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Variation for potassium and sodium accumulation in a family from a cross between grapevine rootstocks K 51-40 and 140 Ruggeri

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Summary

The variation in potassium (K^+) and sodium (Na^+) accumulation was investigated between 60 hybrids within a family obtained by crossing grapevine rootstocks K 51-40 (*Vitis champinii* 'Dogridge' × *V. riparia* 'Gloire', seed parent) with 140 Ruggeri (*V. cinerea* var. *helleri* 'Resseguier #2' × *V. rupestris* 'St. George', pollen parent), which are known to result in higher and lower concentrations of K^+, respectively, but similar concentrations of Na^+, in grape juice and resultant wine from scions grafted to them. The hybrids, their parents and two standard rootstocks, Ramsey (*V. champinii* 'Ramsey') and 1103 Paulsen (*V. cinerea* var. *helleri* 'Resseguier #2' x *V. rupestris* 'St. George') were replicated by clonal propagation and grown under glasshouse conditions either in potting mix, drip-irrigated with a nutrient solution containing 50, 1.7 and 30 mM Cl^-, K^+ and Na^+, respectively, or in aerated nutrient solution containing 25, 1.7 and 15 mM Cl^-, K^+ and Na^+, respectively. In both pot and solution culture trials, there were significant ($P < 0.001$) differences between parents for mean K^+ (but not Na^+) concentrations, and between hybrids for mean K^+ and Na^+ concentrations in laminae. This variation between the hybrids was continuous, indicating multiple rather than single gene control for K^+ and Na^+ accumulation within the family. Differences among the hybrids for lamina K^+ accumulation were not strongly associated with plant vigour. While the ranking of some hybrids for K^+ and Na^+ accumulation was consistent between the trials, others responded differently, suggesting the environment of the rootzone may affect the K^+ and Na^+ accumulation phenotype.

Key words: rootstock, salinity, potassium and sodium accumulation, 140 Ruggeri, K 51-40.

Introduction

Grapevines are considered moderately sensitive to rootzone salinity (Maas and Hoffman 1977, Fisarakis *et al.* 2001), and in many instances they accumulate Na^+ to a lesser extent than chloride (Cl^-) in shoot tissues (Walker *et al.* 2004). Accumulation of Na^+ under saline conditions has been linked to reduced accumulation of K^+ (Roychoudhury *et al.* 2011). Accumulation of K^+ in grapevine shoots has been shown to be affected by the interaction between rootstock and scion, with total K^+ uptake increasing with total root length, total root surface area and percentage of smaller diameter roots (Kodur *et al.* 2010 a, b). Excessive K^+ accumulation in grape berries may result in wines that have high pH with poor colour stability and taste (Somers 1975). However, apart from a limited number of prior studies, for example, Rühl (1989) for K^+ and Sykes (1992) for Na^+, little is known about the variation for K^+ and Na^+ accumulation in grapevines. Rühl (1989) demonstrated strong positive correlations between K^+ concentration in petioles of ungrafted rootstocks and the grape juice pH of the scion varieties 'Chardonnay' and 'Ruby Cabernet' grafted to the rootstocks. Unlike the situation for Cl^- ion uptake, where several studies have documented variation for Cl^- accumulation in hybrid families of grapevine (Sykes 1985, 1987, Gong *et al.* 2011), that have reported single gene (Sykes 1987) and multigene (Sykes 1985, Gong *et al.* 2011) control, we are unaware of prior information on the variation for Na^+ accumulation in grapevines. Sykes (1992) demonstrated continuous variation in Na^+ accumulation in hybrids between the citrus rootstocks Rangpur lime and Trifoliate orange, and concluded that the ability to exclude Cl^- and Na^+ in citrus is due to two different mechanisms.

When used as a rootstock with grapevine scions 'Chardonnay' and 'Shiraz', 140 Ruggeri (*V. cinerea* var. *helleri* 'Resseguier #2' × *V. rupestris* 'St. George') has been observed to result in lower concentrations of K^+ in grape juice and resultant wine than when the same scions are grafted to K 51-40 rootstock (*V. champinii* 'Dogridge' × *V. riparia* 'Gloire') (Walker and Blackmore 2012). This suggests differences between the two rootstock genotypes in their capacity to regulate the uptake and accumulation of K^+. Since the inheritance of K^+ and Na^+ accumulation in grapevine is unclear, we investigated the variation for K^+ and Na^+ accumulation between individuals within a family of 60 hybrids obtained by crossing K 51-40 (seed parent) with 140 Ruggeri (pollen parent). The aims of the research were to determine whether one or more genes were involved in each case, and to quantify heritable versus non-heritable variation in K^+ and Na^+ accumulation within the hybrid family.

Material and Methods

The vines used in the trials: Controlled crosses were made between K 51-40 and 140 Ruggeri in 1985 and 2005 from which 80 hybrids were obtained.

