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Uptake, transport, accumulation and retranslocation of potassium in grapevine rootstocks (*Vitis*)

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Summary

The concentration and content of potassium (K) within grapevine can be regulated by selective use of rootstocks. However, the mechanisms by which rootstocks differ in the accumulation of K in the shoot of grapevine are not well understood. Therefore, the current study addresses these issues. Ungrafted rootstocks 140 Ruggeri (140 R) and 101-14 Millardet de Grasset (101-14) were exposed to K tracer rubidium (Rb) in a glasshouse, for 4 hours through roots to study uptake and transport of Rb from roots to shoot, and for 24 hours through leaf to study downward transport of Rb, in each case assessed up to 48 hours following exposure to Rb. Transpiration rates and root traits were also measured. Results showed similar total Rb uptake and similar downward transport of Rb between the two rootstocks but lower accumulation of Rb in the shoot and lower shoot/roots Rb concentration (as a result of higher retention of Rb in roots), in 140 R than that in 101-14. Transpiration rates and total root length (but not total root surface area) remained similar between two rootstocks. The study shows that short term differences in the accumulation of K in roots and shoot between rootstocks are due to differences in the transport of K from roots to the shoot, rather than by differences in net uptake or retranslocation of K. In addition, such differences were not affected by transpiration rates. The results highlight that accumulation of K in shoot of grapevine rootstocks is regulated mainly by roots.

K e y w o r d s : Cation, nutrient, root, shoot, translocation, transpiration.

Introduction

Grapevine rootstocks (*Vitis*) differ in the accumulation of potassium (K) in various plant parts (Rühl 1989, 1991, Kodur *et al.* 2010 a, b). This differentiation provides a basis for selection of rootstocks to meet specific viticulture and winemaking requirements, for example, by selection and use of high K accumulating rootstocks in soils with low concentrations of available K and *vice versa*. Studies on the accumulation of K in the shoot (or shoot parts) and roots help to predict the accumulation of K in the grape berries, and our previous research (Kodur *et al.* 2010 a, b) showed that some rootstocks under controlled (glasshouse) conditions accumulate low concentrations of K in the shoot (e.g. 140 Ruggeri; hereafter called 140 R) but others accumulate high concentrations in the shoot (e.g. 101-14 Millardet de Grasset; hereafter called 101-14). In addition, such accumulation of K in rootstocks is positively affected by factors such as root traits (e.g. root length, root surface area, amount of fine roots), root pressure and/or growth and vigour, but not by transpiration rate or water use (Kodur *et al.* 2010 a, b). However, the different mechanisms or mode of accumulation of K in shoot between these rootstocks are not well understood, and hence, the current study addresses these issues. In particular, we aimed to determine whether the difference in the accumulation of K in the shoot was due to net uptake of K, transport of K from the roots to the shoot via the xylem, and/or the retranslocation (or downward transport) of K from the shoot to the roots via the phloem. The effect of transpiration rate and root traits on accumulation of K in grapevine was also determined to substantiate the results. An understanding about such mechanisms of accumulation of K will help to identify the specific sites of regulation of K in rootstocks, and for selection of the most appropriate rootstocks for specific soils and climates.

Material and Methods

In two short term experiments, we applied rubidium (Rb) as a tracer for K (Benlloch *et al.* 1989, Kuppelwieser and Feller 1991, Keunecke *et al.* 2001, Lima Filho and Alavolta 2003, Abshagen-Keunecke and Hansen 2007, Metzner *et al.* 2008) to a) roots for 4 h followed by up to 48 h assessment to monitor uptake, roots to shoot transport and accumulation of Rb in shoot (and also potential retranslocation to roots), with stem portion girdled or non-girdled (Experiment 1), and b) leaf for 24 h, followed by up to 48 h assessment, to monitor downward transport of Rb from leaf to roots (Experiment 2). To avoid possible discrepancy between Rb and K in absorption, adequate concentration of Ca (e.g. 1 mM) was maintained in the nutrient solution, thus, preventing impairment of cellular membranes (Läuchli and Epstein 1970). The difference between rootstocks 140 R and 101-14 in the accumulation of K in shoot was established previously (Kodur *et al.* 2010 a, b) and further confirmed under the growing conditions used in the study.

