012).

Within the framework of their response to edaphoclimatic conditions individual rootstocks also show differences in growth capacity of their roots, water uptake, transport of water into annual shoots, metabolic activity and storage of carbon.

Water uptake and its transport represent one of the most important functions of roots. The distribution of roots in soil and the root turnover are the key parameters of water uptake; they are also important for the hydraulic redistribution (Bauerle et al., 2008a).

Root architecture refers to the spatial configuration of the root system, specifically focusing on the geometric properties of root axes and laterals, mostly concerned with the entire root system characteristics (Lynch, 1995). Typically, root distribution studies include root biomass or root length as a function of soil depth, distance from the plant stem, and position between neighbouring plants (Bassoi et al., 2003).

The available soil volume is probably the most important factor dictating the size and the distribution of root system (Saayman, 1982). The spatial root distribution is predominantly a function of the soil environment, while root density is a function of rootstock (Southey & Archer, 1988).

From the viewpoint of tolerance to abiotic factors associated with climatic and soil conditions it is important to study and understand both vertical and horizontal distribution of roots in soil. For example the Dog Ridge and Salt Creek rootstocks, which belong to *Vitis champinii*, put forth prolific root systems of thickness of < 2 mm and 2-5 mm in the top depths of 0-30 cm up to 60 cm away from the trunk, and later thicker roots of > 5 mm beyond 60 cm from the trunk. However, St. George, which belongs to *Vitis rupestris*, has less root length in all categories at all blocks horizontally up to a 150 cm distance from the trunk. In the vertical direction, Salt Creek showed the greatest root length in the category of < 2 mm at a depth of 0-30 cm, while Dog Ridge and St. George were at par for root length. However, at depths of 31-60 cm and 61-90 cm, Dog Ridge produced the greatest root length, followed by Salt Creek and St. George (Simkuwar et al., 2012).

The rootstock shows a significant effect not only on the distribution of roots in soil but also on the architecture of the root system. In *Vitis rupestris,* major roots create vertically a narrow angle and can penetrate deep into the bottom soil layers. On the other hand, roots of *Vitis riparia* are distributed in a wide angle and most of them are situated in a shallow top layer of soil (Perold, 1927). Swanepoel & Southey (1989) analysed the distribution of roots within a wider spectrum of rootstocks growing under conditions of South Africa (Table 1).

Also abiotic factors may influence growth and development of the root system. In this case, above all the vertical distribution of roots within the soil horizon is important.

Rootstock	Number of roots per m²	Rooting index	Number of roots per diameter (mm) class				
			<0.5	0.5-2	2-5	5-10	>10
Berlandieri 13/5	2069	39.6	1792	226	38	10	3
101-14 Mgt	1604	27.1	1210	337	43	11	3
775 P	1006	44.7	839	145	16	4	2
1103 P	2660	41.9	2199	399	53	6	3
99 R	1138	28.9	833	267	30	8	0
110 R	1468	29.9	1103	319	37	9	0
140 Ru	635	20.2	483	122	21	6	3

Table 1. Distribution of roots of different rootstocks cultivated under conditions of South Africa (Swanepoel & Southey, 1989). (Rooting index = number of roots <2 mm/ number of roots ≥2 mm).

To assure a good tolerance of plants to drought and lime is necessary assure a proper development of the root system (Figure 1). Deep loosening of soil is also very important (Figure 2).

Figure 1. Root system of a five-year-old vine in clay loam soil.

Figure 2. Deep lossening of soil in clay loam soil.

An adequate care about the root system and its proper development is very important and should be started immediately after the establishment of a new vineyard. This means that it is necessary to create and maintain a required ratio between thick and thin roots. The root system can be modelled by means of a cut off of roots so that they produce more branches, the total volume of root mass increases and the sorption area for the uptake of nutrients grows up. Usually and most frequently, this cut off takes place during the process of deep soil loosening and/or deep supplementary fertilisation. After these operations, the total volume of roots is partly reduced but the recovery is very quick. If, however, this intervention is too drastic, it may show a negative effect on the overall growth process of grapevine plants. The cutoff and shortening of roots should be performed at best at the beginning of the growing season, i.e. in the period of exogene dormancy, and should not be done every year because the optimum development of roots would be disturbed and plants could be under a permanent stress. It is recommended to use a deep additional fertilisation in three-year cycles.

A good understanding of effects of a limited availability of water on the growth of the root system and its functions has a principal influence on the selection of a suitable method of vineyard management (Schultz, 2010) and also on the selection of a suitable rootstock. In both temperate and Mediterranean regions, the growth of grapevine root system takes place above all within the period starting on flowering and finishing at the beginning of softening of berries (Comas et al., 2010). Drought-resistant rootstocks (e.g. 1103P) show a capability to create new

roots also during the periods of summer drought (Alsina et al., 2010). In these periods, the majority of roots is formed in depths below 60 cm, where the groundwater is available (Bauerle et al., 2008b).

To understand well to principles and processes of growth and development of the root system is therefore very important for understanding to stress situations caused by abiotic factors, especially by drought. The architecture of the root system is a genetic characteristic of root-stocks and soil, climatic and growing conditions modify it only very slightly. In the European „cool climate viticulture" rootstocks with *Vitis rupestris* in their pedigree are relatively rare in spite of the fact that their roots penetrate deep into the soil horizon. Practically, the only representative of these rootstocks is the Moravian rootstock Schwarzmann that was selected in Bzenec (Czech Republic) to the end of the 19th century and was very popular in former Czechoslovakia. Unfortunately, the results of introduction of other rootstocks with *Vitis rupestris* in their pedigree into the European „cool climate viticulture" have not been very successful yet.

