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Accumulation of potassium in grapevine rootstocks (*Vitis*) grafted to 'Shiraz' as affected by growth, root-traits and transpiration

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Summary

The concentration of potassium (K) in scions can be controlled by rootstocks (*Vitis*). However, differences between rootstocks in the accumulation of K and mechanisms of regulation of K, when rootstocks are grafted to a scion, are not clearly understood. Therefore, the current study addresses these issues. Rootstocks Freedom, Schwarzmann, Ramsey, 1103 Paulsen, 110 Richter, 140 Ruggeri and 101-14 were grafted with 'Shiraz' and grown in sand for 56 days in a glasshouse, with daily watering using solutions containing 3 mM K. At day 56, Freedom had highest total K uptake. Freedom and 101-14 had the highest and 140 Ruggeri the lowest concentration of K respectively, in shoot and roots. Accumulation of K in grapevine is affected by the interaction between rootstock and scion, with total K uptake increasing with total root length, total root surface area and percentage of roots in small diameter class (< 0.5 mm). Accumulation of K in the whole grapevine or in the shoot was not affected by either shoot/roots dry weight or transpiration, but was positively related to concentration of K (but not Na) in xylem. The current study highlights the positive impact of root based factors, specifically root traits and root pressure than other (e.g. shoot/roots dry weight, transpiration) in the accumulation of K in 'Shiraz' grapevines when assessed as grafted vines on a range of rootstocks. This knowledge will be important in selecting the new rootstocks for appropriate K uptake or accumulation.

K e y w o r d s : graft, laminae, nutrient, rootstock: scion, shoot: root.

Introduction

In most of the hot irrigated grape growing regions of Australia, the concentration of K in the grape juice can sometimes reach high levels. A high concentration of K in the grape juice leads to a high juice pH (> 3.8) and in turn the production of wines of reduced quality [e.g. reduced colour and flavour (Rühl *et al.* 1992)]. Grape juice with high concentrations of K and high pH not only accentuates the need for acid adjustment during winemaking, but also requires extra effort by wine makers to adjust the wine pH (Mpelasoka *et al.* 2003). Hence, maintaining optimum concentration of K and pH, in juice is highly desirable. Grapevine rootstocks can regulate the accumulation of K in shoot (or shoot parts) and roots, and thereby can regulate the concentration or content of K in grapevines (Cirami *et al.* 1993, Rühl 1989). In the field, rootstocks are usually grafted to a scion, and the scion makes up the majority of the shoot portion of a rootstock-scion combination. Therefore, it is expected that the scion also contributes to the regulation of K in the grapevine in addition to rootstock. Hence, with grafted grapevines, the performance of rootstocks in the regulation of K may differ from that of the same rootstock grown on its own-roots. However, the role of rootstocks when grafted to a scion in the regulation of K uptake and accumulation is not clearly understood. Therefore, the current glasshouse study was aimed to determine a) differences between rootstocks grafted to 'Shiraz' in total K uptake and accumulation into the roots and shoot, and b) possible mechanisms or factors (related to growth, root-traits and transpiration) that regulate such differences.

Material and Methods

C u t t i n g p r o p a g a t i o n a n d e s t a b l i s h m e n t : Own-rooted (un-grafted) rootstocks of Freedom, Schwarzmann, Ramsey, 1103 Paulsen (1103 P), 140 Ruggeri (140 R), 110 Richter (110 R) and 101-14 Millardet et de Grasset (101-14) were propagated from dormant cuttings (4 nodes) in a heated sand-bed. The clones used were respectively D11V1, R1A2S10, A11V2, R2A19S4, A5V19, Q45-3A and 2-5-84. Once the roots had formed (3-4 weeks), rooted cuttings were placed in a paper bag containing rooting mix and kept in a shade house for 3-4 weeks for the production of lateral shoots. Each day, cuttings were sprayed with a fine mist of water. The rootstocks were then pruned to one lateral shoot. Growing buds of 'Shiraz' (clone PT23) as a scion were taken from the field from healthy mother grapevines, and 'Shiraz' was bud grafted to each rootstock. The most uniform grapevines were then placed in black plastic pots (8 L) containing washed river sand of fine texture, and transferred to a glasshouse (25/20 °C day/night; 14 h light/10 h dark). To prevent the loss of sand particles through the holes in the base of the pot, and to allow adequate drainage of nutrient solution, the base of each pot was lined with nylon mesh. The surface of the sand in each pot was covered with plastic beads to decrease evaporative loss of water. Treatments were imposed one week after the grapevines were transferred to pots in the glasshouse.