Ungrafted cuttings of 140 R and 101-14 were raised according to the procedure described by Mullins and Ra-

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JASEKARAN (1981) in a glasshouse (25/20 °C day/night; 14 h light/10 h dark) in pots (with bottom holes), with potting mix (perlite: vermiculite: peat at 6: 3: 1 by volume) as the growth medium. Grapevines were watered daily with Solution A (modified Hoagland #1; HOAGLAND and ARNON 1938) containing (mM): NO_3^-, 2.6; Ca^{2+}, 1.0; Mg^{2+}, 0.3; S, 0.5; $H_2PO_4^-$,0.2; H_3BO_3, 7.7 x 10^{-3}; Zn, 1.3 x 10^{-4}; Cu, 5.0 x 10^{-5}; Cl^-, 3; Na^+, 4.0 x 10^{-5}; Mn, 1.5 x 10^{-3}; Mo, 2.0 x 10^{-5}; Co, 1.3 x 10^{-5}; Fe-EDDHA (Iron sequestrine), 2.5 x 10^{-2} and K^+ (as KCl), 3. Each day, before Solution A was applied, each pot was flushed with tap water to remove any nutrients (held in free spaces between the potting mix particles) that remained from the previous day, to avoid differences between treatments in nutrient availability. Inflorescences and extra buds emerging during growth were removed, and 28 d old grapevines containing one lateral shoot with 2 leaves (Experiment 1) or one lateral shoot with 1 leaf (Experiment 2) were then used for the study. At day 28, each grapevine was removed from the pot, roots rinsed (tap water followed by distilled water) and pre-treated for 12 h in a 5 L bucket containing 2 L of Solution A. Solution A was continuously aerated. Roots of each grapevine were then rinsed with 4 mM $CaSO_4$ solution for 3 minutes, followed by another rinse with distilled water for 1 min, and subjected to Rb uptake. Transpiration rate and/or photosynthesis rate were measured in each rootstock a) just before and just after the transfer from potting mix (day 28) to confirm normal functioning of the grapevines after transfer from the potting mix and/or b) during the experiments to determine the effect of transpiration on differential shoot K accumulation in rootstocks. Transpiration rate and/or photosynthesis rate was measured with an LCi Portable Photosynthesis System (ADC BioScientific Ltd, Hoddesdon, England) in each treatment on intact, fully expanded lamina. Experiment 1 had 4 treatments, 140 R girdled, 101-14 girdled, 140 R non-girdled and 101-14 non-girdled. Experiment 2 had 2 (rootstock only) treatments, 140 R and 101-14. In each experiment, there were 5 replicates per sampling time (up to 48 h), and each experiment followed a completely randomised design.

Experiment 1 (Rb applied to the roots): Girdled treatments were included in Experiment 1 to assess possible retranslocation of Rb by comparing the concentration of Rb in the shoot and roots between girdled and non girdled treatments. To prevent retranslocation of Rb from the shoot to roots in the girdled treatments of 140 R and 101-14, blades spaced at 4 mm removed a 4 mm ring of bark from the main stem (just below the node from which the single lateral shoot emerged). The grapevines in each treatment were transferred to 5 L buckets, each containing 2 L of the Flux solution that contained 3 mM Rb but K-free (Flux solution was similar to that of Solution A, except that Rb replaced K), for 4 h, with Flux solution continuously aerated. The top of each bucket was covered with a plastic grid that supported the stem portion to stand upright, while the roots remained in contact with the Flux solution. At the end of 4 hours of uptake of Rb, the rootstocks in each treatment were removed from the bucket. The roots were then rinsed with 4 mM $CaSO_4$ solution for 5 min and rinsed again with distilled water. The grapevines in each treatment were then transferred to 5 L buckets, each containing Solution B that contained 1 mM K but Rb free (Solution B was similar to Solution A except the concentration of K, *i.e.* 1 mM instead of 3 mM), for up to 48 hours, with Solution B continuously aerated. At each sampling time (0, 5, 24 or 48 h) grapevines in each treatment were taken from the bucket, roots rinsed with distilled water for 1 min, and then rinsed with ice-cold Solution B for 3 min. The rootstocks in each treatment were then destructively harvested, separated into various parts, and kept in a cool room (7 °C) for 3 d and subjected to tissue Rb determination.