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These hybrids have been assigned 'MI' and 'HB' code prefixes for the crosses conducted in 1985 and 2005, respectively. Following seed germination, the hybrids were planted and grown to mature vines in CSIRO's experimental vineyard at Merbein, Victoria, Australia (34°13'41"S, 142°2'38"E). Soil characteristics, vineyard management and irrigation practices were the same for the 'MI' and 'HB' vines. Irrigation water was taken from the Murray River and was generally of low salinity (under 0.35 dSm^{-1}).

Vine propagation: Cuttings of each hybrid, their parents and two standard rootstocks, namely Ramsey (*V. champinii* 'Ramsey') and 1103 Paulsen (*V. cinerea* var. *helleri* 'Resseguier #2' × *V. rupestris* 'St. George') (3-bud cuttings for the pot culture experiment and single bud cuttings for the solution culture experiment, selected to be as uniform as possible), were propagated in potting mix held in free-draining plastic boxes (height × width × length of 20 × 30 × 37 cm) placed on heat-beds in a mist house, which was held at or below 25 °C by evaporative cooling, during August 2007 (pot trial) and September 2008 (solution culture trial). The heat-beds were maintained to provide a bottom heat to the cuttings of approximately 25 °C in order to encourage callus formation and root growth. Cuttings were successfully propagated from only 11 and 49 of the 'MI' and 'HB' hybrids, respectively. The remaining vines from each group were of low vigour and weak such that cuttings, if available, were thin and did not strike. Following propagation, six uniform grapevines (about 20-30 cm in height) of each hybrid, their parents and the two standard rootstocks were selected for each trial.

Pot trial: Grapevines of each hybrid, their parents and two standard rootstocks were planted in a mixture of sand and red loam, 40:60 v/v, respectively, held in 4.5 L pots under glasshouse conditions in late October 2007. Vines were laid out on the bench as six randomised blocks with each genotype replicated once per block. The vines were watered daily with excess nutrient solution to ensure adequate leaching via an automated drip-irrigation system. The nutrient solution contained the following elements (mM): Ca^{2+}, 1.2; K^+, 1.7; Mg^{2+}, 0.4; NH_4^+, 0.5; NO_3^-, 4.2; SO_4^{2-}, 0.4; $H_2PO_4^-$, 0.3; H_3BO_3, 8.3×10^{-4}; Zn, 1.9×10^{-3}; Cu, 1.4×10^{-3}; Mn, 4.4×10^{-3}; Mo, 3.2×10^{-5}; EDTA-Fe, 3.0×10^{-2}. The vines were maintained as single shoots by removing lateral shoots and after 28 d salt (as chloride) was added to the nutrient solution at a rate of 10 mM Cl^- (with cations Na^+: Ca^{2+}: Mg^{2+} in the ratio 6:1:1) per day until 50 mM Cl^- was reached (final concentration of Na^+ being 30 mM). The vines were maintained under these conditions for a further 27 d when they were destructively harvested with all laminae in the middle 60 % of each shoot retained for analysis. This was achieved by discarding 20 % of the shoot proximal to the apex and 20 % distal to the root system. Aerial and rootzone temperatures were monitored in January 2008 with the averages being 27.3 °C (17.7 ~ 39.8°C) and 27.3 °C (18.8 ~ 35.3 °C), respectively.

Solution culture trial: Uniform grapevines were transferred to aerated solution cultures held in 450 L fibreglass tanks (surface area 1 m^2) under glasshouse conditions in mid-November 2008. There was one replicate vine per genotype randomly positioned in each of 6 tanks. The nutrient solution had a similar composition as that used in the pot trial except that NH_4^+ was absent and total NO_3^- was 3.8 mM. Three weeks after vine transfer to culture solution, the concentration of EDTA-Fe was increased from 30 µM to 71 µM, and photoperiod was extended 2 h by supplementary lighting. One week later, salt (as Cl^-) was added to the cultures at a rate of 12.5 mM Cl^- per day (with cations Na^+: Ca^{2+}: Mg^{2+} in the ratio 6:1:1) to give a final Cl^- concentration of 25 mM (final concentration of Na^+ being 15 mM). The youngest leaf on each vine was labelled with a loosely tied cotton thread and shoot length was measured when the salt treatment started. The vines were maintained as single shoots by removing lateral shoots under these conditions for 27 d after which total shoot length and shoot lengths between the labelled leaf and the shoot apex were recorded and they were destructively harvested. As in the pot experiment, all laminae in the middle 60% of each vine were retained for analysis. Aerial and rootzone temperatures were monitored in January 2009 with the averages being 25.9 °C (15.3 ~ 33.3 °C) and 25.6 °C (range 24.5 ~ 27.4 °C), respectively.

Ion analyses: Laminae samples (n = 6) were dried at 60 °C for at least 72 h and finely powdered in a hammer mill to pass through a 0.5 mm mesh. Sodium and potassium were analysed by inductively coupled plasma spectroscopy (Spectroflame ICP, Spectro Analytical Instruments, Kleve, Germany) from extracts of 100-300 mg powdered samples digested in 2 mL of concentrated HNO_3 on a heating block and diluted to 20 mL with deionised water.

