

Effects of juice pH and potassium on juice and wine quality, and regulation of potassium in grapevines through rootstocks (*Vitis*): a short review

S. KODUR

Department of Agricultural Sciences, La Trobe University, Bundoora, Victoria, Australia

Summary

In warm irrigated regions of Australia (such as Sunraysia), pH of grape juice often tends to be high (e.g. > 3.8). A high juice pH is undesirable for the production of quality wines as it results in wines of low quality for example, reduced colour stability and poor taste. Such a high juice pH is typically associated with a high concentration of K in the juice, depending on the scion, rootstock and location. Potassium is an essential nutrient and plant genotypes, including grapevines, differ in the accumulation of K in plant and/or plant parts. This difference in the accumulation of K by genotypes can be exploited to manipulate the concentration and content of K in plants, berries in particular for example, through selection and use of low K accumulating rootstocks to overcome the high pH affects. This paper briefly reviews the effects of juice pH and K on juice and wine quality, and the role and effect of rootstocks in the regulation of K in grapevine. This will provide a basic knowledge about the current research and key future research needed for the maintenance of acceptable quality of grape juice and wine through use of rootstocks.

Key words: Cation, organic acid, variety, woody perennials.

In warm (high mean temperature, e.g. Mean January Temperature > 21 °C) irrigated regions of Australia (such as Sunraysia), the concentration of potassium (K⁺, hereafter referred to as K) in the juice of mature berries can be high (e.g. > 50 mM) depending on the scion, rootstock and location. A high concentration of K in the juice in turn may lead to a high juice pH (e.g. > 3.8), and to wine of lower quality [e.g. reduced colour stability and poor taste (RÜHL *et al.* 1992)]. Winemakers can adjust the pH of the wine, but at increased cost of input (MPELASOKA *et al.* 2003). Therefore, in order to maintain optimum quality of grape juice and wine, excessive uptake of K into the berries should be avoided. The concentration of K in berries and/or the whole grapevine can be controlled by rootstocks that accumulate a low concentration of K (RÜHL 1989, CIRAMI *et al.* 1993, WHITING 2003, KODUR *et al.* 2010 a, b). Thus, an understanding about K, pH and rootstocks will help in the use of rootstocks for the regulation of K and pH in grapevine under practical conditions. Therefore, this short

review briefly gives an insight about the effects of juice K and pH with respect to grape juice and wine quality (e.g. colour, taste), the role of grapevine rootstocks in the regulation of K and the mechanisms and/or factors associated with K regulation in grapevine. This short review will also serve as a starting point to conduct further research in the regulation of K in grapevine through rootstocks.

pH: pH is a measure of the acidity or basicity of a solution. pH is one of the most important factors that affect quality of grape juice and hence the wine (BOULTON 1980, ILAND 1987). The major roles of pH with respect to quality of grape juice and wine are a) perception of acidity and its impact on fruit flavour, acid taste and sugar/acid balance of wines (RÜHL *et al.* 1992), b) stability of soluble grape proteins (MORETTI and BERG 1965) and precipitation of potassium bitartaric acid during winemaking (BERG and KEEPER 1958), c) colour stability of red table wines (SOMERS 1975) and d) occurrence of the malo-lactic fermentation (FORNACHON 1957) and microbial stability of wines (BOULTON 1980).

Unfortunately, in most warm irrigated regions of Australia, pH of the grape juice tends to be too high (e.g. > 3.8) rather than too low (e.g. < 3.0) or optimum, which results in the undesirable effects such as a) reduced quality of colour, for example red wines with a brownish hue (SOMERS 1975, RÜHL *et al.* 1992, MPELASOKA *et al.* 2003), b) poor taste, sugar/acid balance and wine stability, which in the absence of substantial addition of acid result in wines with a flat taste (RÜHL *et al.* 1992) and c) susceptibility of musts and wines to biological spoilage (MPELASOKA *et al.* 2003).