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E x p e r i m e n t a l d e s i g n : Treatments included the rootstocks (grafted to 'Shiraz') a) Freedom, b) Schwarzmann, c) Ramsey, d) 1103 P, d) 110 R, e) 140 R and f) 101-14. There were 5 replicates for each treatment in a completely randomized design.

W a t e r i n g a n d n u t r i t i o n : Grapevines were watered with a half strength Hoagland # 1 solution (Hoagland and Arnon 1938) that contained 3 mM of K and 1 mM Ca. This nutrient solution was applied in excess each day throughout the experiment (so that soil was completely saturated with nutrient solution), and then drained. Before each grapevine was watered with nutrient solution, pots were flushed with tap water in order to remove the nutrients that were already held in free spaces between the sand particles from the previous application of nutrient solution.

W a t e r u s e : Water use (transpiration by the whole grapevine) in each treatment was measured in alternative weeks, from day 14 to day 56. Each pot was weighed after complete drainage and then re-weighed before the next watering. Total water use (total transpiration by the whole grapevine) in each treatment was calculated as the sum of water use from day 1 to day 56.

L a t e r a l s h o o t l e n g t h : The total length of lateral shoots of each grapevine was measured at 14-d intervals from day 14 to day 56. The total length of lateral shoots (15-20 cm) was similar between the grapevines when the experiment began (day 1).

T r a n s p i r a t i o n r a t e : Transpiration rate of laminae was measured for each grapevine on intact, fully expanded and exposed healthy laminae (1 laminae/grapevine) at day 56 between 9 am and 11 am, with an LCi Portable Photosynthesis System, (ADC BioScientific Ltd, Hoddesdon, England).

D e s t r u c t i v e s a m p l i n g : When the experiment began (day 1), 4 extra replicates of each grapevine were destructively sampled to determine the initial status of K and dry weight. At the end of the experiment (day 56), the shoot portion was cut on a slant with a sharp knife at 10 cm above the base. Each harvested shoot portion was separated into stem, lateral shoots and leaves, and stored in a cold room (7 °C). Each pot containing roots plus the remaining stem portion was placed under uniform shade (to prevent the xylem sap from drying). Sap exudation began roughly one hour after the stem was cut, and xylem sap was collected for 3 hours with the help of a transfer pipette (Samco Sci. Corp, San Fernando, USA) from each grapevine. Xylem sap was not sampled after 3 h, as some of the grapevines showed signs of slower exudation. The xylem sap collected from each grapevine was bulked into a 2 mL Eppendorf tube and the sap volume recorded. The xylem sap was then stored in a cold room (7 °C) for nutrient analysis. The remaining stem portion and the root system were then removed from the pots, and roots were carefully washed with tap water followed by distilled water to remove the adhered sand particles. Washed roots were transferred to the laboratory and root-traits analysed. Roots and stem portion were then placed in a cold room with the other harvested parts of grapevines.

R o o t a n a l y s i s : Washed roots of each grapevine were placed on trays that were specially designed for the root scanner. The roots were then scanned with a flatbed scanner, saved as images (TIFF or JPG format) and then analysed with the software package WinRHIZO.pro v.2003b (Regent Instruments Inc). This root-scanning software was used to determine root-traits, such as total root length (cm), total root surface area (cm^2), and the percentage of each of total root length, total root surface area and total number of root tips in 0.0 to 0.5 mm root diameter class. To identify the extent of availability of root length and root surface area to supply K to the whole grapevine, root length and root surface area per g grapevine were each determined as follows. Root length/unit grapevine weight (cm/g) = total root length (cm)/dry weight of whole grapevine (g). Root surface area/unit grapevine weight (cm^2/g) = total root surface area (cm^2)/dry weight of whole grapevine (g).

T i s s u e d r y i n g a n d d e t e r m i n a t i o n o f s h o o t / r o o t s d r y w e i g h t a n d r e l a t i v e g r o w t h r a t e (R G R) : All grapevine parts were oven-dried (65 ^oC) for 3-4 d. The dry weights of individual parts were recorded and the dried samples were stored in an air-tight plastic box for nutrients analysis. Shoot/roots dry weight (ratio between the dry weights of shoot and roots) and RGR were determined as follows. Shoot/roots dry weight = dry weight of (laminae + petioles + lateral shoots + stem)/dry weight of roots. RGR = (ln W_2 - ln W_1) x 1000/ (t_2 - t_1), where W_1 and W_2 are the initial and final dry weight (each in g) of grapevine at time t_1 (day 1) and t_2 (day 56), respectively.