Statistical analysis: Data were subjected to analysis of variance using GenStat Release 11.1 software. Where F-tests were significant ($P < 0.05$), means were separated by least significant differences (Snedecor and Cochran 1967). Significant differences between data for 'HB' and 'MI' hybrids were explored and where none were demonstrated, the data were combined. The intra-class correlation coefficient, a statistic which estimates the degree of genotypic determination and provides an upper estimate of the broad sense heritability was also determined (Falconer and Mackay 1996).

Results

K^+ concentrations for vines in the pot trial: There were significant differences for mean laminae K^+ concentrations at harvest between K 51-40 and 140 Ruggeri vines (Tab. 1), and significant differences were also observed between hybrids (Fig. 1a). The mean concentration for the hybrids was 496.2 µmol·g^{-1} dw, which was approximately the mid-parent value (492.7 µmol·g^{-1} dw). There were no hybrids with significantly higher laminae K^+ concentrations than K 51-40. However, one hybrid (HB28) had significantly lower lamina K^+ concentration than the 140 Ruggeri parent. The intraclass correlation coefficient for lamina K^+ concentrations was 0.43 (Tab. 1).

Table 1

A summary of K^+ and Na^+ concentrations in laminae of vines grown in a potting mix medium. The vines were irrigated daily with a complete nutrient solution containing 50, 1.7 and 30 mM Cl^-, K^+ and Na^+, respectively, for 27 d under glasshouse conditions

	Parents			Hybrids (60)			
	K51-40	140 Ruggeri	F value	Mean	Range	F value	[a]t
K^+ (µmol·g^{-1} dw)	578.5	406.9	12.32*	496.2	261.8~657.2	5.48***	0.43
Na^+ (µmol·g^{-1} dw)	76.0	57.3	ns	100.6	1.7~362.7	9.76***	0.59

ns, not significant at $P \leq 0.05$; *$P < 0.05$; ***$P < 0.001$.

[a]t = intraclass correlation coefficient, which was obtained from the analysis of variance as follows:

Source	Df	Mean square
Between genotypes	n-1	$\sigma_w^2 + p\,\sigma_g^2$
Within genotypes	n (p-1)	σ_w^2

Where n = number of genotypes; p = number of replicates
genotypic variance = σ_g^2; phenotypic variance = $\sigma_g^2 + \sigma_w^2$
$t = \sigma_g^2 / (\sigma_g^2 + \sigma_w^2)$