In order to overcome the adverse effects associated with high pH, organic acids (in particular tartaric acid) or ion exchange materials (to exchange K⁺ for H⁺) are often added to lower the pH of wine (RANKINE 2004). However, these practices are costly and not permitted in some countries, and the wines may be rejected due to consumer demand for chemical-free natural products (RÜHL 1991). Therefore, maintenance of juice and wine quality through use of rootstock is highly desirable.

The pH of grape juice or wine results from the balance between anionic forms of organic acids (mainly malic acid and tartaric acid) and the major cations (mainly K) (BOULTON 1980). Therefore, alteration of the concentration of any of these three factors (malic acid, tartaric acid and K) in grape juice eventually affects the final pH of grape juice.

Potassium (K): Potassium is a predominant cation involved in pH balance. A close correlation between

the pH and concentration of K in grape juice and/or wine, has often been reported (HALE 1977, SOMERS 1977, BOULTON 1980, ILAND 1987). Potassium is an important and essential nutrient element for grapevine growth, yield and desired composition and quality of grape juice and wine. Potassium is the most abundant cation in living plant cells constituting up to 10 % of plant dry matter (LEIGH and WYN-JONES 1984, VERY AND SENTENAC 2003) and membranes of plants are highly permeable to K. Potassium plays an important role for example, in the turgor regulation, charge balance, protein synthesis (LEIGH and WYN-JONES 1984), enzyme activation (WALKER *et al.* 1998) and cellular transport processes (PATRICK *et al.* 2001). However, when K availability is in excess (e.g. juice K > 50 mM), in association with organic acids, K changes qualitative factors of grape juice and wine. The effects associated with K and organic acids are as follows.

a) High concentration of K in grape juice decreases the concentration of free acids (in particular tartaric acid) in juice, and results in an overall increase in the pH of grape juice, must and wine (GAWEL *et al.* 2000). During winemaking, a high concentration of K in wine increases the precipitation of tartaric acid in the salt form of potassium bitartaric acid, and hence decreases the concentration of free tartaric acid. Thus, a high concentration of K in wine makes pH adjustment difficult and expensive. There are many factors which affect the pH of grape juice and thereby the final composition and quality of juice and wine. These factors may be stoichiometric exchange of organic acid hydrogen ions with cations (e.g. K) leading to a decrease in the concentration of free acids, and the tartaric acid/malic acid ratio (GAWEL *et al.* 2000).

b) High concentration of K in juice may decrease the rate of degradation of malic acid through respiration of malic acid, by impeding transfer of malic acid from the vacuole storage pools to the cytoplasm, the site of degradation of malic acid (HALE 1977).

c) High concentration of malic acid increases malolactic fermentation, a secondary fermentation carried out by many lactic acid bacteria and which may have either a positive or negative effect on the organoleptic quality of the wine (MPELASOKA *et al.* 2003). A correlation between the concentration of K and malic acid in juice as the berries ripened (HALE 1977), suggests the positive effect of concentration of K on concentration of malic acid in grape juice.

d) Tartaric acid is a significantly stronger acid than is malic acid. Consequently, at similar values of total acidity, a lower tartaric acid/malic acid ratio may result in a higher pH (BOULTON 1980, GAWEL *et al.* 2000). Tartaric acid gives a crisp and fresh acid taste to the wine (RÜHL 2000), and therefore an optimum concentration of tartaric acid in juice is highly desirable. However, a high concentration of K in grape juice can lead to reduced tartaric acid/malic acid concentration ratio which is undesirable for the production of high quality wines (MPELASOKA *et al.* 2003).

Rootstocks and their effect on K and juice pH in grapevine: For many centuries, cultivars of *Vitis vinifera* were grown on their own roots in the grape-growing regions of Europe. However, problems

such as grape phylloxera (*Daktulosphaira vitifoliae*) and nematode infestation in vineyards encouraged widespread use of rootstocks (WHITING 2003). It has only been during the last 30 years that significant attention has been paid to the effects of rootstocks on the quality of grape juice and wine (RÜHL and WALKER 1990). The commonly-used grapevine rootstocks (from Australian perspective) and their parentage are presented in the Table. Grapevine rootstocks differ in their ability to adapt to different soil conditions, and in their resistance to soil borne pests and diseases. Furthermore, rootstocks can regulate the nutrient levels (including K) of grafted variety (RÜHL 1989, BRANCADORO *et al.* 1994, FISARAKIS *et al.* 2004, ANTONIO IBACACHE and CARLOS SIERRA 2009). Differences between rootstocks in the accumulation of K in grapevines, led to use of certain rootstocks to regulate the concentration of K in shoot parts and hence the juice pH.