Experiment 2 (Rb applied to the leaf): Grapevines of 140 R and 101-14 were each transferred to 2 L of Solution B (containing 1 mM K, Rb-free) in a 5 L bucket for 24 h, where roots were continuously in contact with Solution B. The bucket was covered with a plastic grid that supported the stem portion, with the leaf and lateral shoot portions bent outwards for leaf uptake of Rb. Each leaf on the intact grapevine in each treatment was immersed in the Flux solution (that contained 3 mM Rb, K-free) to enable Rb uptake by leaf for 24 h. The Flux solution (about 300 mL) was placed in each 500 mL plastic container at a height of about 20 cm from ground level. The Flux solution and Solution B were each continuously aerated. At the end of 24 h of leaf uptake of Rb, the leaf was disconnected from the Flux solution, and the grapevines in each treatment were removed from the bucket. The single leaf in each treatment was rinsed for 3 min with 4 mM $CaSO_4$, and then with distilled water for 1 min. Grapevines in each treatment were then transferred to 2 L of fresh Solution B in a 5 L bucket for up to 48 h respectively with Solution B continuously aerated. At the end of each sampling time of 0, 24 or 48 h, each intact grapevine was taken out from the bucket, and roots were rinsed with ice-cold Solution B for 3 min. Grapevines in each treatment were then destructively harvested, separated into various parts, kept in a cold room (7 °C) for 3 days, and subjected to tissue Rb determination.

Tissue analysis and statistical analysis (Experiments 1 and 2): Oven-dried (65 °C) tissue samples were powdered with a hammer mill (mesh size of 1 mm), weighed and digested with a 3:1 (mL) mixture of nitric acid and perchloric acid. The concentration of Rb in each sample was measured with an atomic absorption spectrophotometer (Varian Techtron Pty. Ltd, Mulgrave, Victoria, Australia), and K in leaf and root samples was measured with a flame photometer (Corning, Halstead, Essex, England).

Analysis of variance was conducted with SPSS 14.0.1 for Windows (SPSS Inc, Chicago, Illinois, USA). Means of treatments were compared by least significant difference (l.s.d.) at $P = 0.05$.

Results

Experiment 1 (Rb applied to the roots): The concentrations of K in the leaf (38-44 $\mu mol \cdot g^{-1}$) and in the roots (116-124 $\mu mol \cdot g^{-1}$) of 140 R and 101-14

were roughly similar before treatments began (within the ranges shown). The total uptake of Rb (accumulation of Rb into the whole grapevine) at the end of 4 h of uptake period was also similar between the rootstocks (Table). The accumulation of Rb into the shoot in each treatment was rapid over 5 to 24 h (Fig. 1 A) and at 24 h and 48 h, irrespective of girdling, the concentration of Rb in the shoot was significantly higher in 101-14 than that in 140 R. At 24 and 48 h, the concentration of Rb in the roots of 140 R girdled was significantly higher than that in 101-14 girdled (Fig. 1 B). That is, 140 R girdled retained more Rb in the roots than did 101-14 girdled. A similar result was also true with that of shoot/roots Rb concentration (Fig. 1 C).

During Experiment 1, there was no decrease in the concentration of Rb in the shoot (Fig. 1 A) in any treatments. Furthermore, the concentration of Rb in the shoot of girdled treatments of 140 R and 101-14 was similar to that of their respective non-girdled treatment at each sampling time (Fig. 1 A). There was no significant difference between rootstocks in the transpiration rates of laminae during the treatment period (Table) whereas, irrespective of girdling, 101-14 had significantly higher total root surface area (but not total root length) than 140 R at the end of the treatment period (Table).

Experiment 2 (Rb applied to the leaf): The concentrations of K in the leaf (27-38 µmol·g^{-1}) and in the roots (106-120 µmol·g^{-1}) before the Rb treatment were roughly similar between 140 R and 101-14 (within the ranges shown). The differences between the rootstocks in the concentration of Rb in each of the leaf, lateral shoot, stem and roots (respectively Fig. 2 A, B, C, D) were not significant at 0, 24 and 48 h, except in the main stem at 48 h, where 140 R had significantly higher concentration of Rb than did 101-14 (Fig. 2 C). The concentration of Rb in the leaf at 0 h was approximately 30 and 100 fold higher (Fig. 2 A) than that in the lateral shoot (Fig. 2 B) and roots (Fig. 2 D) respectively. The concentration of Rb in the leaf decreased greatly from 0 to 24 h, with no change at 48 h (Fig. 2 A).

