

Salinity Responses of Grafted Grapevines: Effects of Scion and Rootstock Genotypes

Nuray SIVRITEPE¹⁾, H. Özkan SIVRITEPE¹⁾, Hakan ÇELİK²⁾, A. Vahap KATKAT²⁾

¹⁾Uludag University, Faculty of Agriculture, Department of Horticulture, Görükle Campus, 16059 Bursa, Turkey; nuray@uludag.edu.tr

²⁾Uludag University, Faculty of Agriculture, Department of Soil Science, Görükle Campus, 16059 Bursa, Turkey

Abstract

Two-year-old 'Sultana' and 'Müşküle' vines (*Vitis vinifera* L.) grafted onto Rupestris du Lot (*Vitis rupestris* Scheele) and 110 R (*Vitis berlandieri* × *Vitis rupestris*) were grown in soil, sand, sphagnum peat and farmyard manure mixture (2:1:1:1 v/v) irrigated with 0.3, 2.7 and 5.45 dS m⁻¹ NaCl solutions for a period of 60 days. Biomass accumulation, relative chlorophyll content, leaf water potential, stomatal conductance and transpiration were significantly reduced by salinity in all graft combinations. The inhibiting effect of salinity on growth varied according to the characteristics of the scion genotype and the level of salinity. The results imply the predominance of the scion genotype in determining variation in the leaf-level physiological characteristics of grafted vines because stomatal conductance and transpiration were higher in 'Sultana' than in 'Müşküle' at the same leaf water potential and the level of salinity, regardless of the rootstock genotype. NaCl treatments did not affect leaf Cu concentration while inducing significant Na, K, Ca, N, P, Mg, Fe, Mn and Zn elevations in the leaves of all scion/rootstock combinations. While salinity caused an increase in N content and a decrease in K content in the roots of all graft combinations, it had no influence on Ca, P, Cu and Zn concentrations. In contrast to the 'Sultana' grafted vines, NaCl salinity led to a decrease in Mg, Fe and Mn concentrations in the roots of 'Müşküle' grafted vines. Nevertheless, ion accumulation in leaves and roots of grafted vines under saline or non-saline conditions was controlled predominantly by the genotype of the scion. In response to salinity, 'Sultana' grafts accumulated higher amounts of ions in their leaves than in their roots. However, in 'Müşküle', higher ion concentrations were seen in the roots. Therefore, the increase in the transport of inorganic ions up to the leaves seems to be the major component of osmotic adjustment in salt-stressed 'Sultana' vines.

Keywords: ion contents, leaf water potential, NaCl stress, plant growth, stomatal conductance, *Vitis vinifera*

Introduction

Grape growing is of great importance for Turkey's horticulture, with 482,789 ha in total viticulture area and 3,918,442 tons of grape production (FAO, 2008). More than 90% of the grape-growing area in Turkey is located in the Aegean, Mediterranean and Central Anatolia Regions, which include the major salt-affected soils of Turkey. The environmental conditions of these areas make vineyards susceptible to salt accumulation; these conditions include irrigation with groundwater of variable salt content, the application of deficient irrigation regimes that do not include additional leaching fractions and limited winter rainfall to flush salts from the root zone. Some soils also have poor drainage characteristics, preventing adequate leaching of salts even if water is available to do so. Over time, the above conditions can be expected to result in a gradual increase in soil salinity levels, particularly if there are no heavy rainfalls that leach the salt that has accumulated for years. Under these circumstances, maintaining grape productivity necessitates adopted management practices, as grapevines are moderately sensitive to salinity (Maas, 1990; McCarthy *et al.*, 1992).

The response of grapevines to salinity is composed of two mechanisms (Shani and Ben-Gal, 2005). The first mechanism is reduced transpiration and growth, which begins as soon as salinity is first experienced due to the decreased osmotic potential of the soil solution. The second mechanism involves vine mortality and is correlated with salinity level, a sharp increase in the toxic ion (Na and Cl) content of leaves and the time, delaying the onset of mortality in conditions of lower salinity.

Grafting became a necessary practice in viticulture more than a century after a phylloxera epidemic, and much of the world's viticulture involves rootstocks using the *Vitis vinifera* L scion as a rootstock. However, the choice of rootstock for a particular location depends on the complex interactions between soil type, depth, physical and chemical properties, pests, diseases, water availability and environmental factors. Therefore, the use of certain rootstocks has long been suggested as a cultural practice for improving grapevines salt tolerance by their ability to exclude toxic ions when extracting water from the soil.