D e t e r m i n a t i o n o f l a m i n a e s u r f a c e a r e a , w a t e r u s e / u n i t l a m i n a e a r e a a n d w a t e r u s e / u n i t g r a p e v i n e w e i g h t : Each leaf from each grapevine was further separated into lamina and petiole, and the laminae area for each grapevine was measured with an area measurement system (Delta-T Devices Ltd, Burwell, Cambridge). Water use/unit laminae area (mL/cm^2) was determined as the total water use (mL)/ total laminae area (cm^2). Water use/unit grapevine weight (mL/g) was determined as the total water use (mL)/total dry weight of whole grapevine (g).

T i s s u e a n a l y s i s a n d c a l c u l a t i o n s : Oven-dried (65 °C) samples of laminae, petioles, lateral shoots, stem and roots in each grapevine were powdered with a hammer mill (mesh size of 1 mm). Powdered samples were weighed and digested with a 3:1 volume mixture of nitric acid and perchloric acid. The concentration of K in each tissue sample on a dry weight basis was determined with a flame photometer (Corning, England), and expressed as mg/g dry weight. The xylem sap was diluted 1:10 with distilled water, and the concentrations of K and Na in the xylem sap were each determined with a flame photometer, and expressed as mM. Calculations related to K are as follows. Content of K in tissues (mg/tissue) = concentration of K in tissue (mg/g) x dry weight of tissue (g). Content of K in shoot (mg/shoot) = content of K (mg) in (laminae + petiole + lateral shoots + stem). Content of K in whole grapevine (mg/grapevine) = content of K (mg) in (shoot +

roots). Concentration of K in shoot (mg/g shoot) = content of K (mg) in shoot/dry weight of shoot (g). Concentration of K in whole grapevine (mg/g grapevine) = content of K in whole grapevine (mg/grapevine)/dry weight of whole grapevine (g). Total K uptake (mg/grapevine) = content of K (mg) in (shoot + roots) at day 56 – content of K (mg) in (shoot + roots) at day 1. Translocation efficiency of K = content of K (mg) in shoot/content of K (mg) in (shoot + roots).

Statistical analysis: One-way analysis of variance and correlation analysis of data were performed with SPSS V.12 for Windows. Means of treatments were compared with least significant difference (LSD) at P = 0.05.

Interpretation of the results: In the current study, unless otherwise specified a) all the data refer to the measurements made at the end of the experiment (day 56), and b) 'the differences between rootstocks' refer to the differences between rootstocks that were grafted to 'Shiraz' (as 'Shiraz' used as the common scion).

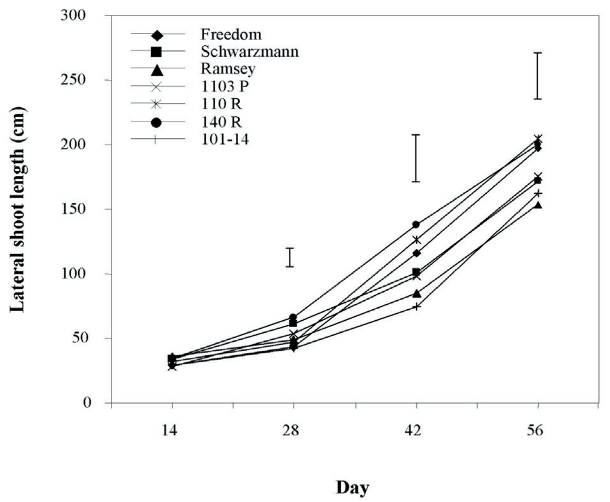

Fig. 1: Lateral shoot length (cm·grapevine^{-1}) of each rootstock grafted to 'Shiraz' from day 14 - day 56. Error bars show least significant difference (P = 0.05) for each sampling time; absence of error bars shows no significant differences between treatments.

Results

Grapevine growth: At day 56 (end of the experiment), there were significant differences between rootstocks in the dry weights of shoot, roots and whole grapevine (Tab. 1). Significant differences were also apparent in shoot/roots dry weight between rootstocks with Ramsey, 101-14 and 140 R significantly higher than that of Schwarzmann and 110 R (Tab. 1). Differences between rootstocks in the lateral shoot length became more apparent from day 28 and at day 56, 110 R and 140 R had significantly higher lateral shoot length compared with those of Ramsey and 101-14 (Fig. 1). A similar result was also true for RGR between rootstocks (Tab. 1).