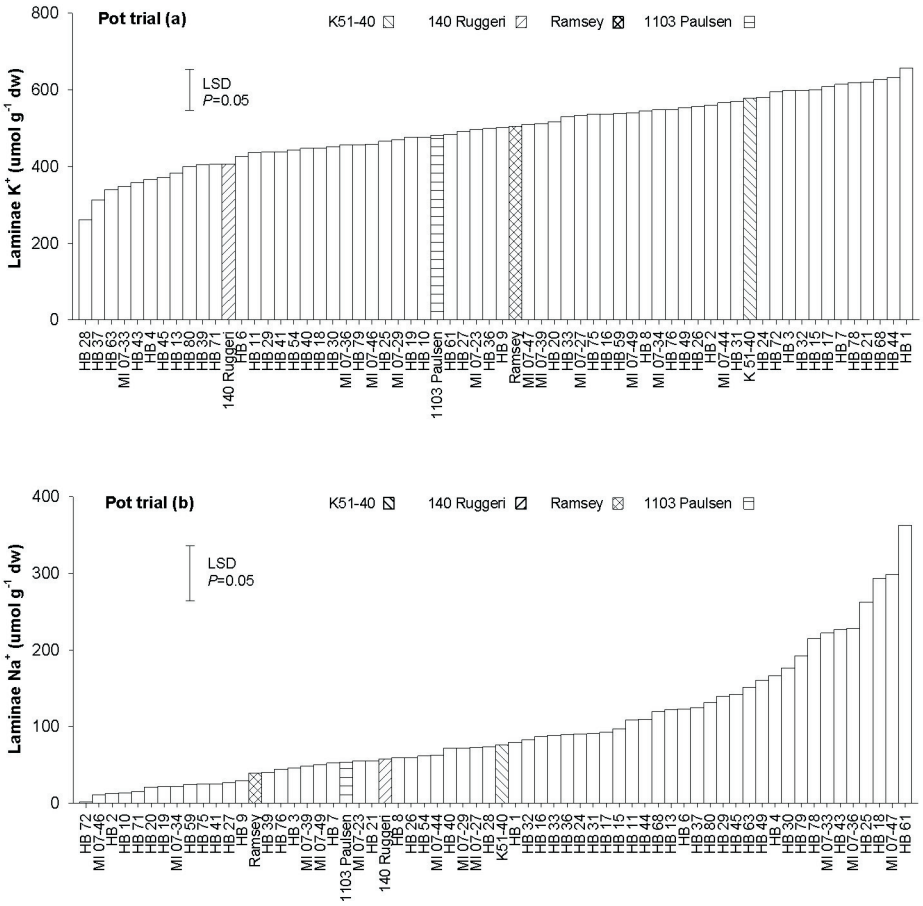

Fig. 1: Mean K^+ (a) and Na^+ (b) concentrations in laminae of grapevines propagated clonally from K 51-40 × 140 Ruggeri hybrids (n = 60) grown in potting mix under glasshouse conditions. The grapevines were irrigated daily with a complete nutrient solution containing 50, 1.7 and 30 mM Cl^-, K^+ and Na^+, respectively, for 27 days before sampling. LSD = least significant difference.

K^+ concentrations for vines in the solution culture trial: There were significant differences in mean laminae K^+ concentrations at harvest between 'HB' and 'MI' hybrids and thus the data for both are presented separately (Fig. 2a, 3a). There were significant differences for mean laminae K^+ concentrations between K 51-40 and 140 Ruggeri vines (Tab. 2), and there were also significant differences between HB hybrids (Fig. 2a). The mean concentration for the HB hybrids was 336.8 µmol·g^{-1} dw (Tab. 2), which was higher than the mid-parent value (301.2 µmol·g^{-1} dw). There were three hybrids (HB1, HB72 and HB79) which had significantly higher laminae K^+ con-

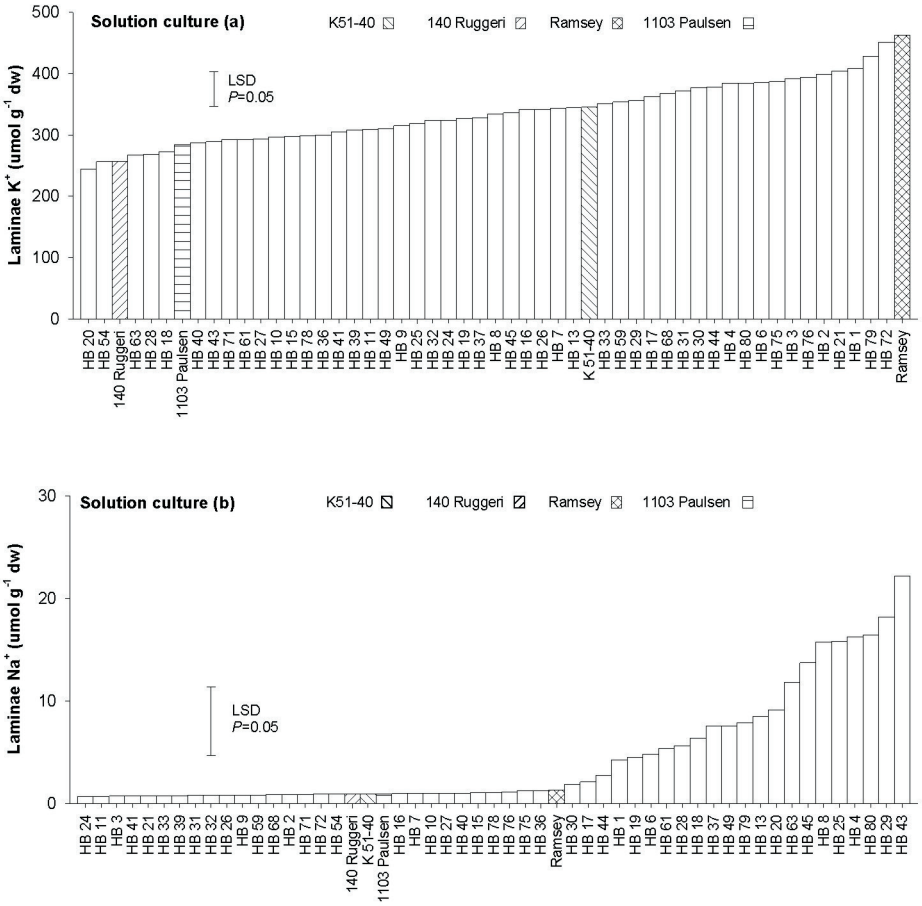

Fig. 2: Mean K^+ (a) and Na^+ (b) concentrations in laminae of grapevines propagated clonally from K 51-40 × 140 Ruggeri hybrids (49 HB hybrids) grown in aerated nutrient culture solution under glasshouse conditions. The grapevines were grown in a complete nutrient solution containing 25, 1.7 and 15 mM Cl^-, K^+ and Na^+, respectively, for 27 days before sampling. LSD = least significant difference.