The most tolerant rootstocks are those capable of maintaining low Cl concentrations in either their own foliage or that of the scion (Alexander and Groot-Obbink, 1971; Downton, 1977a; 1977b) because salt-induced lim-

itations in photosynthesis and stomatal conductance of grapevines are related to high Cl and not to Na contents in the leaves (Prior *et al.*, 1992). When *Vitis vinifera* L. cvs. 'Cardinal' and 'Sultana' were grafted to rootstocks Dog Ridge, 1163-3 and Ramsey, the accumulated chloride content in leaves was only 1/3, 1/10, and 1/16, respectively, of their own-rooted vines (Leon *et al.*, 1969). Under relatively high saline conditions, *Vitis vinifera* L. cv. 'Colombard' grafted onto 25 rootstocks showed different yield and growth performance; 13-5 EVEX, Ramsey, 143-B Mgt, 101-14 Mgt, 1045 P and 140 Ru were recommended for salt tolerance (Southey and Jooste, 1991). When grown at high salinity conditions (i.e., irrigation water salinity 2.3 dS m⁻¹), 'Shiraz' grapes (*Vitis vinifera* L.) had lower leaf Cl concentration grafted onto 140 Ru, 1103 P, Ramsey and 101-14 Mgt than on their own-roots (Walker *et al.*, 2000). However, the highest Cl concentration recorded in mature leaves of own-rooted vines had no significant impact on CO₂ assimilation rates, suggesting that own-rooted vines were not limited photosynthetically compared to grafted vines. This was consistent with the absence of any rootstock effects on fruit yield per vine. It should be noted that in some recent work on the chloride exclusion of rootstocks with long-term saline irrigation it was found that the ability of 1103 P and Ramsey to exclude salt appeared to be deteriorating (Walker *et al.*, 2003).

In contrast with the results obtained from the 'Shiraz' variety, the effect of rootstock on yield performance was evident in 'Sultana' vines grown under long periods of salinity (Walker *et al.*, 2002). High salinity (i.e., irrigation water salinity 3.5 dS m⁻¹) had no effect on five-year mean yields of field grown 'Sultana' vines when grafted on Ramsey, 1103 P and R2 rootstock, while the yield performance of 'Sultana' on own-roots or grafted to J17-69, R1, R3 or R4 decreased significantly. However, Cl and Na concentrations determined in leaf laminae and grape juice of 'Sultana' on J17-69 with poor performance were similar to the levels accumulated by 'Sultana' on Ramsey and 1103 P. Accordingly, no correlation was found between tissue Na and Cl concentrations and the growth and yield reduction in 'Sultana' grown under high salinity (Walker *et al.*, 2004). The authors concluded that salt tolerance in 'Sultana' grapevines (based on yield performance) is not directly connected to rootstock ability of Na and Cl exclusion. This could be associated with the greatest vigor impartment to the scion from the best performing rootstocks (Ramsey, 1103 P and R2).

However, different results have been obtained with regard to the contribution of the root system to the growth and production of the shoot in saline conditions. Yermiyahu *et al.* (2007) observed that while Ramsey rootstock promoted more vigorous vegetative growth than Rugerri, rootstock genotype had no significant effect on the yield performance of 'Sugraone' grapevines grown under high salinity (2.7 dS m⁻¹). In another field study, Hepaksoy *et al.* (2006) also found that salinity (i.e., irrigation water sa-

linity of 1.8 and 3.3 dS m⁻¹) had no significant effect on yield of 'Cabernet Sauvignon' grapes (*Vitis vinifera* L.) grown on Ramsey and Rugerri. Contradictory results have even been found within the same grapevine cultivar, as occurred in 'Sultana' vines (Fisarakis *et al.*, 2001; Walker *et al.*, 2002; 2004). In a short-term greenhouse experiment, despite the higher Cl and Na concentrations in leaves, own-rooted 'Sultana' vines grown under high salinity (i.e., nutrient solution salinity from 1.9 to 12.3 dS m⁻¹) had significantly higher photosynthesizing areas and rates of photosynthesis than those grafted onto 1103 P, 140 Ru, 110 R, SO4 and 41 B rootstocks, resulting in higher values in all the measured growth parameters (Fisarakis *et al.*, 2001). These results showed that own-rooted 'Sultana' vines can cope better with high salinity than those grafted onto rootstocks in competition with the vigor effect of root system to shoot. The authors decided that the higher salt tolerance of own-rooted 'Sultana' vines may be related to the ability of the scion genotype to withstand higher internal ion concentrations, greater ability for osmotic adjustment and/or with mineral uptake interactions like nitrate or potassium, which are all possibilities that need further research.