3. Tolerance of grape rootstocks to lime-induced chlorosis

Lime-induced iron chlorosis, i.e. the condition of a reduced availability of soluble iron to the grapevine plants due high concentrations of bicarbonate ions in calcareous soils, can seriously impair the health condition of vines. The lime-induced chlorosis affects yield and quality of grapevines growing in lots of calcareous areas world-wide (Bavaresco et al., 1994).

A high content of active and total lime in soil can induce symptoms of chlorosis in grapevine plants and, thus, negatively influence the growth and yielding capacity of grapevine plants as well as the quality of harvested grapes. On the other side, however, lime present in soil participates very significantly to the manifestation of sensory proper-ties of wine. From the geological point of view, it is a very important component of „ter-roir", which directly influences the character of produced wine. Wine-growing regions situated on calcareous subsoils can be considered for localities that are very suitable for production of quality wine. As typical examples it is possible to mention French Cham-pagne wine region or Czech limestone Pálava Hills.

Selection of suitable, lime-tolerant rootstocks represents one of possible ways how to react to an increased content of calcium in soil and, at the same time, to preserve quality of plants and harvested grapes. Although the genetic improvement of tolerance of rootstocks to chlorosis represents a very long process, it still represents the best method of fight with iron chlorosis (Nikolic et al., 2000, Pestana et al., 2003). Differences in the uptake and distribution of nutrients within the plant may be influenced by the variety of rootstock because it may show a rather different absorption capacity as far as individual minerals are concerned (Rizk-Alla, et al., 2001). And just these differences in the absorption capacity may be associated also with the occurrence of the lime-induced chlorosis.

Rootstocks 333 EM and 41B (originating from crossing *Vitis berlandieri x Vitis vinifera)* belonged to the first rootstocks selected for a high degree of tolerance to calcium so that they could be

used in vineyards established on calcareous soils. A. Ruggeri, an Italian breeder and selectionist, was the author of the rootstock 140 Ru (*Vitis berlandieri x Vitis rupestris*), which also showed tolerance to lime chlorosis (Fregoni & Bavaresco, 1986). The rootstock Fercal, selected in France by Pouget and Ottenwaeter (1978) is one of the most modern rootstocks showing a very high degree of tolerance to calcium.

3.1. Deficiency symptoms of lime-induced chlorosis

A correct identification of symptoms of lime-induced chlorosis is one of the first presumptions of a successful fight against this deficiency. Iron deficiency chlorosis is one of the major problems affecting a variety of crop species grown in calcareous soils (Gruben & Kosegarten, 2002). Iron deficiency causes various morphological and physiological changes in plants (Bertamini & Nedunchezhian, 2005).

Although the symptoms of lime-induced chlorosis are visible on the whole grapevine plant, the most important ones can be probably observed on leaves.

Iron-deficient plants are characterized by the development of a pronounced intervenial chlorosis similar to that caused by magnesium (Mg) deficiency but occurring first on the youngest leaves. Intervenial chlorosis is sometimes followed by chlorosis of the veins, causing the whole leaf to become yellow. In severe cases, the leaves become white with necrotic lesions (Abadia, 1992).

Typical symptoms of lime-induced chlorosis are the inter-vein yellowing of leaves and a decrease in plant biomass because, under conditions of iron (Fe) deficiency, a decreased photosynthetic performance of plants is induced by a lower content of chlorophyll in leaves (Bavaresco & Poni, 2003). Chlorosis is a disease manifesting itself by yellowing of young leaves, whereas more mature leaves are frequently green. Plant growth is often considerably depressed, independent of whether young leaves are chlorotic or green (Mengel, Bübl, Scherer, 1984). The impaired formation of new leaves and restricted leaf growth is a typical and more sensitive symptom of Fe-deficiency than is leaf chlorosis (Kosegarten *et al.*,1998)

Chlorotic symptoms also vary from year to year as a result of environmental variables, like yields, temperature, rains. In soils where shallow layers are less rich in $CaCO_3$ than deeper layers, it is likely that vines develops chlorosis only when the age and roots explore layers with poor conditions for Fe uptake (Tagliavini & Rombola, 2001).

As the lime-induced chlorosis is the result of the relationship existing between soil conditions and grapevine root system, it is manifested also in growth characteristics of grapevines. The lime-induced chlorosis of grapevine was characterized by a dramatic reduction of shoot growth, grape production and leaf Fe content, and a distribution of dry matter towards roots more than to the clusters (Bavaresco, Giachino, Pezzutto, 2003).

Vines growing on high-bicarbonate soil significantly reduced the dry matter production of individual organs and the total plant weight. Lime stress conditions increased the percent distribution of dry matter in the stem and roots and decreased that one in the fruit (berries and cluster stems) (Bavaresco & Poni, 2003).

A high content of lime mostly causes a low availability of iron, which is a result of its non-solubility occurring in soils showing higher values of pH. Under such conditions, iron cannot be uptaken by roots of plants (Hell & Stephan, 2003).

This lime-induced iron deficiency shows a strong effect not only on grapevine plants but also on some other economically important fruit species cultivated on calcareous soils. It is quite common also in peach, pear, quince-tree, kiwi, and citrus fruit plantations (Tagliavini & Rombola, 2001).

Lime-induced stress conditions show a strong effect on production of grapes and reduce the yield of grapes per vine. When growing grapevine on calcareous soils, a lower number of grapes per annual shoot depends on stress conditions existing in the preceding growing season (when the flower buds were differentiated) while a small size of grapes and berries is a consequence of iron deficiency in the current year (Bavaresco, Presutto, Civardi, 2005).