A close association between K uptake of a rootstock (measured as accumulation of K in the petioles), and the effect of the rootstock on the pH of the scion grape juice (RÜHL and WALKER 1990) shows that increased pH in juice is generally affected by rootstocks. Under some warm irrigated conditions of Australia, pH in grape juice and wine is too high, and such studies have further established the rootstock effects on concentration of K and the pH of grape juice (RÜHL and WALKER 1990, RÜHL 1991). HALE (1977) predicted the non-suitability of rootstocks which accumulate very high concentrations of K in juice of the scion (e.g. 'Dogridge' grafted with 'Shiraz'), when grown under warm irrigated conditions.

Potassium uptake and accumulation in grapevine rootstocks: rootstocks vary in the accumulation of K into the various parts of grapevines. High accumulation of K in petioles (DOWNTON 1985) and in juice and wine (CIRAMI *et al.* 1984) was found for Dogridge. A high concentration of K in shoot parts (e.g. petiole and laminae) was also reported for Freedom (RÜHL 1991), 1613C and Harmony (ANTONIO IBACACHE and CARLOS SIERRA 2009). Ability of rootstocks such as 99 R, 110 R, SO4 and/or 44-53 M to accumulate higher K content in grapevine was also similarly reported (BRANCADORO *et al.* 1994, NIKOLAOU *et al.* 2000, GARCIA *et al.* 2001, FISARAKIS *et al.* 2004). In contrast, a consistent, restricted accumulation of K in the grapevines was found for 140 R (RÜHL and WALKER 1990, RÜHL 1993, KODUR *et al.* 2010 a, b). Existence of these differences between rootstocks means that, the content or concentrations of K in grapevine parts can be regulated by careful selection of rootstocks based on our need (e.g. a low K accumulating rootstock for areas where soils are rich in available K and vice-versa). Such differences between rootstocks in the concentration or content of K in the berry juice of the scion or shoot parts are mainly due to differences in their ability in K uptake from soil and root to shoot transport of K (RÜHL 1989, KODUR *et al.* 2010 a). Potassium is taken up by plant roots from a wide range of external concentrations, varying from 0.1 to 10 mM (HAWKESFORD and MILLER, 2004). Potassium taken up by plants from soil is generally transported to different plant parts at a higher rate than are other nutrients, for example Ca, Mg (MENDEL AND KIRKBY 2001) and K delivery to the

Table

The parentage of some of the commonly used rootstock hybrids in Australia

Parentage	Derivatives (Rootstock hybrids)
<i>V. riparia</i> x <i>V. rupestris</i>	3309 and 3306 Couderc 101-14 Millardet et de-Grasset Schwarzmann
<i>V. berlandieri</i> x <i>V. riparia</i>	SO 4 5BB Kober/5A Teleki 5C Teleki 420A Millardet and de-Grasset
<i>V. berlandieri</i> x <i>V. rupestris</i>	1103 Paulsen 99 Richter 110 Richter 140 Ruggeri
<i>V. vinifera</i> x <i>V. berlandieri</i> <i>V. vinifera</i> x <i>V. rupestris</i>	333EM, 41 B 1202 Couderc, ARG No. 1
<i>V. champinii</i> x <i>V. rupestris</i> , <i>V. champinii</i> x <i>V. riparia</i> , <i>V. champinii</i> x <i>V. Vinifera</i>	Lider's K and J series
(<i>V. vinifera</i> x 333 EM) x <i>V. berlandieri</i> <i>V. longii</i> x Othello (<i>V. labrusca</i> x <i>V. riparia</i> x <i>V. Vinifera</i>) Dogridge x 1613 Couderc	Fercal 1613 Couderc Harmony, Freedom