Although most of the summarized results are contradictory, there is abundant information concerning the effect of grafting and certain rootstocks on salt tolerance in grapevines. However, these results are not sufficient to adequately understand whether the salt tolerance of grafted vines is controlled predominantly by the root or shoot genotype and/or the rootstock characteristics that are able to induce salt tolerance to the shoot depending on the salt tolerance mechanism of the scion genotype. More work has to be conducted in the field of rootstock/scion relationships in terms of salt tolerance in grapevines.

The growth and physiological responses of the grafted grapevines were determined using two grapevine cultivars with different degrees of salt sensitivity and two distinctly different rootstock genotypes in their vigor and salt tolerance with the aim of determining whether salt tolerance is predominantly a function of rootstock or scion cultivar.

Materials and methods

Two-year-old 'Sultana' and 'Müşküle' vines grafted on two rootstocks, Rupestris du Lot (*Vitis rupestris* Scheele) and 110 R (*V. berlandieri* × *V. rupestris*), were used in the experiment. 'Sultana' on own roots with a yield threshold of approximately 1.8 dS m⁻¹ soil saturation paste salinity (Tee *et al.*, 2003) is known to be more tolerant to salt than 'Müşküle' (Sivritepe, 1995; 2000). Rootstocks 110 R and Rupestris du Lot with contrasting vigor potentials are classified as moderately sensitive (yield threshold EC_{sat}: 2.5 dS m⁻¹) and moderately tolerant to salinity (yield threshold EC_{sat}: 3.3 dS m⁻¹), respectively (Tee *et al.*, 2003).

All vines were pruned back to single shoots with two buds and planted in 8 L pots containing a mixture of soil,

sand, sphagnum peat and farmyard manure (2:1:1:1 v/v). The pots were placed in a polyethylene greenhouse with one layer of green shade cloth (manufacturer's shade rating of 30%). During the plant establishment period, the average maximum/minimum temperatures were 35/15°C, respectively, and the relative humidity (RH) ranged from 33 to 98%. Plants were irrigated automatically with local irrigation water [electrical conductivity (EC) of 0.3 dS m⁻¹] when the soil moisture content decreased between 30 and 40 centibars as measured by a soil moisture probe (2900FI Quick Draw, Soilmoisture Equipment Corp., USA) and fertilized at 15 day intervals with a commercial water-soluble fertilizer containing macro and micro nutrients (Rocket 20-20-20 NPK, Turkey).

Uniform plants with two newly developed shoots (approximately 0.5-0.7 m long with about seven to nine leaves) with approximately equal leaf area were selected and placed in a polyethylene greenhouse with 0.7 x 0.5 m between and within row distances, respectively. The salinity treatments were applied 8 weeks after transplantation and were maintained for a duration of 60 days (from the 6th June to the 4th of August).

Salinity treatments consisted of three levels (control, 2.7 and 5.45 dS m⁻¹) of irrigation solution. The two higher salinity levels were achieved by adding NaCl to local irrigation water used for control. The plants were irrigated using a drip irrigation system with 2 l h⁻¹ drippers when the soil moisture content decreased between 30 and 40 centibars. Oversupply (leaching fraction about 30±5%) ensured that the EC of the drain water (which was monitored) was practically the same as the EC of the salinity treatments. Additionally, changes in the EC of the growing media were observed during the experiment. Soil samples were taken before salinity treatments started and at fifteen day intervals during the irrigation period from each of the cultivar x rootstock x NaCl salinity combinations with three replicates. Air-dried soil samples were ground and sieved to separate the 2 mm fraction. Saturated pastes were made from 200 g of soil and deionized water. Electrical conductivity from saturated pastes was determined using a 0.01 dS m⁻¹ conductivity cell. The changes in EC values of growing media during the salt treatment period were presented depending on the NaCl salinity (Tab. 1), while other variables were combined. This was justified as there was no statistical difference related to these factors and their interactions (as shown by 3-way ANOVA).

Tab. 1. The changes in the EC (± sd) of growing media during the salt treatment period

NaCl salinity (dS m ⁻¹)	Treatment period (days)				
	0	15	30	45	60
Control	1.14±0.11	0.89±0.11	1.02±0.16	1.08±0.15	1.04±0.20
2.70	1.14±0.11	1.56±0.12	2.29±0.17	3.17±0.55	3.85±0.57
5.45	1.14±0.11	2.70±0.14	4.63±0.27	7.06±0.30	7.63±0.60

At the end of the experimental period, 8 plants per replicate were sampled and evaluated for their response to salinity. At harvest, the plants were dissected into leaves, stems and roots and the number of leaves on each plant were recorded. The samples were dried at 70°C to a constant weight and the dry matter of the leaves, stems and roots was measured.