Because the lime-induced chlorosis affects above all the growth of grapevine plants, influences the total leaf area capable of photosynthetic activities and thus also yield and quality of fruit and for that reason it is possible to say that iron deficiency is caused mainly by higher levels of calcium carbonate and the resulting high contents of bicarbonates in soil. These high levels of bicarbonate ion are typical just for these calcareous soils (Pestana, Faria, De Varennes, 2004; Mengel, Breininget, Bübl, 1984). Under such conditions, the occurrence of chlorosis symptoms is quite common and for that reason this type of chlorosis may be defined as a lime-induced iron chlorosis or, abbreviated, lime-induced chlorosis (Pestana *et al.*, 2004).

The identification of chlorosis symptoms in vineyards is very important because it enables to perform protection of plants against mechanisms that induce this plant disease. The identification can be performed by means of leaf analysis that enables to estimate contents of individual macro and microelements in leaf blades and/or leaf petioles.

The leaf analysis enables to identify all factors that can influence the availability of nutrients in soil and their uptake by plants; it also can provide information about the nutrient balance of plants in the moment of sampling (Pestana et al., 2003).

3.2. Causes of the occurrence of lime-induced chlorosis

Although the reasons of the occurrence of this type of chlorosis seem to be relatively definite, the mechanism of its occurrence is still not explicitly defined. It seems that different forms of iron present in soil and their availability for plants contribute a lot to the occurrence of this type of chlorosis. Even in very small amounts, iron represents one of those minerals, which are utilised by plants to assure their sound growth. Iron is used by plants in two forms, viz. as Fe^{2+} and Fe^{3+}.

Iron chlorosis affects susceptible plants growing on calcareous soils. Different kinds of carbonates induce different degree of chlorosis. Chlorosis is high for magnesite, hydromagnesite and calcite and low for aragonite and nil for dolomite (Fregoni, 1980). There are several different views concerning iron concentration in soil and its relationship to the occurrence of chlorosis. In some cases the lime-induced chlorosis can occur under conditions of a low content

of iron in soil and leaves (Bavaresco et al., 1992) while in other its symptoms may be observed at very high levels of iron in leaves (Mengel et al., 1984b). Iron also plays an important role in activities of the enzymatic system of plants: it actively participates in photosynthetic reduction-oxidation reactions, respiration, biosynthesis of proteins and chlorophyll, biological binding of atmospheric oxygen, and in reduction of nitrates and nitrites (Tagliavini & Rombola, 2001).

Cultivated plants differ in their susceptibility to Fe deficiency in calcareous soil; some are not much affected while others show severe leaf symptoms of chlorosis (Tagliavini & Rombola, 2001). In cultivars grown under conditions of a high content of carbonates in soil the content of chlorophyll can decrease dramatically with the increasing age of plants (Shaaban et al., 2007).

The total content of lime in soil is not very useful for predicting the development of the occurrence of this type of chlorosis. Active carbonates (active lime) is more reactive and, therefore, able to build and maintain high levels of HCO_3^-; for that reason it is a more reliable indicator (Tagliavini & Rombola, 2001). In viticulture, the evaluation of conditions suitable for the induction of chlorosis the following parameters are usually taken into account: total carbonates (%), active lime (%) and CPI (chlorotic power index). Evaluated rootstocks are then classified on the base of these analytic parameters. This concept resulted in the so-called "chlorotic power index" (CPI) (Juste & Pouget, 1972. In: Huglin & Schneider, 1998). This means that the amount of active lime is related to the amount of Fe extracted by ammonium oxalate. Table 2 shows degrees of chlorosis intensity in relation to different values of CPI (Lupascu et al., 2009).

CPI value	Intensity of chlorosis
0	None
≤ 5	Small
6 - 15	Medium
16 -35	High
≥ 36	Very high

Table 2. Degrees of chlorosis intensity in relation to different values of CPI (LUPASCU et al., 2009).

The content of active lime in soil is a parameter, which is frequently used when selecting rootstocks for cultivation of grapevine plants in calcareous soils (Champagnol, 1984).

The susceptibility to chlorosis is the most important selection criterion for rootstocks in many European wine-growing regions where such a condition is prevalent due to occurrence of highly calcareous soils.

Two basic strategies how to classify grapevine plants according to their capability to adapt themselves to conditions, under which the lime-induced chlorosis can occur (Bavaresco, 1990):

- Strategy I involves four types of response in the roots as follows: a) enhancement of H-ions release, b) formation of rhizodermal or hypodermal transfer cells, c) enhancement of ferric

iron reduction to ferrous iron, d) enhancement of release of reducing/chelating compounds e.g. phenols.

- Strategy II is characterized by an enhancement of release of non-proteinogenic amino acids and by a high affinity uptake system.

Bavaresco (1990) formulated the following hypothesis: the response mechanism of tolerant grapevine rootstocks corresponds probably with Strategy I (Bavaresco et al., 1989) however, the vines are normally grafted and the behaviour of the whole plant towards lime-induced chlorosis is governed by the following two properties: (i) by the ability of roots to satisfy iron requirement of leaves; (ii) by the iron requirement of leaves to secure a normal iron nutrition of the plant (Pouget & Ottenwalter, 1973).

The reason that Fe deficiency results in a rapid inhibition of chlorophyll formation is not fully understood, even though this problem has been studied for many years (Bertamini & Nedunchezhian, 2005). The reduction of plant biomass of susceptible plants is related to a reduced root growth due to soil bicarbonate and to a lower photosynthesis rate which also depends by a decrease of leaf chlorophyll, under Fe stress conditions (Bavaresco, Giachino, Pezzutto, 2003). According to the growth rate of sink tissues and such organs as the roots, shoot apex, fruits and storage organs can be limited by supply of photosynthates from the source leaves or by a limited capacity of the sink to utilize the photosynthates (Marschner, 1995). In some cases, lime-induced chlorosis is related to a low Fe uptake and its translocation to leaves (Bavaresco et al., 1992), in others to a high content of Fe in leaves, which has to be somehow inactivated (Mengel, Breininget, Bübl, 1984; Bavaresco et al., 1993).