Table 1

Dry weights of shoot, roots and whole grapevine and shoot/roots dry weight each at the end of the experiment (day 56), and relative growth rate (RGR), for each rootstock grafted to 'Shiraz'

Rootstock	Shoot (g)	Roots (g)	Whole grapevine (g)	Shoot/roots	RGR[a] (mg·g^{-1b}·day^{-1})
Freedom	30	3.3	33	9	16
Schwarzmann	28	3.9	32	8	13
Ramsey	25	2.0	27	12	12
1103 P	26	2.8	29	10	14
110 R	34	4.2	38	8	17
140 R	36	3.4	40	11	17
101-14	25	2.0	27	12	12
LSD	9	1.5	10	2	4

LSD = least significant difference (P = 0.05). [a]RGR = (ln W_2 - ln W_1) x 1000/(t_2 - t_1), where W_1 and W_2 are the initial and final dry weight (each in g) of grapevine at time t_1 (day 1) and t_2 (day 56), respectively. [b]Dry weight.

Water use and transpiration rate. Water use: Water use by each rootstock increased steadily with time (Fig. 2), and rootstocks differed significantly at each sampling time. The total water use was significantly higher for 110 R and 140 R compared with 101-14 and Ramsey, but not the other rootstocks (Tab. 2). The pattern of water use by rootstocks (Fig. 2) was roughly similar to the pattern of lateral shoot length (Fig. 1), during the growth period. Total water use was positively correlated with the dry weight of whole grapevine (r = 0.95, P = 0.01).

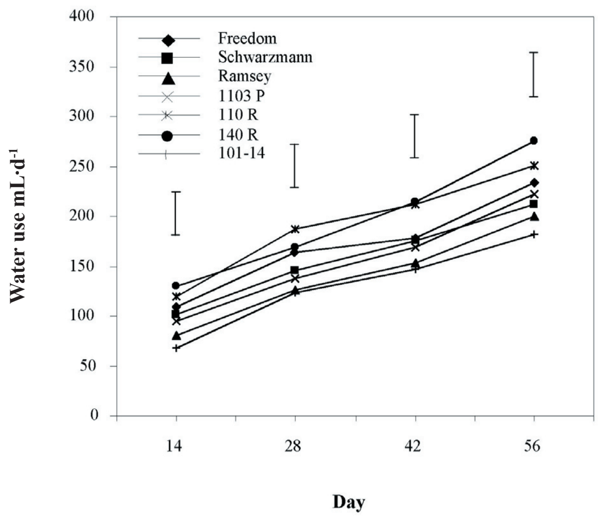

Fig. 2: Water use (mL·d) by each rootstock grafted to 'Shiraz'. Error bars show least significant difference (P = 0.05) for each sampling time.

Water use/unit laminae area was significantly higher for 101-14 compared with all other rootstocks (Tab. 2), however, there were no differences between other rootstocks. This is because rootstocks with higher total water use also

Table 2

Total water use (TWU), total laminae area (TLA), water use/unit laminae area (WU/LA), water use/unit grapevine weight (WU/GW), and transpiration rate (TR) at the end of the experiment (day 56) for each rootstock grafted to 'Shiraz'

Rootstock	TWU[a] (L·56 d^{-1})	TLA (cm^2)	WU/LA (mL·cm^{-2})	WU/GW[b] (mL·g^{-1})	TR (mmol·m^{-2}·s^{-1})
Freedom	9.6	1593	6.3	292	2.7
Schwarzmann	8.9	1498	6.5	290	2.2
Ramsey	7.8	1181	6.7	294	2.5
1103 P	8.7	1275	6.9	298	2.4
110 R	10.8	1945	5.8	285	3.4
140 R	10.8	2008	5.9	275	2.6
101-14	7.3	826	8.9	272	3.5
LSD	2.5	722	1.5	n.s	1.1

LSD = least significant difference (P = 0.05).
n.s. = not significant.
[a]Determined as the sum of water use from Day 1 to Day 56.
[b]Dry weight.

had higher total laminae area (Tab. 2), and total water use was positively correlated with the total laminae area (r = 0.70, P=0.01). On the other hand, the water use/unit grapevine weight was similar between rootstocks (Tab. 2).

Transpiration rate: Rootstocks 110 R and 101-14 had significantly higher transpiration rate than did Schwarzmann (but not the other rootstocks) at day 56 (Tab. 2).