To determine the mineral composition of leaves and roots, previously dried and ground materials were extracted in nitric-perchloric acid. In the extract, Na, K and Ca concentrations were analyzed by flame-photometry (Eppendorf Elex 6361, Hamburg, Germany) and Mg, Fe, Mn, Zn and Cu concentrations were determined by atomic absorption spectrometry (Unicam PU 9200X, Cambridge, UK). Phosphorus was determined colorimetrically by the ammonium phosphovanadomolybdate method and N was determined by Kjeldahl's procedure.

Fully-expanded mature leaves from the mid-shoot area of each sampled plant were measured one day before plant harvesting. Stomatal conductance (G_s) and transpiration (T) were determined between 12:00 and 14:00 using a portable steady-state porometer (LI-1600M, LI-COR, Nebraska, USA).

Chlorophyll content was estimated in these leaves using a SPAD meter (*Minolta 502*, Osaka, Japan). Leaf water potential at noon (Ψ_n), was measured with a pressure chamber (A.R.I Flow Control Accessories, Kibbutz Kfar-Charuv, Israel).

Plants were also scored for visible symptoms of salt injury on a scale of 1 to 4 as follows: 1 - no injury, 2 - damage on shoot-tips and leaf edges, 3 - necroses on the whole leaf and/or on part of the stem, and 4 - dead. Following this, salt injury index (SI) was calculated according to the following formula:

SI = $\sum(n_i \times i)/N$, where n_i is the number of plants receiving the mark "i" (from 1 to 4) and N is the total number of plants in each salt concentration.

The layout of the experiment was a Factorial Randomized Plots Design. There were three replicates in each treatment group and 12 plants in each replicate. All the resulting data were subjected to a three way ANOVA (NaCl Salinity x Cultivars x Rootstocks). For discrimination of significant values, means were compared by the LSD test at p<0.05.

Results and discussion

Salt stress resulted in a considerable decrease in the dry biomass of leaves, shoots and roots of all scion-rootstock combinations (Tab. 2). The decrease in plant dry matter production under salt stress in grapevines is a confirmation of previously reported results (Ben-Asher *et al.*, 2006a; Shani and Ben-Gal, 2005). Under saline conditions, the grafts with 'Sultana' shoots produced more leaf biomass than those of 'Müşküle' shoots, regardless of the rootstock genotype. Moreover, the root biomass of the grafted plant

Tab. 2. The effect of NaCl salinity on dry biomass of leaves, shoots and roots, and salt injury index in different graft combinations of grapevines

NaCl salinity (dS m ⁻¹)	Rootstocks	Dry biomass of leaves (% of control)		Dry biomass of shoots (% of control)		Dry biomass of roots (% of control)		Salt injury Index	
		'Müşküle'	'Sultana'	'Müşküle'	'Sultana'	'Müşküle'	'Sultana'	'Müşküle'	'Sultana'
Control	Rup. du Lot	100.00	100.00	100.00	100.00	100.00 a*	100.00 a	1.00 d	1.00 d
	110 R	100.00	100.00	100.00	100.00	100.00 a	100.00 a	1.00 d	1.00 d
2.70	Rup. du Lot	84.20	102.76	92.06	93.33	80.57 c	65.34 de	1.20 d	1.73 c
	110 R	97.23	106.32	92.98	92.86	77.75 c	86.69 b	1.73 c	1.60 c
5.45	Rup. du Lot	78.14	92.36	84.12	70.00	65.31 de	41.85 f	2.27 a	1.93 bc
	110 R	85.23	98.97	87.72	80.95	62.56 e	69.60 d	2.20 ab	2.13 ab
ANOVA									
NaCl salinity (A)		**		**		**		**	
Rootstock (B)		**		ns		**		ns	
Cultivar (C)		**		ns		**		**	
A x B		ns		ns		**		ns	
A x C		**		**		**		ns	
B x C		ns		ns		**		ns	
A x B x C		ns		ns		**		**	

* Values not associated with the same letter are significantly different (P<0.05); ** significant at 0.05 level; ns: not significant

depended on the shoot genotype. Thus, the scion genotype played a major role in establishing the growth rate of grafted vines, regardless of the rootstock genotype, as previously observed in salt stressed citrus and tomato grafts (Banuls and Primo-Millo, 1995; Chen *et al.*, 2003; Santa-Cruz *et al.*, 2002).