root surface is predominantly brought about by diffusion (SEIFFERT *et al.* 1995). In plant system, K transport into the cells involves multiple mechanisms, and movement of K inside plants is mediated by plant K transporters and channels. Potassium carriers mediate energized high and low affinity uptake whereas potassium channels mediate passive low affinity potassium transport across plant cell membranes. The high-affinity transport system relates to K uptake at low external K concentrations (< 1 mM) whereas low affinity transport system relates to high external K concentrations (> 1 mM). The K channels and/or transporters in plants, their importance and functions have been well discussed (FOX and GUERINOT 1998, VERY and SENTENAC, 2003, ASHLEY *et al.* 2006, GIERTH and MASER 2007, CHEN *et al.* 2008, SZCZERBA *et al.* 2009). It has been shown that cultivars of grapevine may vary with respect to free space properties (MAGGIONI and VARANINI, 1983) and transport at plasma membrane level (PINTON *et al.* 1990).

Plant roots (or root-based factors) play an important role in K uptake and/or accumulation in grapevine. Plant genotypes vary with respect to their rooting morphology (e.g. root length) and the rooting pattern (e.g. branching) which may have a large effect on the pattern of K uptake from the soil. The differences in the root morphology and density in the soil profile between genotypes may affect differential acquisition of K (SWANEPOEL and SOUTHEY 1989). Root hairs are the major region of nutrient absorption and they enhance the absorptive surface area of roots (WANG *et al.* 2006). The importance of root hairs in K uptake and transport was revealed in Arabidopsis (AHN *et al.* 2004). Root exudates also play predominant role in the mineral nutrition of grapevine, by either containing signals for the

regulation of microbial activity, or by providing molecules to control rhizosphere processes to increase nutrient acquisition (DAKORA and PHILLIPS 2002). Root pressure on the other hand found to enhance K uptake and roots to shoot transport of K, particularly in young grapevines (KODUR *et al.* 2010 a, b).

Other factors that affect K uptake and/or accumulation in grapevine may include plant growth and vigour; shoot demand for K in relation to the root size, shoot/roots weight, interaction between K and other ions (e.g. Na, Mg), scion used in the study and rootstock-scion interaction. A series of experiments on a range of rootstocks grown as ungrafted (KODUR *et al.* 2010 a) or grafted with 'Shiraz' scion (KODUR *et al.* 2010 b) showed that a) irrespective of grafting, total uptake of K in grapevine was positively affected by grapevine growth and vigour but not affected by total water use, b) accumulation of K in the shoot of grapevine (ungrafted) was positively affected by shoot vigour, shoot demand for K in relation to the root size, shoot/roots dry weight and root pressure, but not affected by transpiration rate, and c) accumulation of K in the shoot of grapevine (grafted with 'Shiraz') was positively affected by root pressure, but not affected by either shoot/roots dry weight or transpiration rate. The accumulation of K in grapevine is also affected by vineyard management practices. For example, increased K supply to soil found to increase K levels in various parts of grapevine (MORRIS *et al.* 1980, PONI *et al.* 2003) while shoot trimming (which affect the source sink balance in grapevine) found to decrease K concentration in leaf blade (PONI *et al.* 2003). Therefore, any kind of differences in the response between rootstocks to one or more of these factors, in particular root-based, will contribute to differences

in the pattern of K uptake, transport and accumulation in grapevine.