Table 2

A summary of K^+ and Na^+ concentrations in laminae of vines grown in an aerated complete nutrient solution containing 25, 1.7 and 15 mM Cl^-, K^+ and Na^+, respectively, for 27 d under glasshouse conditions

	Parents			Hybrids (HB: n = 49; MI: n = 11)				
	K51-40	140 Ruggeri	F value	Hybrid source	Mean	Range	F value	[a]t
K^+ (µmol g^{-1} dw)	345.6	256.8	29.60**	HB	336.8	244.3 ~ 451.4	5.91***	0.45
				MI	349.3	308.9 ~ 414.2	4.09***	0.34
Na^+ (µmol g^{-1} dw)	0.95	0.90	ns	HB	4.74	0.69 ~ 22.2	5.44***	0.43
				MI	18.2	0.87 ~ 109.1	4.65***	0.38

[a]t = intraclass correlation coefficient. The calculation is as shown in Tab. 1.
ns, not significant at $P \leq 0.05$; **$P < 0.01$; ***$P < 0.001$.

centration than K 51-40. However, there were no hybrids with significantly lower lamina K^+ concentration than the 140 Ruggeri parent. The intraclass correlation coefficient for lamina K^+ concentrations was 0.45 (Tab. 2).

For the MI hybrids, there were significant differences between hybrids (Fig. 3a). The mean K^+ concentration in laminae for the hybrids was 349.3 µmol·g^{-1} dw, which was similar to that for K 51-40. There was one hybrid (MI 07-44) with significantly higher lamina K^+ concentration than the K 51-40 parent (Fig. 3a). The intraclass correlation coefficient for lamina K^+ concentrations was 0.34 (Tab. 2).

Sodium concentrations for vines in the pot trial: There was no significant difference for mean laminae Na^+ concentrations at harvest between K 51-40 and 140 Ruggeri vines (Tab. 1), but there were significant differences between the hybrids (Fig. 1b). The mean concentration for the hybrids was 100.6 µmol·g^{-1}dw, which exceeded that for either parent. There were 13 hybrids which had significantly higher laminae Na^+ con-

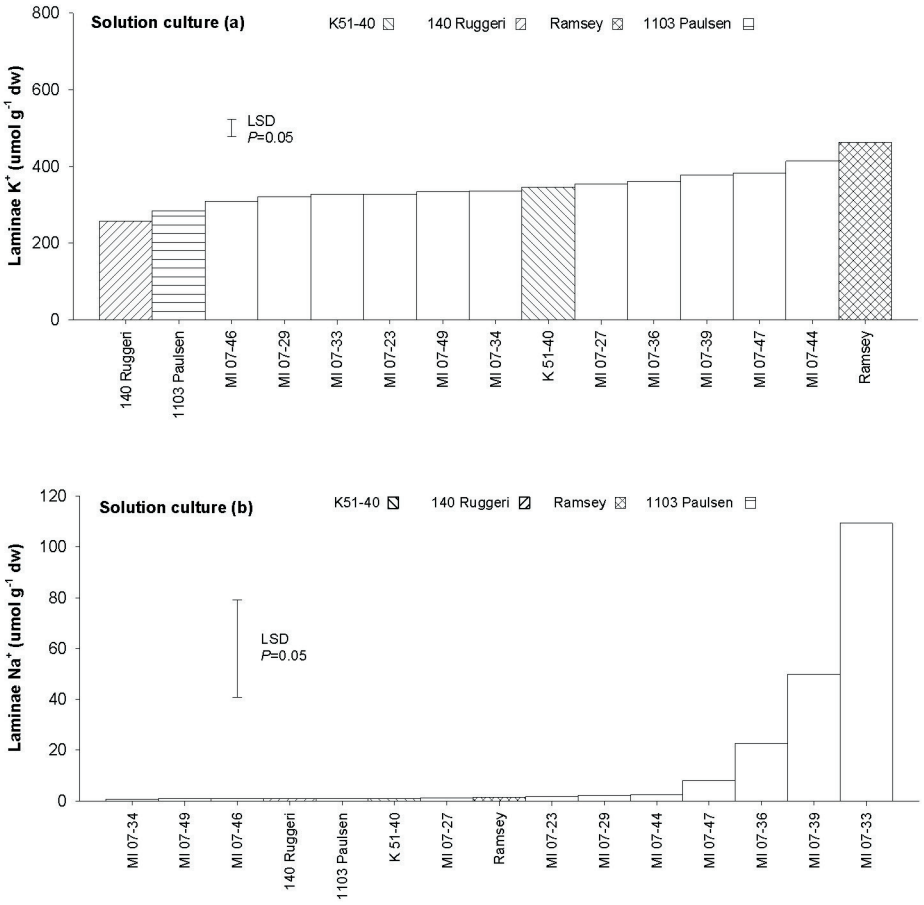

Fig. 3: Mean K^+ (a) and Na^+ (b) concentrations in laminae of grapevines propagated clonally from K 51-40 × 140 Ruggeri hybrids (11 MI hybrids) grown in aerated nutrient culture solution under glasshouse conditions. The grapevines were grown in a complete nutrient solution containing 25, 1.7 and 15 mM Cl^-, K^+ and Na^+, respectively, for 27 days before sampling. LSD = least significant difference.

centrations than either parents. These were HB4, HB18, HB25, HB30, HB43, HB49, HB61, HB63, HB78, HB79, MI33, MI36 and MI47. The distribution for Na^+ accumulation was skewed and different from that of K^+ (Fig. 1a). The intraclass correlation coefficient for lamina Na^+ concentrations was 0.59 (Tab. 1).