According to Munns (1993), the decrease in plant biomass production due to salinity may be attributed to low external water potential, ion toxicity and ion imbalance. The response of grapevines to salinity includes reduced transpiration and biomass production due to decreases in osmotic potential of soil solution. In fact, the osmotic ef-

fect of salinity on transpiration and growth begins as soon as salinity is experienced. The chemical potential of the saline media initially establishes a water potential imbalance between the apoplast and symplast, which leads to a decrease in pressure potential, potentially causing a reduction in growth (Bohnert *et al.*, 1995). In a saline environment, leaf cells lose water, creating a lower osmotic potential. Like the results of Gibberd *et al.* (2003) and Vincent *et al.* (2007), we found a marked reduction in leaf water potential of all graft combinations grown under saline conditions (Tab. 3). The same decreasing trend was also seen for stomatal conductance and transpiration in

Tab. 3. The effect of NaCl salinity on relative chlorophyll content, leaf water potential, stomatal conductance and transpiration in different graft combinations of grapevines

NaCl salinity (dS m ⁻¹)	Rootstocks	Relative chlorophyll content (SPAD)		Leaf water potential (-MPa)		Stomatal conductance (mmol m ⁻² s ⁻¹)		Transpiration (mmol m ⁻² s ⁻¹)	
		'Müşküle'	'Sultana'	'Müşküle'	'Sultana'	'Müşküle'	'Sultana'	'Müşküle'	'Sultana'
Control	Rup. du Lot	28.84	28.73	1.91	1.77	53.10 c*	80.06 b	2.65 c	4.62 b
	110 R	29.46	28.69	1.53	1.66	54.80 c	137.20 a	2.69 c	5.51 a
2.70	Rup. du Lot	27.56	28.20	1.97	1.80	20.35 de	50.46 c	0.87 cfg	2.20 cd
	110 R	25.81	30.25	1.85	1.90	32.80 d	29.85 d	1.67 de	1.31 ef
5.45	Rup. du Lot	22.61	22.06	2.15	2.25	1.65 f	11.67 ef	0.09 g	0.50 fg
	110 R	26.63	21.48	2.04	1.97	3.84 f	10.58 ef	0.20 g	1.34 def
ANOVA									
NaCl salinity (A)		**		**		**		**	
Rootstock (B)		ns		**		**		ns	
Cultivar (C)		ns		ns		**		**	
A x B		ns		ns		**		ns	
A x C		**		ns		**		**	
B x C		ns		ns		ns		ns	
A x B x C		ns		ns		**		**	

* Values not associated with the same letter are significantly different (P<0.05); ** significant at 0.05 level; ns: not significant

salt-stressed grafted vines (Tab. 3). Similar results were noticed previously when own-rooted and grafted grapevines were exposed to salinity (Ben-Asher *et al.*, 2006b; Fisarakis *et al.*, 2001; Sivritepe, 2000). However, our results imply predominance of the scion genotype in determining variation in the leaf-level physiological characteristics of grafted vines because both parameters were higher in 'Sultana' than in 'Müşküle' at the same leaf water potential and regardless of the rootstock genotype.

As observed in the water relation parameters, the relative chlorophyll contents in the leaves of all grafted plants were reduced by salinity (Tab. 3). Salt stress is known to reduce the life-span of leaves. This causes accelerated senescence and, as a consequence, chlorophyll degradation (Yeo and Flowers, 1984). In the present study, salt-induced chlorophyll degradation is accompanied by visible symptoms of salt injury (Tab. 2). Similarly, in addition to chlorophyll degradation, salt-induced necroses on leaf tissues were observed in grapevines (Sivritepe, 1995). In addition, rootstock genotype caused practically no difference in chlorophyll content and the level of salt injury of both grapevine cultivars. When comparing the two cultivars grafted on the same rootstock, salt damage was more striking in the leaves of 'Müşküle' than in 'Sultana'. Moreover, significant differences in chlorophyll content were found between scion genotypes in response to salinity, with 'Sultana' appearing to be more salt tolerant. Therefore, the shoot genotype again played the dominant role in determining chlorophyll content and level of visible symptoms of salt damage in grafted grapevines exposed to salinity.