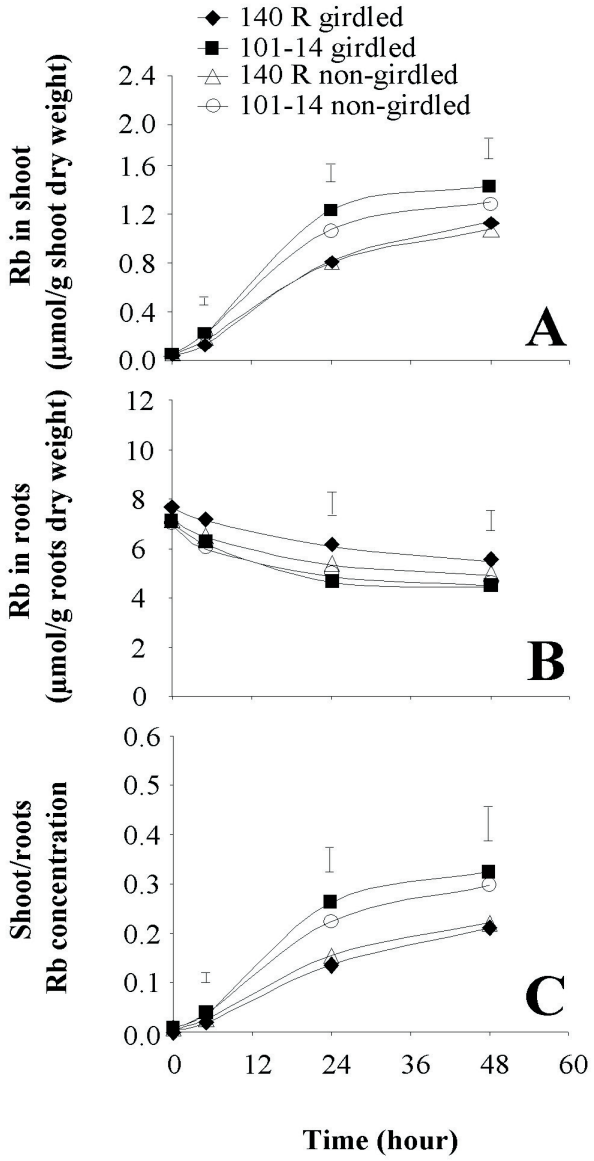

Fig. 1: Concentrations of Rb in shoot (**A**) and roots (**B**); and shoot/roots Rb concentration (**C**), for 140 R and 101-14 rootstocks (girdled and non-girdled) at various sampling times after 4 hours of Rb uptake through the roots (Experiment 1). Error bars show least significant difference (P = 0.05) between treatments. Absence of error bars shows no significant differences. Note: Differences in scales of y-axis between Fig. 1 A, B and C. Girdled, stem girdled; non-girdled, stem non-girdled; 140 R, 140 Ruggeri; 101-14, 101-14 Millardet et de Grasset.

Discussion

Experiment 1 (Rb applied to the roots): The differential accumulation of K in the shoot between two rootstocks was due to difference in the root

Table

Total Rb uptake, transpiration rate, total root surface area and total root length each for girdled and non girdled rootstocks of 140 R and 101-14 (Experiment 1)

Treatment	Total Rb uptake (µmol/grapevine)	Transpiration rate (mmol m^{-2} s^{-1})		Total root surface area (cm^2)	Total root length (cm)
	Hour 0	Hour 24	Hour 48	Hour 48	Hour 48
140 R girdled	2.15	1.92	2.32	281	1104
101-14 girdled	1.80	2.33	1.80	364	1242
140 R non girdled	1.94	2.01	2.54	272	989
101-14 non girdled	1.99	2.14	2.66	328	1118
LSD (P = 0.05)	n.s	n.s	n.s	42	n.s

n.s = not significant; hours 0, 24 and 48 respectively refer to 0, 24 and 48 hours after 4 hours of Rb uptake.