Sodium concentrations for vines in the solution culture trial: There were significant differences in mean laminae Na^+ concentrations at harvest between 'HB' and 'MI' hybrids and the data for them are presented in Fig. 2b and Fig. 3b, respectively. There was no significant difference for mean laminae Na^+ concentrations between K 51-40 and 140 Ruggeri vines (Tab. 2), but there were significant differences ($P < 0.001$) between hybrids in each group of hybrids (Fig. 2b, 3b). The hybrids showed a skewed frequency distribution (Fig. 2b, 3b), with skewness being 1.42 and 1.96 for HB and MI hybrids, respectively. The intraclass correlation coefficients for laminae Na^+ concentrations were 0.43 and 0.38 for HB and MI hybrids, respectively (Tab. 2).

K^+/Na^+ ratio in pot and solution culture trials: In the pot trial, the lamina K^+/Na^+ ratios at harvest were under 50, with one exception, where the ratio exceeded 350 (hybrid HB72). HB72 had significantly higher K^+/Na^+ ratio than all other HB hybrids, and there was no significant difference in K^+/Na^+ ratio between the other hybrids (data not shown). Higher K^+/Na^+ ratio in HB72 might have been due to much lower accumulation of Na^+ than any other hybrid (Fig. 1b). In the solution culture trial, due to low laminae Na^+ concentrations, the majority of hybrids had lamina K^+/Na^+ ratios at harvest of 200 or higher, but there was no significant difference between hybrids in either the HB or MI hybrid groups (data not shown).

Correlations between K^+ or Na^+ concentrations and shoot growth parameters in solution culture trial: In the HB hybrids, there were significant negative correlations between lamina K^+ concentrations at harvest and shoot growth during the experiment, shoot length at harvest and shoot dry weight at harvest, but the relationships were weak (Tab. 3). In the MI hybrids, the correlations between lamina K^+ concentration at harvest and shoot lengths at start of the experiment and at harvest and with shoot dry weight at harvest were not significant.

No significant correlations between lamina Na^+ concentration at harvest and shoot growth parameters were observed in either HB or MI hybrids, with the exception of shoot dry weight at harvest for MI hybrids (Tab. 3). No significant correlations between lamina K^+/Na^+ ratio at harvest and shoot growth parameters were observed in HB hybrids but significant correlations were obtained with MI hybrids (Tab. 3).

Table 3

Correlations between laminae K^+ concentrations and shoot growth parameters for K 51-40 × 140 Ruggeri hybrids grown in an aerated complete nutrient solution containing 25, 1.7 and 15 mM Cl^-, K^+ and Na^+, respectively for 27 d under glasshouse conditions

Shoot growth parameter	HB (n = 49)				MI (n = 11)			
	K^+ concentration (μmol g^{-1}dw)							
	r	y = a + bx	b ± se	*P*	r	y = a + bx	b ± se	*P*
Shoot length at stress start (cm)	-0.261	y = 125.2–0.125x	-0.125 ± 0.068	0.070	-0.502	y = 131.0-0.189x	-0.189 ± 0.090	0.057
Shoot growth (length from tag to tip, cm)	-0.430	y = 249.0–0.236x	-0.236 ± 0.072	0.002	-0.530	y = 235.9-0.245x	-0.245 ± 0.109	0.042
Shoot length at harvest (cm)	-0.368	y = 374.9–0.364x	-0.364 ± 0.134	0.009	-0.506	y = 360.0-0.423x	-0.423 ± 0.200	0.054
Shoot dry weight (g)	-0.300	y = 42.8–0.069x	-0.069 ± 0.032	0.036	-0.388	y = 26.7-0.045x	-0.045 ± 0.030	0.153
	Na^+ concentration (μmol g^{-1}dw)							
Shoot length at stress start (cm)	-0.227	y = 87.3-0.893x	-0.893 ± 0.559	0.117	-0.464	y = 69.6-0.299x	-0.299 ± 0.158	0.082
Shoot growth (length from tag to tip, cm)	-0.096	y = 171.5-0.430x	-0.430 ± 0.653	0.513	-0.438	y = 155.9-0.345x	-0.345 ± 0.197	0.103
Shoot length at harvest (cm)	-0.169	y = 258.8-1.364x	-1.364 ± 1.164	0.247	-0.464	y = 222.7-0.662x	-0.662 ± 0.350	0.081
Shoot dry weight (g)	-0.217	y = 21.6-0.407x	-0.407 ± 0.267	0.135	-0.536	y = 12.5-0.107x	-0.107 ± 0.047	0.039
	K^+/Na^+ ratio							
Shoot length at stress start (cm)	0.149	y = 78.6+0.019x	0.019 ± 0.018	0.306	0.559	y = 50.1+0.068x	0.068 ± 0.028	0.030
Shoot growth (length from tag to tip, cm)	0.022	y = 168.7+0.003x	0.003 ± 0.021	0.882	0.592	y = 131.2+0.089x	0.089 ± 0.033	0.020
Shoot length at harvest (cm)	0.085	y = 247.1+0.022x	0.022 ± 0.037	0.561	0.618	y = 175.9+0.167x	0.167 ± 0.059	0.014
Shoot dry weight (g)	0.182	y = 17.0+0.011x	0.011 ± 0.009	0.211	0.746	y = 4.716+0.028x	0.028 ± 0.007	0.001