Screening tests of tolerance to chlorosis are performed on plants grown under conditions of a high content of bicarbonates in soil. This evaluation can be performed also *in vitro* on a medium containing a high level of bicarbonates (Bavaresco et al., 1993). The identification of real causes of the occurrence of the lime-induced chlorosis under conditions of a given vineyard is very important for the improvement and/or elimination of these biotic stress situations. The selection of a suitable rootstock is very important above all in situations when the uptake of iron is blocked due to a high content of lime in soil and also due to unsuitably chosen rotstocks.

3.3. Tolerance to lime-induced chlorosis in wild species and rootstocks varieties

Rootstocks represent a very important part of the concept how to prevent the occurrence of lime-induced chlorosis in vineyards. A perfect knowledge of soil conditions existing in a given locality and also of the resistance of individual rootstocks to lime enables to optimise the management of selection of rootstocks on the base of soil conditions.

Use of genotypes tolerant to chlorosis induced by iron blocking is a reliable tool how to solve problems of chlorosis occurrence (Jimenez *et al.*, 2008).

Chlorosis resistance or susceptibility of grapevine varieties and rootstocks is related not only to the root ability to supply adequate iron to the leaves, but also to their iron requirements, which can differ between genotypes. On the basis of this concept, the grapevine varieties were ranked according to their chlorosis resistance or tolerance (Branas, 1974). Breeding also greatly

contributes to the selection of lime-resistant rootstocks. Breeding efforts to get proper geno-types included successfully crossing between wild grape species, and some chlorosis-resistant rootstocks are now available for the grapevine growers of the many calcareous areas world-wide (Fregoni, 1980; Pouget, 1980; Bavareso, Fraschini, Perino, 1993). Lime-tolerant grapevine rootstocks have some specific physiological mechanism to overcome chlorosis when grown on calcareous soils, including and improvement of root Fe uptake and reducing capacity (Varanini & Magioni, 1982; Bavaresco, Fregoni, Fraschini, 1991).

Vitis riparia and *Vitis rupestris* are very important species in the history of the rootstock breeding activities. These two species are not very tolerant to calcareous soils. *Vitis berlandieri* is recognized for adaptation to calcareous soils. *Vitis vinifera* is species tolerant to calcareous soils (Cousins, 2005). Knowing the characteristics of the important parental species and rootstock varieties used in rootstock development helps us to understand the viticultural attributes of individual rootstocks families.

Data about the tolerance of rootstocks to lime-induced chlorosis, as mentioned by Cousins (2005) and Chauvet & Reynier (1979) are presented in Table 3.

Rootstocks	Tolerance to chlorosis	Reference
SO 4	Medium	COUSINS (2005)
Börner	Low	
420 A	Good	CHAUVET & REYNIER (1979)
Kober 5BB SO4	Medium	
140 Ruggeri	Very Good	
1103 Paulsen 110 Richter	Medium	
Fercal	Very Good	

Table 3. Tolerance of rootstocks to chlorosis (after Cousins, 2005, Chauvet & Reyiner, 1979).

From the viewpoint of the resistance to chlorosis, the rootstocks registered in the State Variety Book of the Czech Republic can be ranked from the most resistant to the most sensitive as follows: *Craciunel 2 – SO 4 – Kober 125 AA – Kober 5 BB – Teleki 5 C – Amos – LE-K-1*. These results are very important from the viewpoint of the use of rootstock varieties for propagation and growing of grapevine in the Czech Republic (Pavloušek, 2008).

In table 4, the classification of rootstock variety, content of active lime and values of CPI are described (Juste & Pouget, 1972 In: Huglin & Schneider (1998).

Rootstock	Content of active lime (%)	CPI value
Vialla	-	2
Riparia Gloire	6	5
196-17	6	-
101-14	9	10
216-3	9	-
44-53	10	-
3309	11	10
1616	11	-
Rupestris du Lot	14	20
99R,110R,1103P,SO4	17	30
5BB,420A, 34 EM	20	40
161-49	25	50
140 Ru	25	90
41B	40	60
333 EM	40	70
Fercal	-	120

Table 4. Classification of rootstocks on the base of the content of active lime and CPI (Juste & Pouget, 1972. In: Huglin & Schneider, 1998).

Recently, the species *Vitis cinerea* is very often used when selecting new rootstock types. In the Czech Republic, rootstock breeders used the German rootstock Börner and the Czech hybrid Bruci [(*Vitis berlandieri x Vitis rupestris) x Vitis cinerea*] as donors of resistance to phyloxera. Hybrids with a very high tolerance to chlorosis originated from parent combinations [Binova x (Binova x Teleki 5C) x Börner] and (Teleki 5C x Börner). These hybrids originated from combinations of *Vitis berlandieri, Vitis riparia* and *Vitis cinerea*. Hybrid combinations with *Vitis rupestris* and *Vitis amurensis* showed mostly only a medium tolerance to chlorosis. A simple hybrid (Binova x Börner) showed also a medium tolerance to lime-induced chlorosis (Pavloušek, 2009).

4. Tolerance of grape rootstocks to drought

Drought stress is one of the most important abiotic stress factors which are generally accompanied by heat stress (Zulini *et al.*, 2007).

In recent years, climatic changes can be observed worldwide. Warm years are more frequent and periods of drought are longer. This means that modern viticulture must look for methods how to react to this increasing frequency of periods of drought.

The grapevine (*Vitis vinifera*) has different physiological and morphological mechanisms enabling it to maintain growth and production also under conditons of water deficiency (Kondouras et al., 2008).