Root-traits: At day 56, rootstocks Freedom and 101-14 had significantly higher total root length compared with that of Ramsey and Schwarzmann, while Freedom also had significantly higher total root surface area than did Ramsey (Tab. 3). Rootstocks 110 R and 140 R had a significantly higher average root diameter than did 101-14 (Tab. 3). Rootstock 140 R contained significantly lower a) root length/unit grapevine weight than did 101-14 (Tab. 1), and b) root surface area/unit grapevine weight than did Freedom (Tab. 1).

Table 3

Total root length (TRL), root length/unit grapevine weight (RL/GW), total root surface area (TRSA), root surface area/unit grapevine weight (RSA/GW) and average root diameter (ARD), at the end of the experiment (day 56) for each rootstock grafted to 'Shiraz'

Rootstock	TRL (cm)	RL/GW[a] (cm·g^{-1})	TRSA (cm^2)	RSA/GW[a] (cm^2·g^{-1})	ARD (mm)
Freedom	2823	89	960	30	1.1
Schwarzmann	2474	83	719	23	1.1
Ramsey	2187	83	608	23	1.1
1103 P	2576	91	744	25	1.1
110 R	2784	77	907	24	1.2
140 R	2753	71	911	23	1.2
101-14	2997	115	730	27	0.9
LSD	341	23	246	5	0.2

LSD = least significant difference (P = 0.05).
[a]Dry weight.

At day 56, rootstocks 101-14 and Freedom had greater percentage of total root length (Figure 3A) and total number of root tips (Fig. 3 C) each in 0.0 to 0.5 mm diameter class of roots than did 140 R. However, the percentage of total root surface area in 0.0 to 0.5 mm diameter class of roots was similar between rootstocks (Fig. 3 B).

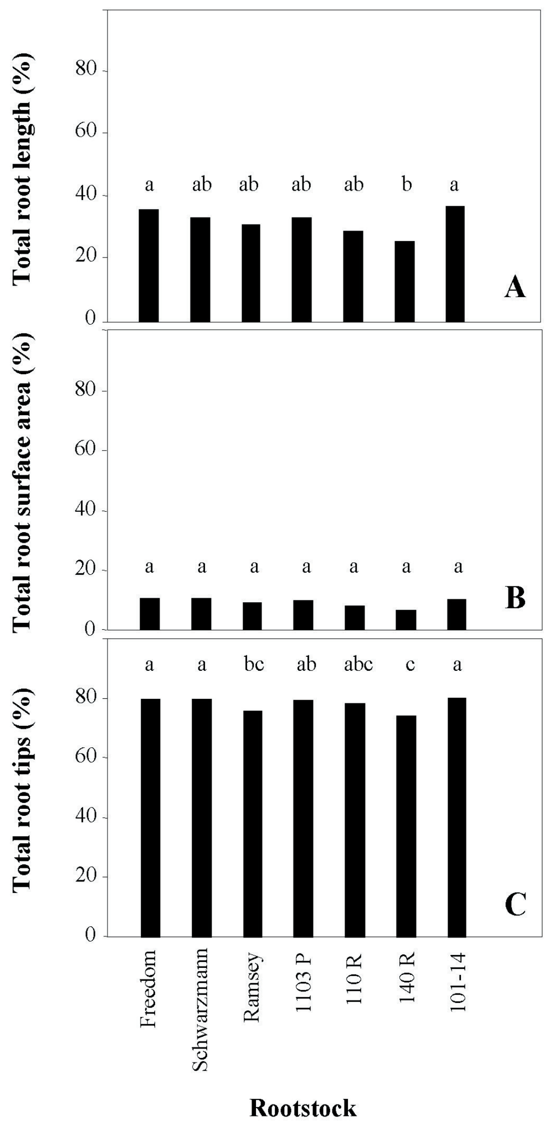

Fig. 3: The percentage of, the total root length (**A**), total root surface area (**B**) and total number of root tips (**C**), each in 0.0 to 0.5 mm diameter class of roots for each rootstock grafted to 'Shiraz' at the end of the experiment (day 56). Different letters indicate significant difference (P = 0.05) between treatments.