r = correlation coefficient; a = the intercept; b = the slope; se = standard error; *P* = probability related to b - the slope.

Comparison of data obtained in pot and solution culture trials: Mean lamina K^+ and Na^+ concentrations at harvest of vines grown in the solution culture trial showed significant, but very weak relationships with respective lamina K^+ and Na^+ concentrations in the pot trial (R^2 = 0.16 and 0.11, respectively). There was a poor relationship between lamina K^+ and Na^+ in both the solution culture trial and pot culture trial (R^2 = 0.069 and 0.006 for pot trial and solution culture trial, respectively).

Comparisons between K^+ and Cl^- and between Na^+ and Cl^- accumulation in laminae: Laminae Cl^- concentrations at harvest for the hybrids in both the pot and solution culture experiments were reported previously (GONG *et al.* 2011). Laminae K^+ accumulation showed a weak-moderate positive correlation with laminae Cl^- accumulation in the pot culture trial (R^2 = 0.29; $P < 0.001$) (Fig. 4a), but not in the solution culture trial (R^2 = 0.07; P = 0.062) (data not shown). Laminae Na^+ accumulation showed a very weak positive correlation with laminae Cl^- accumulation in the pot culture trial (R^2 = 0.12; $P < 0.05$) (Fig. 4b) and also in the solution culture trial (R^2 = 0.16; P = 0.001) (data not shown).

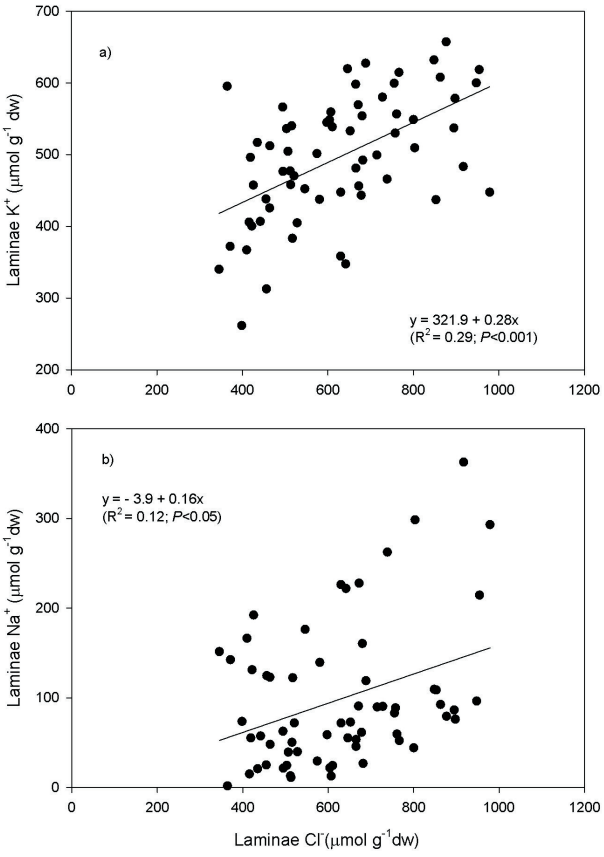

Fig. 4: Regression (**a**) of laminae K^+ concentration on laminae Cl^- concentration, and (**b**) of lamina Na^+ concentration on lamina Cl^- concentration for the pot trial. Chloride concentration data were obtained from the same study but reported in a previous paper (GONG *et al.* 2011).

Discussion

In both pot and solution culture trials, K 51-40 showed a better capacity than 140 Ruggeri for K^+ accumulation, but not Na^+ accumulation, in laminae (Tabs 1 and 2). Furthermore, the hybrids of K 51-40 × 140 Ruggeri showed a continuous variation in K^+ and Na^+ accumulation in laminae under the experimental conditions described. There were poor correlations for both K^+ and Na^+ concentrations in laminae at harvest between the pot and solution culture trials (data not shown). This may have been due to differ-

ences in root morphology due to the two growth media (Storey 1995, Tregeagle 2007, Tregeagle *et al.* 2010) or may have been associated with different seasons in which the cuttings were collected and trials conducted (2007-08 and 2008-09 for the pot and solution culture trials, respectively).