In Europe, varieties of *Vitis vinifera* are traditionally cultivated in non-irrigated regions. Yield of grapes as well as the quality of berries is therefore dependent on the adaptability of grapevine plants to drought. A good understanding and control of the water regime of plants as well as influencing their tolerance to drought stress on the base of application our knowledge of plant physiology and molecular biology may significantly increase not only productivity of plants but also quality of environmental conditions.

In grapevine, water supply of plants plays an important role in processes of plant growth and formation of berries. A limited supply of water reduces not only the growth of annual shoots but also the weight of berries and the final yield of grapes. A marked lack of water may result in reduced yields and an impaired quality of grapes. This means that in the course of the growing season the occurrence of stress induced by water deficit shows a significant effect on physiological functions of grapevine plants. Although the grapevine (*Vitis vinifera*) is a species showing a very good tolerance to drought, a severe stress may sometimes markedly influence qualitative properties and parameters of grapes. When using plant material adapted to drought conditions, it is possible to avoid losses caused by a severe water stress (Van Leeuwen *et al.*, 2009).

Selection and breeding of grapevine rootstocks and varieties with a higher water-use efficiency represents a possibility how to adapt viticultural production to current climatic changes (Vandeleur et al., 2009, Flexas et al., 2010).

4.1. Properties influencing the tolerance of grapevine plants to drought

In the course of phylogenesis the grapevine (*Vitis vinifera* L.) plants have developed various physiological and morphological mechanisms, which enable them to maintain their growth and fertility even under conditions of a limited availability of water.

Although grapevine (*Vitis vinifera* L.) is considered to be a species adapted to drought stress, the combined effect of high irradiation, high temperatures and low atmospheric water pressure tension would presumably act as major constraint for the leaf photosynthesis, particularly under conditions of severe soil water deficits usually encountered by this crop (Flexas *et al.*, 1998).

Physiological responses of plants to water deficit are linked to a condition of recognition of stress by the root system, turgor changes and water potential and consequently stomatal conductance, internal CO_2 concentration and photosynthetic activity decrease. From a molecular perspective, several genes expressed under stress conditions are activated, such as genes linked to the biosynthesis of abscisic acid and synthesis of specific proteins (Chavaria & Pessoa Dos Santos, 2012). This means that in plants the water stress is manifested by many different mechanisms.

A limitation of growth of annual shoots and leaves represents one of the first symptoms of water deficiency (Stevens et al., 1995). The sensitivity of roots is usually lower than that of annual shoots (Dry *et al.*, 2000). The growth intensity of annual shoots can be used as one of very sensitive indicators of grapevine water status (Patil et al., 1995, Pellegrino et al., 2006, Lebon et al., 2006, Pavloušek, 2011b).

In summer, water available to the plant can often be insufficient because of a lack of precipitation or a low level of its reserves in soil. This can lead to a reduction in the vigour of the plant, its productivity, and quality of the crop. The growth of above-ground parts of grapevine plants is associated also with the growth of roots and this is directly dependent on the availability of water in soil. In periods of drought, roots of some grapevine rootstock varieties can penetrate deep into the soil horizon and thus produce new and new roots.

The growth of roots is also dependent on the relationship, which exists between the rootstock variety and soil conditions (Morlat & Jacquet, 2003). Rootstock genotype has a major influence on root density (Southey & Archer, 1988; Williams & Smith, 1991) even though the distribution of grapevine roots is significantly dependent on both edaphic conditions (Smart *et al.*, 2006) and vine (Archer & Strauss, 1985). In extremely drought soils, however, the growth of roots of some botanical species may be significantly reduced (Comas et al., 2005).

The tolerance of grapevine to drought is also dependent on the quality of the root system, its architecture, the distribution of individual types of roots within the soil and the density of the root system in the place of water and nutrients uptake. On the other hand, however, the architecture of the root system can be influenced also by spacing of planarity and method of vineyard tillage.

Roots are usually the first point where the stress is perceived by plants and where they respond to the existing stress conditions. The grapevine tolerance to drought is *de facto* the capability of plants to produce selectively new roots in those places where the groundwater is available. The water stress has a dominant effect on the growth of the grapevine and affects both the growth and the development of grapevines.

The growth inhibition of annual shoots decreases transpiration of plants and reduces the total volume of conductive tissues (Lovisolo et al., 2010). The transport of water from soil to roots and (via conductive tissues) also to annual shoots and other above-ground parts of grapevine plants is dependent on activities of aquaporins. Aquaporins are members of the major membrane intrinsic protein family, where can act as water channels and can regulate cell-to-cell water transport (Maurel et al., 2008). Aquaporins play an important role in the process of water absorption. The availability of aquaporins on the surface of roots is changing during the day and depends on the photoperiodicity (Chavaria & Pessoa Dos Santos, 2012).

The physiological mechanisms related to drought tolerance vary from genotype to genotype. It is necessary to screen genotypes for drought tolerance and take into consideration all important aspects, e.g. photosynthesis rate, transpiration rate, stomatal conductance and relative water content occurring at different level of water stress (Satisha *et al.*, 2006). Grapevine varieties adapt themselves to water deficits by means of various mechanisms, e.g. by changes

in the leaf area (Gómez Del Campo *et al.*, 2003), xylem vessel size, and/or conductivity (Lovisolo & Schubert, 1998).

Stomata enable a control of water regime in plants because they balance and stabilise values of water potential existing between their leaves and the atmosphere. Stomatal closure is one of the first responses to soil drying, and a parallel decline in photosynthesis and stomatal conductance under progressive water stress has already been reported (Medrano *et al.*, 1997). Within the framework of stomatal activities there are relationships among metabolism of abscisic acid (ABA), hydraulic signals, regulation of activities of aquaporins and electric signals that are manifested when measuring the water potential of leaves (Lovisolo et al., 2010). This means that the reaction of stomata is mediated by ABA, which is produced within the framework of a response to the stress induced by drought in roots; this newly synthesised ABA is then transported into other parts of the plant (Loveys et al., 1984).