Accumulation of K: At day 56, total K uptake was significantly higher for Freedom, 140 R and 110 R compared with 1103 P (Tab. 4). Freedom and 110 R also showed a higher content of K in the shoot compared with that in 1103 P and Ramsey (Tab. 4), whereas Freedom and 140 R showed higher content of K in roots than did 1103 P and 101-14 (Tab. 4). Rootstocks 110 R and 101-14 had

Table 4

Content of K in shoot and roots, total K uptake and translocation efficiency of K each at the end of the experiment (day 56) for each rootstock grafted to ‘Shiraz’

Rootstock	Shoot (mg·shoot^{-1a})	Roots (mg·roots^{-1a})	Total K uptake (mg·grapevine^{-1a})	Translocation efficiency of K[b]
Freedom	642	66	655	0.90
Schwarzmann	538	57	554	0.90
Ramsey	395	44	404	0.90
1103 P	387	38	393	0.91
110 R	621	51	632	0.93
140 R	602	78	641	0.88
101-14	506	41	515	0.92
LSD	223	23	226	0.03

LSD=least significant difference (P = 0.05)
[a]Dry weight.
[b]Translocation efficiency of K = content of K in shoot/content of K in (shoot + roots).

higher translocation efficiency of K compared with 140 R (Table 4).

The total K uptake was correlated with a) the dry weight of whole grapevine (r = 0.85, P = 0.01), b) total root length (r = 0.40, P = 0.05), c) total root surface area (r = 0.72, P = 0.01) and d) average root diameter (r = 0.63, P = 0.01).

At day 56, the concentration of K in the shoot and in the whole grapevine was significantly higher for Freedom and 101-14 compared with that for 140 R, 1103 P and Ramsey (Tab. 5). Rootstock 101-14 also had significantly higher concentration of K in laminae than did 140 R, Schwarzmann and 1103 P (Tab. 5). However, the concentration of K in roots was significantly higher for 140 R than that for 110 R, 1103 P and Schwarzmann (Tab. 5). On the other hand, the shoot/roots concentration of K was significantly higher for 110 R than that for 140 R, Ramsey and 101-14 (Tab. 5).

Table 5

Concentration of K (mg·g^{-1} dry weight) in laminae, shoot, roots and whole grapevine, and shoot/roots concentration of K each at the end of the experiment (day 56) for each rootstock grafted to ‘Shiraz’

Rootstock	Laminae	Shoot	Roots	Whole grapevine	Shoot/roots concentration
Freedom	19.9	21.7	20.5	21.6	1.1
Schwarzmann	16.8	18.5	16.2	18.2	1.2
Ramsey	18.9	16.0	21.2	16.4	0.9
1103 P	17.0	14.6	13.9	14.6	1.1
110 R	18.9	18.2	12.1	17.5	1.5
140 R	15.6	16.6	24.2	17.2	0.8
101-14	21.6	20.4	20.5	20.4	1.0
LSD	4.5	3.5	7.1	3.1	0.4

LSD = least significant difference (P = 0.05).

Concentrations of K and Na in the xylem sap and the xylem sap volume: At Day 56, the concentration of K in the xylem sap was significantly higher for 101-14 than that for Schwarzmann, Ramsey and 140 R (Tab. 6), whereas the concentration of Na in the xylem sap was significantly higher for 1103 P than that for Schwarzmann and 140 R (Tab. 6). The xylem sap volume was higher for Freedom and 110 R compared with Ramsey (Tab. 6). A significant correlation existed between the concentration of K in the xylem sap and the concentration of K in the shoot of grapevines (r = 0.42, P = 0.05).

Table 6

Concentrations of K and Na in the xylem sap[a], and the xylem sap volume, each at the end of the experiment (day 56) for each rootstock grafted to ‘Shiraz’

Rootstock	K (mM)	Na (mM)	Xylem sap volume (μL·grapevine^{-1})
Freedom	10.8	1.3	750
Schwarzmann	8.0	0.6	700
Ramsey	9.1	1.0	600
1103 P	11.3	1.4	640
110 R	10.6	0.9	760
140 R	9.0	0.8	630
101-14	12.2	1.3	700
LSD	3	0.5	145

LSD = least significant difference (P = 0.05).
[a]Xylem sap was collected for 3 h.

Discussion

Accumulation of K in grapevines and the role of rootstocks and scion: Significant differences in total K uptake (Tab. 4) and accumulation of K into the roots and shoot (Tabs 4 and 5) by grapevine rootstocks grafted to ‘Shiraz’ show the ability of rootstocks and/or the specific combination effect of rootstock with ‘Shiraz’ in the regulation of K in grapevine. As ‘Shiraz’ was the common scion for all rootstocks, the differences between grapevines in the accumulation of K were largely due to rootstocks. These results also show that the mechanisms of accumulation of K in scion are controlled by rootstocks (Rühl 1991). However, the role of the scion in accumulation of K in grapevines is not clearly understood.