Two groups of hybrids (HB and MI) from crosses made 20 years apart were used. There were no differences between the groups with respect to K^+ and Na^+ accumulation in the pot study. However, there were differences between the groups with respect to K^+ and Na^+ accumulation in the solution culture study. Root morphology differences between the pot and solution culture studies (Storey 1995, Tregeagle 2007, Tregeagle *et al.* 2010) may have been a factor, together with other possible reasons, for example, an environmental effect associated with the different field locations of the MI and HB source vines or an age effect of the parent vines from which cuttings were taken. Alternatively, it may have just been a chance occurrence due to family size and gene segregation.

There were significant negative correlations between lamina K^+ concentrations at harvest and shoot growth during the experiment, shoot length at harvest and shoot dry weight at harvest for HB hybrids in the solution culture trial (Tab. 3), yet the R^2 values were quite low (≤ 0.19). The correlations in MI hybrids were inconclusive (no significant correlation with shoot length at start or at harvest or with shoot dry weight at harvest). Therefore, differences among the hybrids for K^+ accumulation were not strongly associated with plant vigour (Tab. 3). Determination of a vine vigour and K^+ accumulation index was not an objective of the study, mainly because the large size of the experiments (384 vines in each case) which precluded inclusion of a nutrient solution only control. In a previous study, Kodur *et al.* (2010a) found that K^+ uptake by vines was positively related to the vine biomass and relative growth rate. The difference in results between this study and their study might be due to the fact that in this study the plants were grown in solution culture containing 25 mM Cl^- and 15 mM Na^+, whereas in the Kodur *et al.* (2010a) study, no additional Cl^- and Na^+ were added. Furthermore, the Kodur *et al.* (2010a) study was a pot culture study, whereas this study was a solution culture study, and it is well known that there are differences in root morphology between grapevines grown in potting mix and solution culture grown plants (Tregeagle 2007, Tregeagle *et al.* 2010). Root traits play an important role in K^+ uptake, as has been observed by Kodur *et al.* (2010b). Whether there are differences in the root traits among the hybrids remain to be investigated.

No correlations existed between laminae Na^+ concentrations and shoot growth, also suggesting that Na^+ accumulation was not related to plant vigour (Tab. 3).

The present results suggest involvement of more than one gene in the variation or K^+ accumulation by the rootstock genotypes investigated in these experiments. To our knowledge, there are no previous reports on inheritance of K^+ accumulation in grapevine. Similarly, the results suggest involvement of more than one gene in Na^+ accumulation in grapevine. This is consistent with the conclusion by Sykes (1992), who observed a continuous variation in Na^+ accumulation in hybrids between the citrus rootstocks Rangpur lime and Trifoliate orange and concluded involvement of more than one gene in Na^+ accumulation. The variability for K^+ and Na^+ accumulation in leaves indicated an extensive genetic variation for the ability by the hybrids to exclude K^+ and Na^+ from their leaves. The values obtained for the intra-class correlation coefficient, a statistic which estimates the degree of genotypic determination (Falconer and Mackay 1996) and, thus, an upper estimate of the broad sense heritability, supported this argument. As the vines grown in the experiments were clonal, estimates of broad sense heritability from intra-class correlation coefficients indicated that 43 % and 34-45 % of the total phenotypic variation in K^+ accumulation of this hybrid family could be attributed to heritable sources in the pot and solution culture trials respectively. Similarly, estimates of broad sense heritability from intra-class correlation coefficients indicated that 59 % and around 40 % of the total phenotypic variation in Na^+ accumulation could be attributed to heritable sources in the pot and solution culture trials, respectively.

The statistically significant ($P < 0.001$) correlation that was observed between K^+ and Cl^- concentrations of the hybrids in laminae for the pot trial ($R^2 = 0.29$; Fig. 4a) and the stronger relationship between laminae K^+ and Cl^- than between laminae Na^+ and Cl^- concentrations suggests that the mechanisms for excluding K^+ and Cl^- may be partially related. However, lack of a similar significant correlation between laminae K^+ and Cl^- concentrations for data from the solution culture trial (Fig. 3B) indicates involvement of other factors. The difference in rootzone concentrations of Cl^- (50 *vs.* 25 mM) may be one factor. The significant changes in root morphology between plants grown in pot culture *vs.* solution culture (Storey 1995, Tregeagle 2007, Tregeagle *et al.* 2010) may be another factor.

In summary, the variation in K^+ and Na^+ accumulation within a hybrid family from a cross between K 51-40 and 140 Ruggeri in each case appeared to be controlled by more than one gene. Further work and analysis would involve studying quantitative trait loci for K^+ and Na^+ exclusion using a larger family.

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