Plants respond to the lack of water by a quick closing of stomatal opening so that a further loss of water via transpiration is prevented. This mechanism represents a very efficient protection of plants against drought-induced stress.

A lack of water in soil and a leaf water deficit result also in a gradual reduction of photosynthesis and changes in assimilation of carbon and nitrogen (Chavaria & Pessoa Dos Santos, 2012, Zlatev &Cebola Lidon, 2012). Drought-induced decrease in photosynthesis is primarily due to a stomatal closure, which lowers CO_2 availability in the mesophyll, not due to a direct effect on the capacity of the photosynthetic apparatus (Escalona *et al.*, 1999). Osmotic stress is a common feature of many abiotic stress factors, that affect grapevines (Gramer, 2010). Some biochemical characteristics, e.g. the stability of chlorophyll, can be used for selection of cultivars resistant to drought conditions (Sinbha & Patil, 1986, Pavloušek, 2011b).

Water-use efficiency (Wue) can be considered for the most important indicator of water management of plants (and also in grapevine). The Wue can be defined as a balance existing between the biomass gain (expressed in kilograms of produced biomass or in mols of assimilated CO_2) and losses of water (expressed as cubic meters of consumed water or mols of transpired water). From the agronomic point of view the Wue can be defined as the volume of yield produced per unit of consumed water (Tomás, et al., 2012). Quality of grapes is very markedly dependent on the amount of water consumed by plants and for that reason an improvement in efficiency of water use represents the major requirement concerning crop sustainability and quality of grapes (Medrano et al., 2012). New aspects of Wue and actual data concerning this indicator were dealt with and studied in many recent studies (Flexas et al., 2010, Schultz & Stoll, 2010, Lovisolo et al., 2010, Tomás et al., 2012, Medrano et al., 2012). The Wue is a key parameter that enables to evaluate the efficiency of water use within the agrarian sector. It is dependent on the total amount of water consumed by plants in the course of the growing season. This sum represents the amount of water used by plants plus water losses caused by transpiration (Flexas et al., 2010).

For that reason it can be expected that there is a relationship between Wue on the one hand and genetic foundations (i.e. genomes) of cultivars or rootstocks on the other. Basing on the knowledge of Wue of individual species, rootstocks or cultivars it could be therefore possible

to recommend them for planting in individual sites/localities with regard to their availability of water.

Some studies dealt with the Wue of individual botanic species and rootstocks. A higher Wue value was found out in *Vitis rupestris* while a lower one in *Vitis doaniana, Vitis californica* and *Vitis candicans* (Padgett-Johnson, et al., 2003). Higher Wue values were also described in *Vitis riparia* (Flexas et al., 1999) and the rootstock 110 R (Pou et al., 2008).

Soar *et al.* (2006) reported that rootstock effect on gas exchange of vineyard-grown grapevines is most likely due to differences in the relative capacity of rootstocks to extract and provide scions with water. Rootstocks have been reported to affect the efficiency of water transport to the shoots via conductivity constrains imposed by the anatomy of xylem vessels (De Herralde *et al.*, 2006).

Greenspan (2006) differentiates between terms "drought-tolerance" and "drought-avoidance". Drought-tolerance refers to the ability of the rootstock to support grapevine physiological functions during periods of low soil moisture availability. Rootstocks may exhibit drought-tolerance through several mechanisms:

Maintaining a low hydraulic resistance to water flow, even under dry conditions.

1. Maintaining photosynthetic activity in leaves, even under low water availability conditions.

2. Preventing the abscission of leaves during periods of low water availability.

Drought-avoidance refers to the ability of the rootstock to prevent low vine water status by one or more of many mechanisms, including:

1. Deep or extensive root exploration to fully exploit soil moisture reserves.

2. Conservation of vine water use by inducing closure of the leaf stomatal pores to limit transpiration.

3. Restricting vine vigour, thereby limiting the amount of transpiring leaf surface area.

The relationship existing between the response of plants and the drought-induced stress influences, through physiological reactions of plants, also the development of important qualitative parameters of grapes (Lovisolo et al., 2010):

1. Effects of plant metabolism, above all photosynthesis and transpiration, on accumulation of sugars and secondary metabolites in berries.

2. Consequences at the berry level of both the chemically-mediated long distance signalling between root and shoot (essentially cytokinin and ABA) and the whole-plant hydraulic control via both the xylem and the phloem from root to berry.

3. Adaptation of berry metabolism to a severe osmotic stress existing in berry cells.

ABA, which is present in xylem fluid represents a key signal of root-shoot in plants that are stressed by drought (Schachtmann & Gooder, 2008).

The grapevine belongs to plants, in which a the existence of a very strong relationship between ABA produced in drought-exposed and stressed roots on the one hand and quality of grapes on the other.

Abscisic acid (ABA) is therefore the most important plant hormone that influences ripening and quality of grapevine berries. The participation of ABA is high at the beginning of development of berries and decrease till the period of berry softening. Its content increases again during the initial stages of accumulation of sugars and reaches the maximum approximately 2–3 weeks later (Davies & Böttcher, 2009). The content of ABA in the skin is higher than in the pulp (Coombe and Hall, 1973). Also grapevine seeds contain more of this acid than pulp (Zhang et al., 2003). ABA participates also in biosynthesis of anthocyanins and, according to Davies & Böttcher (2009) in the accumulation of sugars in berries. Drought-induced stress supports the formation of ABA and show a positive effect on the formation of secondary metabolites, above all of flavonoids, which involve anthocyanins and tannins. Under conditions of water stress, concentrations of anthocyanins and proanthocyanidins in the skin increase independently on the size of berries; this process is dependent above all on the availability of water (Roby et al., 2004).