The accumulation of K in grapevine may also depend on the rootstock parentage. For example, RÜHL (1989) showed that in the shoot, concentration of K in the progenies from the crosses between *V. berlandieri* and *V. rupestris* (110 R, 140 R and 1103 P) was low, but b) *V. champinii* selection cv. Dogridge was high. Similarly, Freedom, a descendant of Dogridge, is also known to accumulate high concentration of K in shoot parts. A lower K accumulation in petioles of rootstocks with *V. berlandieri* background is also evident from other reports (e.g. WOLPERT *et al.* 2005). On the other hand, the evaluation of red wines made on a small scale (juice not adjusted for high pH) shows that the use of *V. champinii* rootstocks may impact negatively on the quality of red wine in some situations, which is due to the high content of K in the juice (MAY 1994). These studies indicate the differences between rootstocks in the accumulation of K and the possible association of genetic factors in such accumulation, in particular to the shoot parts of rootstocks. If this were the case, rootstocks bred for low K absorption, and low transport from roots to shoot may help in the regulation of K in grapevines. Such breeding is in progress elsewhere (WALKER and CLINGELEFFER 2009), yet information on the genes involved, and the nature of genes related to the regulation of K is limited.

However, the performance of some grapevine rootstocks in the accumulation of K into the grapevine parts is not always similar. For example, a high accumulation of K in 1103 P and a low accumulation of K in Dogridge, in the grapevine were reported by SCIENZA *et al.* (1986). Nevertheless, these differences in the accumulation of K into some rootstocks between different studies could be due to differences in the growing environments (field, glasshouse, grafted with a scion, grown on own-roots), use of different clones of the same rootstocks and differences in sampling time and stage. As with rootstocks, the scion may affect the accumulation of K into the juice, which may also depend on external supply of K. Biomass allocation within the plant and root development in grafted grapevine depends on scion genotypes (TANDONNET *et al.* 2010) and exploitation of genetic variability in mineral nutrition is high when a scion is grafted to rootstocks due to interspecific variation among rootstocks in nutrient uptake and translocation to the scion (GABLEMAN *et al.* 1986). Therefore, scion used in the study and the interaction between rootstock-scion is also of prime consideration while assessing the effect of rootstocks in the K accumulation. Nevertheless, the studies on the mechanisms by which rootstocks and/or scions regulate the accumulation of K are limited and needs further research. Based on the current knowledge, some of the possible fruitful areas of further research are listed below.

Key future research: a) Studies on the relative impact of the climate and in particular soil factors on the long term performance of the grafted grapevines (rootstocks-scion interaction) in the regulation of juice pH and K in juice.

b) In depth studies to determine the specific role and the mechanisms by which the scion inter-relates with the

rootstock to regulate the accumulation of K in the grapevines, in a particular rootstock-scion combination. Experiments that involve an identical rootstock but grafted with different scions may show the possible role of scion/s on a particular rootstock, or the combined effect of a rootstock-scion combination.

c) Given the importance of growth as a driver of accumulation of K in grapevines, comparative studies between rootstocks with high vigour and low vigour in the extent of accumulation of K in vegetative tissues and berries of a common scion.

d) Studies to determine the differences between rootstocks in the retranslocation of K from leaves to the berries, on various scions (particularly in a well established vineyard where genotypic differences between grapevines in shoot growth and internal status of K differ largely).

e) Detailed microscopic studies to identify the location of retention, and restriction of movement of K within the roots of 140 R and other promising rootstocks that can restrict the accumulation of K into the berries (e.g. studies that involve cross and longitudinal sections of roots, to identify the pattern of distribution of K in various root zones and parts).

f) Genetic, physiological and molecular physiological studies to identify the inheritance of rootstock ability to limit the accumulation of K in grapevines and the gene/s that may be involved.

Conclusions

The current short review shows the adverse effects associated with high juice pH and high concentration of K in juice on the quality of wine (e.g. reduced colour stability and poor taste) and highlights the practical suitability of rootstocks in the regulation of K in grapevine and in turn the juice pH. Consideration of the basic knowledge provided in this review and further research on mechanisms by which rootstocks differ in the accumulation of potassium in grapevine will help in the maintenance of acceptable quality of grape juice and wine through selective use of rootstocks.

Acknowledgements

This study was supported by an International Postgraduate Research Scholarship and a La-Trobe University Postgraduate Research Scholarship.