In a previous study, Fisarakis *et al.* (2001) reported a strong correlation between leaf Na concentration and salt toxicity symptoms in own-rooted and grafted 'Sultana' vines. In the present study, salinity treatments significantly increased leaf Na concentration, particularly in leaves of 'Sultana' vines grafted on Rupestris du Lot (Tab. 4). However, the higher accumulation of Na ions in the leaves of the 'Sultana'-Rupestris du Lot combination caused no excess in the level of chlorophyll degradation and the level of visible symptoms of salt injury compared to other scion-rootstock combinations at the same level of salinity (Tab. 2 and 3). Furthermore, the effect of rootstock on the Na accumulation in leaves of salt-treated plants varied depending on the shoot genotype. Consequently, rootstock genotype caused no differences in the accumulation of Na ions in the leaves of 'Müşküle' vines after exposure to salinity. The results obtained from 'Müşküle' corroborate similar findings of Hepaksoy *et al.* (2006) in 'Cabernet Sauvignon' grapes grafted onto Rugerri and Ramsey rootstocks. Moreover, roots accumulated higher amounts of Na than other vine parts, especially in 'Müşküle' scion grafts (Tab. 4). Our results are consistent with previous studies conducted on salt-stressed grapevines (Fisarakis *et al.*, 2001; Garcia and Charbaji, 1993; Storey *et al.*, 2003). It is interesting to note that Na concentration in the roots of grafted vines under saline or non-saline conditions was controlled by shoot genotype and not by rootstock genotype. Shoot genotype domination of root Na concentration in response to salinity was also observed in grafted tomato plants (Chen *et al.*, 2003).

Tab. 4. The effect of NaCl salinity on Na, K and Ca concentrations (% d.w.) in leaves and roots of different graft combinations of grapevines

NaCl salinity (dS m ⁻¹)	Rootstocks	Na				K				Ca			
		Leaves		Roots		Leaves		Roots		Leaves		Roots	
		'Müşküle'	'Sultana'	'Müşküle'	'Sultana'	'Müşküle'	'Sultana'	'Müşküle'	'Sultana'	'Müşküle'	'Sultana'	'Müşküle'	'Sultana'
Control	Rup. du Lot	0.04 e*	0.11 de	0.33	0.17	1.35 cd	1.37 cd	1.28	0.93	1.18 f	1.59 de	1.65	0.84
	110 R	0.02 e	0.03 e	0.32	0.20	1.35 cd	1.22 d	1.39	0.86	1.31 f	1.77 c	1.67	1.19
2.70	Rup. du Lot	0.18 d	0.48 c	0.87	0.48	1.54 b	1.49 bc	1.00	0.92	1.53 e	1.56 de	1.58	0.92
	110 R	0.12 de	0.06 de	0.76	0.51	1.62 b	1.23 d	0.99	0.75	1.55 de	2.09 b	1.48	1.28
5.45	Rup. du Lot	0.47 c	1.43 a	1.36	0.70	1.88 a	1.62 b	0.81	0.76	1.71 cd	1.65 cde	1.44	0.98
	110 R	0.57 bc	0.65 b	1.28	0.85	1.91 a	2.04 a	0.92	0.65	1.66 cde	2.42 a	1.44	1.37
ANOVA													
NaCl salinity (A)		**		**		**		**		**			ns
Rootstock (B)		**		ns		ns		ns		**		**	**
Cultivar (C)		**		**		**		**		**		**	**
A x B		**		ns		**		**		ns		ns	ns
A x C		**		**		ns		**		ns		**	**
B x C		**		**		ns		**		**		**	**
A x B x C		**		ns		**		ns		**		ns	ns

* Values not associated with the same letter are significantly different (P<0.05); ** significant at 0.05 level; ns: not significant

Although the reduction of K and Ca uptake in grapevines by Na is a competitive process, NaCl treatment enhanced accumulation of both ions in the leaves (Tab. 4), which balanced the increased concentration of Na ions. These results are in agreement with those of Fisarakis *et al.* (2004), who reported that the ability of vines to maintain high K and Ca levels in leaves may act as the major monovalent cationic osmoticum in the presence of high external salt concentrations. In addition to K and Ca, NaCl salin-

ity induced significant N, P, Mg, Fe, Mn and Zn accumulation in the leaves of all grafted vines (Tab. 4-7). Nevertheless, under saline conditions, the level of accumulated ions in the leaves of grafted vines significantly varied by shoot genotype in such a way that 'Sultana' leaves had higher ion concentrations than leaves of 'Müşküle' vines. Thus, the effect of rootstock on the ion accumulation of leaves of salt-treated plants was limited by cultivar and the level of salinity. Accordingly, only 'Sultana' scions had higher leaf

Tab. 5. The effect of NaCl salinity on N, P and Mg concentrations (% d.w.) in leaves and roots of different graft combinations of grapevines