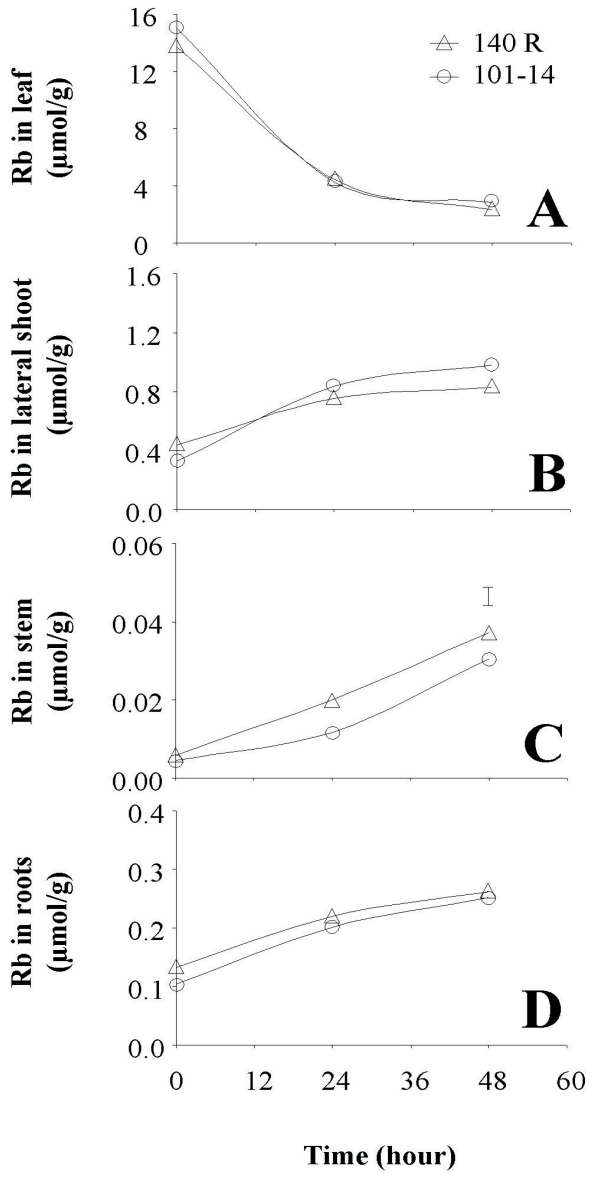

Fig. 2: Concentrations of Rb in leaf (**A**), lateral shoot (**B**), stem (**C**), and roots (**D**), for 140 R and 101-14 rootstocks at various sampling times after 24 hours of Rb uptake through the leaf (Experiment 2). Error bars show least significant difference (P = 0.05) between treatments. Absence of error bars shows no significant differences. Note: Differences in scales of y-axis between Fig. 2 A, B, C and D. 140 R, 140 Ruggeri; 101-14, 101-14 Millardet et de Grasset.

to shoot transport of K. A similar total uptake of Rb by the two rootstocks but difference in the concentrations of Rb in shoot, roots and shoot/roots supports this view. The difference in the transport of K from roots to shoot may imply difference between two rootstocks in loading of K into the xylem. A restricted accumulation of K into the shoot or shoot parts of 140 R relative to 101-14 has been reported previously for grapevines grown in glasshouse (KODUR *et al.* 2010 a, b), whereas in the field, results appear to be site dependent (R. R. Walker and D. H. Blackmore, personal communication). A restricted shoot K accumulation in 140 R (pot-grown) was due to its ability to retain more K in the roots, root vacuoles in particular (RÜHL 1993).

The differential accumulation of K in the shoot between two rootstocks was not related to the retranslocation of K. Absence of significant difference in the concentration of Rb in the shoot between girdled and non girdled grapevines (101-14 and 140 R), and no decrease in the concentration of Rb in shoot over 48 hours in non-girdled treatments (Fig. 1), show that there was no detectable retranslocation of Rb from shoots to the roots in these two rootstocks. These results further substantiate roots to shoot transport of K as the governing mechanism for differential accumulation of K in the shoot of rootstocks. A significant retranslocation of Rb from shoot back to the roots via the phloem seems to have been unlikely in Experiment 1, as the concentration of Rb in the shoot of each treatment was much lower than that in the roots, and/or due to lack of downward transport of Rb from shoot to the roots during the course of Experiment 1.