Similar to rootstocks, the scion can regulate the accumulation of K in grapevines. The scion contributes the majority of the shoot in a grafted grapevine, and in the current study, nearly 85 % of dry weight of whole grapevine was constituted by 'Shiraz' scion. A positive correlation between dry weight of whole grapevine and total K uptake suggests that rootstock-scion interaction and/or scion may regulate K uptake. Similar to K uptake, transport of K from roots to shoot may be controlled by scion. Efficient K transport systems in some scion varieties were also observed in a model experiment with grafted grapevines (Miklós and Hajdu 2003). Exploitation of genetic variability in mineral nutrition is high when a scion is grafted to rootstocks, due to interspecific variation between rootstocks in nutrient uptake and translocation to the scion (Gableman *et al.* 1986). On the other hand, non-significant differences in the shoot dry weights between 5 of the 7 tested rootstocks grafted to 'Shiraz' in the current study show that the shoot size was not severely affected by rootstocks and may reflect the dominant effect of the scion in the regulation of shoot morphology in grafted grapevines. Shoot morphology affected the transport and accumulation of K into the shoot of grapevine on own-roots (Kodur *et al.* 2010).

Differences between rootstocks grafted to 'Shiraz' in the accumulation of K: K uptake and accumulation into the roots and shoot of grapevine depends on the type of rootstock (grafted to 'Shiraz'). Differences between rootstock genotype in K uptake from the soil were previously reported (Downton 1985, Scienza *et al.* 1986, and Rühl 1989). A high total K uptake and accumulation into the shoot, plus a high concentration of K in the whole grapevine and in shoot with Freedom, suggest that Freedom takes up K more efficiently from the soil and accumulates more K in the shoot, than does 140 R. A high accumulation of K into the shoot of 'Shiraz' grafted to Freedom agrees with other authors (Downton 1985, Rühl 1989). On the other hand, a high concentration of K in roots (but not in the shoot) in 140 R suggests the ability of 140 R to restrict the accumulation of K into the shoot. A restricted accumulation of K in the grapevines of 140 R was similarly reported (Rühl 1989, 1993). However, a high total K uptake (but not concentration of K in the whole grapevine) by 140 R shows the effect of high dry matter production and consequence of dilution of K within the grapevine.

Shoot/roots dry weight *vs.* accumulation of K into the shoot of root stocks grafted to 'Shiraz': Accumulation of K into the shoot was not affected by the shoot/roots dry weight in grapevine rootstocks (grafted to 'Shiraz'). For example, Ramsey had higher shoot/roots dry weight but had lower content of K in the shoot, than did 110 R. The lack of relationship was also true between shoot/roots dry weight and translocation efficiency of K. However, shoot/roots dry weight was positively related to the accumulation of K into the shoot and translocation efficiency of K, when these rootstocks were on own-roots (data not shown). The similarities between majority of tested rootstocks in their shoot size (as a result of grafting to common scion) and the constitution of majority of the dry weight of whole grapevine by shoot (scion), may explain why accumulation of K in to the shoot of grafted grapevine is not affected by shoot/root dry weight.

Uptake of K as affected by root-traits in rootstocks grafted to 'Shiraz': In the current study, K uptake increased with increase in total root length and total root surface area of rootstocks (grafted to 'Shiraz'). The significant correlation between total K uptake and these root-traits (root length and root surface area) further suggests that root-traits positively affect K uptake. The differences between rootstocks in the rooting pattern may affect the uptake efficiency of nutrients, and hence reflect the nutrient status of the grapevine (Williams and Smith 1991). A higher total root length and higher total root surface area in rootstocks may be due to a) larger grapevine (e.g. 140 R and 110 R), or b) larger root system (in terms of root length and root surface area) than the shoot system (e.g. Freedom and 101-14). The larger root system (than shoot system) coupled with a high concentration of K in the whole grapevine in Freedom and 101-14 may show high efficiency of their roots in K uptake.

Rootstocks Freedom and 101-14 were also associated with a high percentage of roots in the small diameter class (0-0.5 mm root diameter). This smaller diameter class comprises of fine roots, which are thought to contribute to most of the water and nutrient uptake of root systems (Tyree *et al.* 1998), including woody perennials (Richards 1983).