NaCl salinity (dS m ⁻¹)	Rootstocks	N				P				Mg			
		Leaves		Roots		Leaves		Roots		Leaves		Roots	
		'Müşküle'	'Sultana'	'Müşküle'	'Sultana'	'Müşküle'	'Sultana'	'Müşküle'	'Sultana'	'Müşküle'	'Sultana'	'Müşküle'	'Sultana'
Control	Rup. du Lot	1.48 g*	1.78 de	0.94	0.56	0.20 f	0.41 d	0.26	0.21	0.40 f	0.45 de	0.46 b	0.21 g
	110 R	1.48 g	1.85 cd	0.99	0.54	0.23 f	0.41 d	0.28	0.17	0.43 ef	0.44 de	0.50 a	0.21 g
2.70	Rup. du Lot	1.63 f	2.11 a	0.93	0.70	0.24 f	0.44 cd	0.23	0.22	0.45 de	0.42 ef	0.46 b	0.28 f
	110 R	1.74 e	1.97 b	0.97	0.60	0.32 e	0.51 b	0.24	0.16	0.47 cd	0.45 de	0.40 d	0.27 f
5.45	Rup. du Lot	1.78 de	2.14 a	1.04	0.79	0.30 e	0.49 bc	0.22	0.21	0.55 a	0.42 ef	0.45 bc	0.30 ef
	110 R	1.93 bc	2.10 a	1.08	0.83	0.30 e	0.61 a	0.25	0.18	0.49 bc	0.52 ab	0.42 cd	0.33 e
ANOVA													
NaCl salinity (A)		**		**		**		ns		**		**	
Rootstock (B)		ns		ns		**		ns		**		ns	
Cultivar (C)		**		**		**		**		ns		**	
A x B		ns		ns		**		ns		ns		**	
A x C		ns		**		ns		ns		**		**	
B x C		**		ns		ns		**		**		ns	
A x B x C		**		ns		**		ns		**		**	

* Values not associated with the same letter are significantly different (P<0.05); ** significant at 0.05 level; ns: not significant

Tab. 6. The effect of NaCl salinity on Fe and Mn concentrations (% d.w.) in leaves and roots of different graft combinations of grapevines

NaCl salinity (dS m ⁻¹)	Rootstocks	Fe				Mn			
		Leaves		Roots		Leaves		Roots	
		'Müşküle'	'Sultana'	'Müşküle'	'Sultana'	'Müşküle'	'Sultana'	'Müşküle'	'Sultana'
Control	Rup. du Lot	54.67 g*	83.67 cd	3544	816	57.00 d	45.67 e	115.67	34.33
	110 R	64.67 efg	84.00 cd	3059	589	64.67 c	46.33 e	121.67	31.00
2.70	Rup. du Lot	60.00 fg	106.00 a	3462	930	77.67 b	49.33 e	128.67	38.00
	110 R	85.33 bcd	91.00 bc	2779	785	70.67 c	56.00 d	106.00	39.00
5.45	Rup. du Lot	70.33 ef	96.67 ab	2738	1106	86.33 a	46.33 e	119.67	40.00
	110 R	73.67 de	104.33 a	2377	1168	81.00 ab	69.67 c	106.67	49.00
ANOVA									
NaCl salinity (A)		**		ns		**		ns	
Rootstock (B)		**		**		**		ns	
Cultivar (C)		**		**		**		**	
A x B		ns		ns		**		ns	
A x C		ns		**		**		ns	
B x C		**		ns		**		ns	
A x B x C		**		ns		**		ns	

* Values not associated with the same letter are significantly different (P<0.05); ** significant at 0.05 level; ns: not significant

Tab. 7. The effect of NaCl salinity on Zn and Cu concentrations (% d.w.) in leaves and roots of different graft combinations of grapevines

NaCl salinity (dS m ⁻¹)	Rootstocks	Zn				Cu			
		Leaves		Roots		Leaves		Roots	
		'Müşküle'	'Sultana'	'Müşküle'	'Sultana'	'Müşküle'	'Sultana'	'Müşküle'	'Sultana'
Control	Rup. du Lot	13.00	17.33	56.67	34.33	4.17	6.17	39.83	14.33
	110 R	11.67	15.00	57.67	33.33	3.83	7.17	43.50	18.67
2.70	Rup. du Lot	11.33	17.00	45.67	38.33	5.17	5.17	44.83	19.67
	110 R	12.33	16.00	47.33	35.33	4.17	6.83	40.50	17.67
5.45	Rup. du Lot	13.33	18.67	44.67	41.33	5.50	5.83	38.17	21.67
	110 R	15.00	17.67	49.67	43.00	4.17	6.17	38.10	17.67
ANOVA									
NaCl salinity (A)		**		ns		ns		ns	
Rootstock (B)		ns		ns		ns		ns	
Cultivar (C)		**		**		**		**	
A x B		ns		ns		ns		**	
A x C		ns		**		ns		ns	
B x C		**		ns		**		ns	
A x B x C		ns		ns		ns		ns	