The differential accumulation of K in the shoot between two rootstocks was not affected by transpiration but may be related to root based factors. A similar transpiration rate between 140 R and 101-14 throughout the experiment (Table), but differences in the transport and subsequent accumulation of K in the shoot suggest that these processes may be regulated by differences in the xylem loading of K as affected by roots but not transpiration (TANNER and BEEVERS 2001). The importance of root-based factors (e.g. root pressure) in the accumulation of K in grapevine was similarly highlighted elsewhere (KODUR 2011). The current study also demonstrates a positive association between K accumulation and specific root traits for example, higher total root surface area in 101-14 compared with that of 140 R. This, in turn, may have contributed to improved nutrient uptake and subsequent nutrient transport in 101-14, on a longer term (e.g. > 48 h), as seen previously (KODUR *et al.* 2010 a, b).

Experiment 2 (Rb applied to the leaf): As shown by downward movement of Rb within each treatment, the two rootstocks may differ in the retranslocation of K from leaf to stem (and in turn to roots) beyond 48 h, but not up to 48 h, in particular to the roots (Fig. 2). Despite the similarities between two rootstocks in the downward transport of Rb, results show that the downward transport of K is rapid and occurs in the short-term (< 48 h), provided conditions favour retranslocation (e.g. high concentration of K in leaf). Potassium is a phloem-mobile element, and experiments with tomato plants (*Lycopersicon esculentum*) have shown that around 20 % of K flux in the xylem stream was associated with retranslocation (ARMSTRONG and KIRKBY 1979). Although the observed difference between rootstocks in the concentration of Rb in the stem (at 48 h) between rootstocks was marginal, differences in Rb content may have been large. That is, since the stem contributes most of the total dry weight of the grapevine, the differences between rootstocks in the content (quantity) of Rb in stem would have been large. This may subsequently have resulted in increased retranslocation of K from stem to the roots beyond 48 h.

The major factors that determine the retranslocation of K are growth (particularly the shoot), and the status of K in

the external solution and within the grapevine. For example, studies with tree species found that nutrient retranslocation occurs in response to production of new shoots (Fife *et al.* 2008), and in particular the growth and production of leaves (Saur *et al.* 2000). Similarly, a very high K supply (e.g. 10 mM) in the external medium may enhance the internal status of K and may increase the retranslocation of K, depending on shoot demand for K (Marschner 1995). Retranslocation of K is also enhanced by other factors, such as artificial shading (Saur *et al.* 2000), whereas the retranslocation efficiency is enhanced by high soil fertility, rapid nutrient uptake, and growth (Nambiar and Fife 1991). The lack of consistent and major differences between two rootstocks in downward transport of Rb in particular to roots in Experiment 2 implies similarities between two rootstocks in relation to the above factors and/or mechanisms responsible for retranslocation of K (in 48 h). Nevertheless, Experiment 2 shows rapid downward transport of Rb in both rootstocks with evidence for possible differences in the retranslocation of Rb beyond 48 h. This suggests the need for further studies to determine the differences in retranslocation of K between rootstocks over long-term to various parts (e.g. roots, and berries in particular), with conditions favouring retranslocation of K (e.g. good shoot growth, high K concentration in leaves or shoot).

Conclusions

The differences between 140 R and 101-14 in the accumulation of K (Rb) into the roots and shoot in short-term (48 h) were mainly due to the difference in upward transport of K from roots to shoot (as a result of differences in the retention of K in roots), rather than to the difference in either net uptake of K into the whole shoot and roots or retranslocation of K from shoot in particular to the roots. Such differences in the accumulation of K in shoot of rootstocks were not affected by transpiration but related to the roots or root based factors. The study also shows rapid downward transport of K on short-term (e.g. < 48 h) when applied through the leaf, with evidence for possible difference between rootstocks in the downward transport of K in the longer-term (e.g. > 48 h).

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