References

- AHN, S. J.; SHIN, R.; SCHACHTMAN, D. P.; 2004: Expression of KT/KUP genes in *Arabidopsis* and the role of root hairs in K⁺ uptake. *Plant Physiol.* **134**, 1135-1145.
- ANTONIO IBACACHE, G.; CARLOS SIERRA, B.; 2009: Influence of rootstocks on nitrogen, phosphorus and potassium content in petioles of four table grape varieties. *Chilean J. Agric. Res.* **69**, 503-508.
- ASHLEY, M. K.; GRANT, M.; GRABOV, A.; 2006: Plant responses to potassium deficiencies: a role for potassium transport proteins. *J. Exp. Bot.* **57**, 425-436.

- BERG, H. W.; KEEFER, R. M.; 1958: Analytical determination of tartrate stability in wine. I. Potassium bitartrate. *Am. J. Enol. Vitic.* **9**, 180-193.
- BOULTON, R.; 1980: The general relationship between potassium, sodium and pH in grape juice and wine. *Am. J. Enol. Vitic.* **31**, 182-186.
- BRANCADORO, L.; VALENTI, L.; REINA, A.; SCIENZA, A.; 1994: Potassium content of grapevine during the vegetative period: The role of the rootstock. *J. Plant Nutr.* **17**, 2165-2175.
- CIRAMI, R. M.; MCCARTHY, M. G.; GLENN, T.; 1984: Comparison of the effects of rootstocks on crop, juice and wine composition in a replanted nematode-infected Barossa Valley vineyard. *Aust. J. Exp. Agric. Anim. Hus.* **24**, 283-289.
- CIRAMI, R. M.; MCCARTHY, M. G.; NICHOLAS, P. R.; 1993: Clonal selection and evaluation to improve production of Cabernet Sauvignon grapevines in South Australia. *Aust. J. Exp. Agric.* **33**, 213-220.
- CHEN, Y. F.; WANG, Y.; WU, W. H.; 2008: Membrane transporters for nitrogen, phosphate and potassium uptake in plants. *J. Integr. Plant Biol.* **50**, 835-848.
- DAKORA, F. D.; PHILLIPS, D. A.; 2002: Root exudates as mediators of mineral acquisition in low-nutrient environments. *Plant Soil* **245**, 35-47.
- DOWNTON, W. J. S.; 1985: Growth and mineral composition of the Sultana grapevine as influenced by salinity and rootstock. *Aust. J. Agric. Res.* **36**, 425-434.
- FISARAKIS, I.; NIKOLAOU, N.; TSICALAS, P.; THERIOS, I.; STAVRAKAS, D.; 2004: Effect of salinity and rootstock on concentration of potassium, calcium, magnesium, phosphorus, and nitrate-nitrogen in Thompson Seedless grapevine. *J. Plant Nutr.* **27**, 2117-2134.
- FORNACHON, J. C. M.; 1957: The occurrence of malo-lactic fermentation in Australian wines. *Aust. J. Appl. Sci.* **8**, 120-129.
- FOX, T. C.; GUERINOT, M. L.; 1998: molecular biology of cation transport in plants. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **49**, 669-696.
- GABLEMAN, W. H.; GERLOFF, G. C.; SCHETTINI, T.; COLTMAN, R.; 1986: Genetic variability in root systems associated with nutrient acquisition and use. *HortScience* **21**, 971-973.
- GARCIA, M.; GALLEGRO, P.; DAVEREDE, C.; IBRAHIM, H.; 2001: Effect of three rootstocks on grapevine (*Vitis vinifera* L.) cv. Negrette, grown hydroponically. I. Potassium, calcium and magnesium nutrition. *S. Afr. Enol. Vitic.* **22**, 101-103.
- GAWEL, R.; EWART, A.; CIRAMI, R.; 2000: Effect of rootstock on must and wine composition and the sensory properties of Cabernet Sauvignon grown at Langhorne Creek, South Australia. *Aust. NZ. Wine Ind. J.* **15**, 67-73.