In grapevine plants suffering from drought-induced stress, the synthesis of reserve substances may be impaired due to an inhibited photosynthesis. This means that the plants are not adequately prepared for overwintering. This stress markedly influences the quality of grapes. Contents of amino acids, organic acids and also sugars are usually reduced. Stressed plants show a decreased uptake of minerals from soil and, thus, lower extract in wine. In extreme cases it is possible to observe negative effects on smell and taste of wine as well as the occurrence of the ATA phenomenon (atypical aging – ATA). Due to a high content of polyphenols, the taste of stressed wines is bitter, disharmonic and „short".

From the viewpoint of quality of harvested gapes, a proper evaluation of the drought-induced stress risk is very important. In white wine varieties, this type of stress may show more negative effects than in varieties used for making of red wines because in this case the synthesis of ABA may show a positive effect on formation of phenolic substances.

4.2. Tolerance to drought in wild species and rootstocks varieties

The use of rootstocks makes it possible to give plants a certain capacity to adapt drought conditions. A good knowledge of tolerance of rootstocks is important above all with regard to the use of these genetic resources in the process of breeding and selection of plants tolerant to drought.

The capability of plants to create a root system efficiently penetrating into the soil is an important factor, which enables them to survive during longer periods of drought and water-stress.

The assessment and evaluation of tolerance of rootstocks to drought represents an important component of the process of selection of suitable rootstocks and for further breeding work. The classification of rootstocks into five groups according to their tolerance to drought is presented in Table 5 (Carbonneau, 1985).

Degree of resistance	Rootstock variety
Highly resistant	R 110, R 140, 44-53,
Resistant	P 1103, 196-17, P 1447, SO4, R 99, 7383,
Less resistant	3309, 7405, 7903, 420 A, Fercal, RSB1, 7921, 5 BB, 161-49, 41 B, Rupestris du Lot, 101-14
Susceptible	Rupestris du Lot, 101-14, EM 333, 7924, Yuga,
Highly susceptible	7542, Vialla

Table 5. Evaluation of drought tolerance of individual rootstock varieties (Carbonneau, 1985).

It is well-known that there are really remarkable differences in tolerance to drought. Some rootstocks (e.g. 101-14 and Schwarzmann) show a low tolerance while in others (e.g. Lider 116-60, Ramsey, 1103 Paulsen, 140 Ruggeri, and Kober 5 BB) this property is better (Sommer, 2009). Also Cirami *et al.*, (1994) observed a good tolerance to drought in rootstocks Ramsey, 1103 Paulsen, and 140 Ruggeri.

Table 6 presents tolerance to drought in some rootstocks varieties after Lavrenčič et al. (2007) and Pouget & Delas (1989).
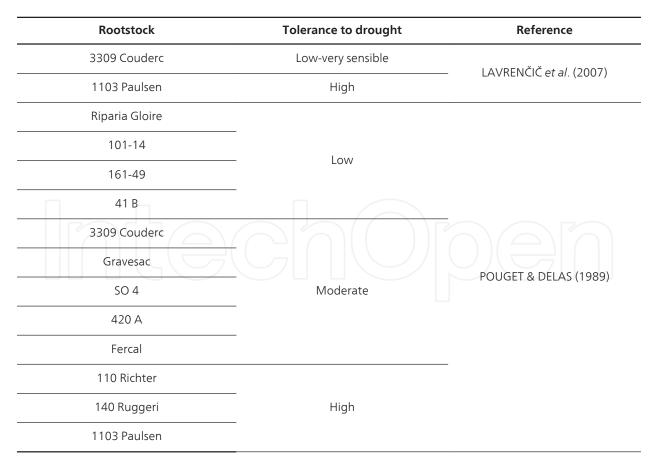
Rootstock	Tolerance to drought	Reference
3309 Couderc	Low-very sensible	LAVRENČIČ *et al.* (2007)
1103 Paulsen	High	
Riparia Gloire	Low	POUGET & DELAS (1989)
101-14		
161-49		
41 B		
3309 Couderc	Moderate	
Gravesac		
SO 4		
420 A		
Fercal		
110 Richter	High	
140 Ruggeri		
1103 Paulsen		

Table 6. Tolerance of rootstocks to drought (Lavrenčič et al., 2007, Pouget & Delas, 1989).

Cregg (2004) stated that to compare the relative tolerance among different genotypes, the variables to evaluate are as follows: survival potential, growth capacity, and water use efficiency based of morphological and physiological adaptations that might occur in the plant.

The most drought-tolerant grapevine species are V. arizonica, V. californica, V. champinii, V. doaniana, V. gidriana, and V. longii. The lowest tolerance was observed in V. berlandieri, V. cinerea, V. lincecumii, V. riparia, and V. solonis. V. rupestris showed only a moderate tolerance to drought (Padgett-Johnson, et al., 2003).

V. cinerea can assure not only a complete phylloxera resistance; it also shows a positive influence on scion performance especially in shallow, gravely, and consequently dry soils. Phylloxera-resistant *V. cinerea* hybrids are therefore recommended for vineyards established in sites with generally dry conditions. In dry locations *V. riparia x V. cinerea* hybrids represent a valuable expansion of the range of rootstocks currently available in Germany. Particularly on steep slopes and in seasons with rare rainfall the results obtained with these hybrids were superior (Schmidt *et al.*, 2005).

Basing on the evaluation of all traits of tolerance to drought of research in the Czech Republic it is possible to conclude that the highest number of drought-tolerant hybrids originated from the crossing of Binova x Börner so that there is a very good chance to use the rootstock Börner and *Vitis cinerea* for further breeding and selection of rootstock resistant to drought stress. However, hybrids with *Vitis rupestris* and *Vitis amurensis* in their pedigrees show only a medium resistance to drought stress. (Pavloušek, 2011b).