Transpiration vs. K uptake and accumulation of K into the shoot of rootstocks grafted to 'Shiraz': Tabs 2 and 4 show that water use alone does not increase the K uptake from the soil in rootstocks (grafted to 'Shiraz'). Furthermore, a similar water use/unit laminae area, and water use/unit grapevine weight, by most of the rootstocks suggests that a higher water use in some rootstocks was specifically due to a greater total laminae area, or generally due to increased dry weight of the grapevines. Significant correlations between total water use and a) laminae area, and b) dry weight of whole grapevine, support these conclusions. On the other hand, the positive relationship between dry weight of whole grapevine and total K uptake shows the general effect of dry weight on K uptake. Therefore, the difference between rootstocks grafted to 'Shiraz' in the total transpiration, by either the whole grapevine and/or per total laminae area, does not account for the differences in total K uptake.

The transpiration rate (at day 56) also had poor effect on the accumulation of K into the shoot or shoot parts of rootstocks (grafted to 'Shiraz') (Tabs 2 and 5). A non significant correlation between transpiration rate and each of concentration of K in a) laminae or b) in the shoot further substantiates these results. Although studies on the affect of transpiration rate on accumulation of K in grafted plants are limited, research on field crops showed that accumulation of K is not affected (Hooymans 1969) or negatively affected (Brag 1972), by transpiration rate. However, unlike water use, the transpiration rate was measured only at day 56 in the current study, and thus warrants further investigation. Nevertheless, the results show that water use (Day 1-56), and transpiration rate (at day 56) do not account for the accumulation of K in rootstocks grafted to 'Shiraz'.

Root pressure vs accumulation of K into the shoot of rootstocks grafted to 'Shiraz': In contrast to the effect of a) shoot/roots dry weight and b) transpiration, accumulation of K into the shoot of rootstocks (grafted to 'Shiraz') was positively affected by the root pressure. The positive correlation between the concentration of K in the xylem sap and the concentration of K in the shoot (but not Na), of rootstocks supports this conclusion, as the xylem sap was collected from decapitated stem (where root pressure was a driving force but not transpiration). The differences between rootstocks in the concentration of K in the xylem sap show the relative differences in their xylem loading of K. If this were the case, rootstocks 101-14 and Freedom (with a high concentration of K in the shoot of intact grapevines) may have had higher rates of xylem loading of K than 140 R. Similarly, in the current study, rootstocks (e.g.110 R and Freedom) with a higher xylem volume also had higher shoot content of K compared with 1103 P. This shows that root pressure may regulate the transport of K from roots to the shoot. The volume of xylem sap collected shows the net translocation efficiency of nutrients such as K (Marschner 1995), which means that rootstocks Freedom, in addition to a high rate of xylem loading of K, may also have had a high rate of transport of K from roots to the shoot. These results highlight the importance of root pressure in transport and accumulation of K into the shoot of grapevine rootstocks grafted to 'Shiraz'.

From the current study, it is evident that the accumulation of K in the grapevine is positively affected by root-traits and root pressure but not by transpiration, when rootstocks were grafted to 'Shiraz'. A similar result was also true when the same rootstocks were grown on their own-roots that is, rootstocks without 'Shiraz' (Kodur *et al.* 2010). This further highlights the positive affect of root-traits and root pressure, and a poor affect of transpiration, in the accumulation of K in grapevines. These results also show that in grapevines, irrespective of grafting or on own-roots, the factors (or mechanisms) affecting the accumulation of K into the grapevine are mostly similar. However, in contrast to when grafted with 'Shiraz' scion, accumulation of K into the shoot of these rootstocks when grown on their own roots (ungrafted vines) was positively affected by the shoot/roots dry weight (Kodur *et al.* 2010). This demonstrates that the interaction of the rootstock with the scion, which largely affects the shoot/roots dry weight pattern of the grapevine in the accumulation of K.

Conclusions

The current study shows the differences between rootstocks grafted to 'Shiraz' in the accumulation of K in whole grapevine or its parts, and highlights the role of rootstock-scion interaction in the regulation of K. Accumulation of K in 'Shiraz' grapevines grafted to a range of rootstocks is positively affected by the root-traits and root pressure but poorly affected by the shoot/roots dry weight and transpiration, highlighting the importance of root based factors/mechanisms in the accumulation of K. Consideration of the factors that affect the accumulation of K in rootstocks grafted to a common scion will help in the selection of particular rootstocks and/or rootstock-scion combination for lower accumulation of K in K rich soils or for higher accumulation of K in K deficient soils.

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