- GIERTH, M.; MASER, P.; 2007: Potassium transporters in plants-Involvement in K⁺ acquisition, redistribution and homeostasis. *FEBS Lett.* **581**, 2348-2356.
- HALE, C. R.; 1977: Relation between potassium and the malate and tartrate contents of grape berries. *Vitis* **16**, 9-19.
- HAWKESFORD, M. J.; MILLER, A. J.; 2004: Ion-coupled transport of inorganic solutes. In: M. R. BLATT (Eds): *Membrane Transport in Plants: Annual Plant Reviews* **15**, 105-134. Oxford: Blackwell publishing Ltd.
- ILAND, P. G.; 1987: Interpretation of acidity parameters in grapes and wine. *Aust. Grapegrower Winemaker* **5**, 81-85.
- KODUR, S.; TISDALL, J. M.; TANG, C.; WALKER, R. R.; 2010: Accumulation of potassium in grapevine rootstocks (*Vitis*) as affected by dry matter partitioning, root-traits and transpiration. *Aust. J. Grape Wine Res.* **16**, 273-282.
- KODUR, S.; TISDALL, J. M.; TANG, C.; WALKER, R. R.; 2010: Accumulation of potassium in grapevine rootstocks (*Vitis*) grafted to Shiraz as affected by growth, root-traits and transpiration. *Vitis* **49**, 7-13.
- LEIGH, R. A.; WYN-JONES, R. G.; 1984: A hypothesis relating critical potassium concentrations for growth to the distribution and functions of this ion in the plant cell. *New Phytol.* **97**, 1-13.
- MAGGIONI, A.; VARANINI, Z.; 1983: Free-space binding and uptake of ions by excised roots of grapevine. In: M. R. Saric; B. C. Loughman (Eds): *Genetic aspects of plant nutrition*, 133-137. Martinus Nijhoff/Dr. W. Junk Publishers, The Hague, Boston, Lancaster.
- MAY, P.; 1994: *Using Grapevine Rootstocks: The Australian Perspective*. Winetitles: Adelaide.
- MENDEL, K.; KIRKBY, E. A.; 2001: *Principles of Plant Nutrition*. Kluwer Acad. Publ., London.
- MORRIS, J. R.; CAWTHORN, P. L.; FLEMING, J. W.; 1980: Effect of high rates of potassium fertilization on raw product quality and changes in pH and acidity during storage of Concord grape juice. *Am. J. Enol. Vitic.* **31**, 323-328.
- MPELASOKA, B. S.; SCHACHMAN, D. P.; TREEBY, M. T.; THOMAS, M. R.; 2003: A review of potassium nutrition in grapevines with special emphasis on berry accumulation. *Aust. J. Grape Wine Res.* **9**, 154-168.
- MORETTI, R. H.; BERG, H. W.; 1965: Variability among wines to protein clouding. *Am. J. Enol. Vitic.* **16**, 69-78.
- NICOLAOU, N.; KOUKOURIKOU, M. A.; KARAGIANNIDIS, N.; 2000: Effects of various rootstocks on xylem exudates cytokinin content, nutrient uptake and growth patterns of grapevine *Vitis Vinifera* L. cv. Thompson Seedless. *Agronomie* **20**, 363-373.
- PATRICK, J. W.; ZHANG, W.; TYERMAN, S. D.; OFFLER, C. E.; WALKER, N. A.; 2001: Role of membrane transport in phloem translocation of assimilates and water. *Aust. J. Plant Physiol.* **28**, 695-707.
- PINTON, R.; VARANINI, Z.; MAGGIONI, A.; 1990: Properties of potassium uptake by seedling roots of grape cultivars. *Plant and Soil* **123**, 175-179.
- PONI, S.; QUARTIERI, M.; TAGLIAVINI, M.; 2003: Potassium nutrition of Cabernet Sauvignon grapevines (*Vitis vinifera* L.) as affected by shoot trimming. *Plant and Soil* **253**, 341-351.
- RANKINE, B. C.; 2004: *Making Good Wine; with an Introduction by M. A. AMERINE*. Pan Macmillan, Sydney.
- RÜHL, E. H.; 1989: Uptake and distribution of potassium by grapevine rootstocks and its implication for grape juice pH of scion varieties. *Aust. J. Exp. Agric.* **29**, 707-712.