The occurrence of drought is also very closely correlated with the overall soil conditions of the site. For that reason it is recommended to select individual rootstocks with regard to the type of soil and also to contents of loamy, clayey and sandy particles within the soil profile.

White (2009) arranged rootstocks with regard to their drought tolerance and pedological conditions of the site in the following manner (Table 7):

Soil profile characteristics	Vineyard water status	Recommended rootstocks
Soil depth < 20 cm: sand, loam or clay including any root-impeding subsoil	Dry soil	110 Richter, 140 Ruggeri, 1103 Paulsen
	Irrigated soil	110 R, 140 Ru, 1103 P, Ramsey
Soil depth 20-75 cm, sands, loams or clays, with no root-impeding subsoil.	Dry soil	99R, 110R, 140 Ru, 1103P, Ramsey, Kober 5 BB
	Irrigated soil	99R, 110R, Ramsey, Kober 5BB, Teleki 5C, Schwarzmann, SO4, 420A, 101-14 (in loams and clays).
Soil depth"/> 75 cm, uniform or gradational profile of sand, loam or clay.	Dry soil	99R, 110R, 1103P, Ramsey (in sand), Kober 5BB.
	Irrigated soil	SO4, 101-14, Teleki 5C, Schwarzmann, 3306 a 3309 Couderc, 420A.

Table 7. Dependence of tolerance drought and chlorosis of rootstocks on soil conditions (WHITE, 2009).

A good understanding of physiological mechanism that enable plants to adapt themselves to the water deficit and to maintain growth also during stress periods could help within the framework of individual breeding programs to screen and select stress-tolerant genotypes (Winter *et al.*, 1988).

5. Conclusion

Regarding climatic changes and a more and more frequent occurrence of periods of drought within the growing season, the problem of lime-induced chlorosis and drought damage of grapevine plants becomes to be more and more important.

Hofäcker (2004) presented a general evaluation of the drought and chlorosis resistance of rootstocks most commonly grown in Europe; results of this analysis are presented in Table 8.

Rootstock	Parentage	Country of origin	*Drought resistance	*Chlorosis resistance
5 BB	*V. berlandieri x V. riparia*	Austria	+++	+++
SO4	*V. berlandieri x V. riparia*	Germany	+++(+)	++++
Binova	*V. berlandieri x V. riparia*	Germany	+++(+)	++++
125 AA	*V. berlandieri x V. riparia*	Austria	++(+)	+++(+)
5C	*V. berlandieri x V. riparia*	Hungary	+(+)	++/+++
Teleki 8B	*V. berlandieri x V. riparia*	Hungary	+++(+)	++++
420A	*V. berlandieri x V. riparia*	France	++++	++(+)
161-49 Couderc	*V. berlandieri x V. riparia*	France	+	+++++
R.S.B.1	*V. berlandieri*	France	+++	+++++
140 Ruggeri	*V. berlandieri x V. rupestris*	Italy	++++	++++
1103 Paulsen	*V. berlandieri x V. rupestris*	Italy	++++(+)	++++
775 Paulsen	*V. berlandieri x V. rupestris*	Italy	++++(+)	++++
Richter 110	*V. berlandieri x V. rupestris*	France	++++	++++
Richter 99	*V. berlandieri x V. rupestris*	France	++++	+++
3309 Couderc	*V. riparia x V. rupestris*	France	+++	+(+)
Schwarzmann	*V. riparia x V. rupestris*	Czech Republic	++(+)	++
101-14 Millardet de Grasset	*V. riparia x V. rupestris*	France	+(+)	+(+)
Cosmo 2	*V. berlandieri x V. riparia*	Italy	+++	+++
Cosmo 10	*V. berlandieri x V. riparia*	Italy	+++	+++

Rootstock	Parentage	Country of origin	*Drought resistance	*Chlorosis resistance
Riparia Glorie de Montpellier	*V. riparia*	France	+	+++(+)
Rupestris du Lot	*V. rupestris*	France	++	++
Börner	*V. riparia x V. cinerea*	Germany	+++(+)	++(+)
Rici	*V. riparia x V. cinerea*	Germany	+++(+)	++(+)
Cina	(*V. berlandieri x V. riparia*) x *V. cinerea*	Germany	+++(+)	++(+)
Sori	*V. solonis x V. riparia*	Germany	+++	++
1616 Couderc	*V. solonis x V. riparia*	France	+++	++
Gravesac	161-49 C x 3309 C	France	++++	+++
Fercal	(*V.berlandieri* x Colombard) x / *V.berlandieri* x (*V. riparia x V. rupestris x V. candicans*)/	France	++	+++
Sorisil	Sylvaner x 1616 C	Germany	++++	+++(+)
26 G	Trolinger x *V. riparia*	Germany	+++	++++
41B Millardet de Grasset	Chasselas blanc x *V. berlandieri*	France	++++	+++
333 E.M.	Cabernet Sauvignon x *V. berlandieri*	France	++++	++++
Golia	Castel 156-12 x *V. berlandieri*	Italy	+++(+)	+++
Georgikon 28	Kober 5 BB x *V. vinifera*	Hungary	++++	++++

Note: + = Very low, ++ = Low, +++ = Medium, ++++ = High, +++++ = Very high

Table 8. Drought and chlorosis tolerance of the most common European rootstocks (adapted after *Hofäcker, 2004).

Effects of lime-induced chlorosis and drought of grapevine rootstocks are therefore very important, especially in association with a better understanding of effects of these abiotic factors on grapevine on the one hand and the possibility of the use of such a knowledge when breeding and selecting rootstocks on the other.

The aim of this survey of literature is to present a complete overview of rootstock tolerance to two important abiotic factors – lime and drought.

Acknowledgements

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