** significant at 0.05 level; ns: not significant

K, Ca, P, Mg and Fe but lower Na concentrations when grafted onto 110 R. The positive effect of rootstock 110 R on leaf ion concentrations in salt-stressed 'Sultana' vines is comparable with the published data (Fisarakis *et al.*, 2001; 2004).

NaCl salinity did not affect the root Ca, P, Cu and Zn concentrations in any graft combination (Tab. 4, 5 and 7). However, increasing salinity levels resulted in increased N but reduced K concentrations in the roots of all grafted vines (Tab. 4 and 5). Similar patterns of K, Ca, P and N concentrations were also observed by Fisarakis *et al.* (2004). On the other hand, the effect of salinity on root Mg, Fe and Mn concentrations of grafted vines significantly differed by scion genotype (Tab. 5 and 6). In contrast to the 'Sultana' grafted vines, increasing NaCl salinity led to a decrease in Mg, Fe and Mn concentrations in the roots of 'Müşküle'-grafted vines. Nevertheless, both under saline and non-saline conditions, the levels of accumulated ions in the roots of grafted vines were controlled predominantly by shoot genotype. Consequently, at each salinity level, grafts with 'Müşküle' shoots had higher ion concentrations than the roots of 'Sultana' grafted vines, regardless of the rootstock genotype. These findings reinforce the above-mentioned finding of shoot domination of growth rate and the leaf-level physiological characteristics of grafted vines.

In response to salinity, 'Sultana' grafts accumulated higher amounts of ions in their leaves than in the roots. By contrast, in 'Müşküle', higher ion concentrations were seen in the roots. In horticultural crops, salt tolerance is associated with their ability to limit uptake and/or transport of saline ions from the root zone to the leaves (Paranychiakis and Chartzoulakis, 2005). In the present study, together with Na, higher ion accumulations in the leaves (Tab. 4-7)

suggest that this does not occur in 'Sultana' grafted vines. For that reason, an opposite strategy should be used when a moderately salt tolerant cultivar like 'Sultana' is used as a scion; that is, increasing the transport of inorganic solutes up to the leaves seems to be the major component of osmotic adjustment in stressed grapevines. The role of ion accumulation in osmotic adjustment was also observed in drought-stressed grapevines (Patakas *et al.*, 2002). The higher ion concentrations of leaves can be an advantage to plants if the ions are compartmentalized. As the vacuole can make up approximately 90% of the cell volume of a mature cell, ions can act as "cheap osmolytes" in the vacuole (Cramer *et al.*, 2007). The production of sufficient organic osmotica is metabolically expensive and potentially limits plant growth by consuming significant quantities of carbon that could otherwise be used for growth (Patakas *et al.*, 2002). Thus, by using this alternative mechanism of inorganic ion accumulation for osmotic adjustment, 'Sultana' vines seem to save energy, which enables them to grow under saline conditions. This advantage may also be related to their ability to withstand higher internal saline ion concentrations (Fisarakis *et al.*, 2001).

Conclusions

The results of the present study suggest that scion genotype plays a dominant role in determining biomass and inorganic ion accumulation of the grafted vines grown under salt stress. Indeed, the osmotic effect of salt was chiefly responsible for the reduction in growth and leaf water potential under salt stress. However, our results proved that 'Müşküle' and 'Sultana' scions showed a different response to salinity because stomatal conductance and transpiration were always higher in 'Sultana' than in 'Müşküle' sci-

ons at the same leaf water potential and level of salinity. Thus, stomatal conductance and transpiration seems to be affected by the osmotic impact of salinity and showed obvious scion dependency. The level of salt-induced chlorophyll degradation and the level of visible symptoms of salt injury also depended on the salt adaptation capacity of the scion rather than Na toxicity. Total inorganic ion concentration in the leaves seems to be the major component of osmotic adjustment in salt-stressed 'Sultana' vines, and the osmotic adjustment ability accounted for the relative salt tolerance of this cultivar. These results suggest that it is necessary to take into account the salt tolerance mechanism of the shoot genotype before selecting rootstocks for grapevines grown under salinity.

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