- RÜHL, E. H.; 1991: Effect of potassium supply on cation uptake and distribution in grafted *Vitis champinii* and *Vitis berlandieri* × *Vitis rupestris* rootstocks. *Aust. J. Exp. Agric.* **31**, 687-691.
- RÜHL, E. H.; 1993: Effect of K⁺ supply on ion uptake and concentration in expressed root sap and xylem sap of several grapevine rootstock varieties. *Wein. Wiss.* **48**, 61-68.
- RÜHL, E. H.; 2000: Effect of rootstock and K⁺ supply on pH and acidity of grape juice. *Acta Hort.* **512**, 31-37.
- RÜHL, E. H.; FUDA, A. P.; TREEBY, M. T.; 1992: Effect of potassium, magnesium and nitrogen supply on grape berry composition of Riesling, Chardonnay and Cabernet Sauvignon vines. *Aust. J. Exp. Agric.* **32**, 645-649.
- RÜHL, E. H.; WALKER, R. R.; 1990: Rootstock effects on grape juice potassium concentration and pH. In: P. J. Williams; D. M. Davidson; T. H. Lee (Eds) *Proc. 7th Aust. Wine Ind. Techn. Conf.*, 75-78. Adelaide, Australia. (Winetitles: Adelaide).
- SCIENZA, A.; FAILLA, O.; ROMANO, F.; 1986: Investigations on the variety-specific uptake of minerals by grapevines. *Vitis* **25**, 160-168.
- SEIFFERT, S.; KASELOWSKY, J.; JUNGK, A.; CLAASSEN, N.; 1995: Observed and calculated potassium uptake by maize as affected by soil water content and bulk density. *Agron. J.* **87**, 1070-1077.
- SOMERS, T. C.; 1975: In search of quality for red wines. *Food Technol. Aust.* **27**, 49-56.
- SOMERS, T. C.; 1977: A connection between potassium levels in the harvest and relative quality in Australian red wines. *Aust. Wine Brew. Spirit Rev.* **96**, 32-34.
- SWANEPOEL, J. J.; SOUTHEY, J. M.; 1989: The influence of rootstock on the rooting pattern of the grapevine. *S. Afr. J. Enol. Vitic.* **10**, 23-28.
- SZCZERBA, M. W.; BRITTO, D. T.; KRONZUCKER, H. J.; 2009: K⁺ transport in plants: Physiology and molecular biology. *J. Plant Physiol.* **166**, 447-466.
- TANDONNET, J. P.; COOKSON, S. J.; VIVIN, P.; OLLAT, N.; 2010: Scion genotype controls biomass allocation and root development in grafted grapevine. *Aust. J. Grape Wine Res.* **16**, 290-300.
- VERY, A. A.; SENTENAC, H.; 2003: Molecular mechanisms and regulation of K⁺ transport in higher plants. *Annu. Rev. Plant Biol.* **54**, 575-603.
- WALKER, R.; CLINGELEFFER, P.; 2009: Rootstock attributes and selection for Australian conditions. *Aust. Vitic.* **13**, 70-76.
- WALKER, R. R.; CLINGELEFFER, P. R.; KERRIDGE, G. H.; RÜHL, E. H.; NICHOLAS, P. R.; BLACKMORE, D. H.; 1998: Effects of the rootstock Ramsey

- (*Vitis champini*) on ion and organic acid composition of grapes and wine, and on wine spectral characteristics. *Aust. J. Grape Wine. Res.* **4**, 100-110.
- WANG, H.; INUKAI, Y.; YAMAUCHI, A.; 2006: Root development and nutrient uptake. *Crit. Rev. Plant Sci.* **25**, 279–301.
- WHITING, J.; 2003: Selection of Grapevine Rootstocks and Clones for Greater Victoria (Department of primary industries: East Melbourne, Victoria).
- WOLPERT, J. A.; SMART, D. R.; ANDERSON, M.; 2005: Lower petiole potassium concentration at bloom in rootstocks with *Vitis berlandieri* genetic backgrounds. *Am. J. Enol. Vitic.* **56**, 163-169.

Received January 11, 2010