Long-term Response of Grapevines to Salinity: Osmotic Effects and Ion Toxicity

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Abstract: Growth, mortality, transpiration, and ion accumulation were evaluated in grapevines (*Vitis vinifera* L. cv. Sugraone) under variable conditions of salinity to evaluate whether mortality is a consequence of the processes causing growth and transpiration loss or whether it is an independent process coupled with ion toxicity. Six irrigation water salinity levels (electrical conductivity of irrigation water from 0.5 to 12 dS m^{-1} chlorine concentration from 3.8 to 149 mM) were applied in a one-year lysimeter study and four salinity levels (1.8 to 9.0 dS m^{-1}; 10 to 75 mM chlorine) were applied for five years in vineyard conditions. In the lysimeter experiment, salinity-reduced transpiration was measured as early as 30 days after budburst, and biomass production and evapotranspiration were found to be linearly related. In both the lysimeter and field trials, mortality was dynamically associated with salinity level and time and corresponded to extreme accumulation of sodium and chlorine in shoots. Grapevine response to salinity involved two mechanisms: (1) a reduction in transpiration and growth, which began as soon as salinity was experienced; and (2) vine mortality, which was correlated with salinity level, a sharp increase in sodium and chlorine content of leaves, and time. At lower salinities, the onset of mortality occurred later and death rates increased as the duration of exposure to salinity increased.

Key words: salinity, growth, transpiration, mortality, toxicity, grapevine

Salinity acts on plants through nonspecific and specific mechanisms. The nonspecific effect is due to decreased osmotic potential of the soil solution that impedes transpiration and photosynthesis (Munns and Termaat 1986, Shannon and Grieve 1999). Specific effects relate to ion uptake and altered physiological processes resulting from toxicity, deficiency, or changes in mineral balance (Greenway and Munns 1980, Shannon and Grieve 1999, Hasegawa et al. 2000).

Examples of both specific and nonspecific salinity effects have been documented for grapevines. Walker et al. (1981) detailed salinity-induced stomatal closure and subsequent reductions in photosynthesis and shoot growth. Downton et al. (1990) refuted conceptions assuming direct inhibition of photosynthesis by showing that stomatal behavior altered by salinity sufficiently explains the photosynthetic response. In their investigations regarding rootstock salinity tolerance, Downton (1985), Garcia and Charbaji (1993), and Fisarakis et al. (2001) reported sodium (Na) and chlorine (Cl) toxicity as these ions accumulate in grapevines. Specifically, changes in Na-potassium (K) balance and their antagonism have been documented by Downton (1985) and Garcia and Charbaji (1993), who studied the response of Cabernet Sauvignon vines to increasing salinity of a hydroponic solution.

Biomass reductions caused by salinity and drought are associated with equivalent reductions in transpiration (de Wit 1958, Childs and Hanks 1975, Shani and Dudley 2001). There are no data for relationships between whole-plant biomass production and transpiration under conditions of stress for grapevine. Downton et al. (1990) reported a correlation between biomass production and transpiration at the leaf level for Sultana vines and associated photosynthesis inhibition under conditions of salinity to stomatal closure and the subsequent restriction of CO_2 into leaves.

Grapes have been defined as moderately sensitive to salinity (Downton 1977, Maas 1990). Maas (1990) reported threshold values for grapevines of 1.5 dS m^{-1} in saturated paste electrical conductivity (EC_e) and a salinity response of 9.6% yield decrease for every subsequent unit (dS m^{-1}) increase in EC_e. Conclusions concerning vine response to salinity are largely based on short-term studies in hydroponic growing conditions or in potting media, and there have been few studies on mature grapevines over time. In field conditions, Walker et al. (2002) calculated that the yield reduction for own-rooted Sultana vines for each 1.0 dS m^{-1} increase in a root-weighted electrical conductivity

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of the soil saturation paste ($RWEC_e$) above 2.6 dS m^{-1} was 9.3%. In short-term controlled studies, extreme levels of salinity have been found to lead to vine death (Shani et al. 1993, Garcia and Charbaji 1993). In situ observations in commercial vineyards in Israel (U. Shani and A. Ben-Gal, unpublished data, 1996-2002) and in Texas (McEarchern 1995) indicate a slowly materializing increase in vine mortality correlated with conditions of relatively moderate salinity. There is not enough information to adequately understand the response of mature grapevines to salinity under field conditions or the processes leading to vine death because of salinity.

The main objectives of this work were to evaluate processes involved with vine response to salinity and to question whether vine mortality is a result of the processes causing decreased growth and transpiration or is an independent process coupled with ion toxicity. Specifically, grapevine growth and water consumption, ion accumulation in shoots, and mortality rates were investigated as a function of salinity under near-field (lysimeter) and field conditions.

Materials and Methods

Lysimeter study. *Vitis vinifera* L. cv. Sugraone, an early season, seedless table grape, was grafted on Salt Creek (Ramsey) (*Vitis champini*) rootstock and planted in free-standing lysimeters at the research station of Arava Research and Development, Yotvata, in the Arava Valley, Israel (lat. 29°53'N; long. 53°3'E). The lysimeters were filled with 1.0 m^3 of Arava sandy loam soil (Shani et al. 1987) and incorporated a drainage device as described by Ben-Gal and Shani (2002) that prevented saturation in the lower boundary and maintained soil water hydraulic conditions corresponding to those in the field. The lysimeters had automatic systems for preparation and delivery of irrigation water and for collection and measurement of drainage water quantity and electrical conductivity (EC). Desired amounts of pre-prepared concentrated salt and fertilizer solutions were weighed in a mixing tank and brought to final solution with desalinated (EC 0.5 dS m^{-1}) water. The irrigation water was pressurized (25 m) and applied to each lysimeter via four 8-L h^{-1}drippers (Netafim, Tel Aviv, Israel). Drainage water leaching from each lysimeter and collected in containers was pumped daily to a tank where it was weighed. Electrical conductivity was determined by an on-line meter (model BC9; LTH Electronics, Bedfordshire, UK). The weight of each lysimeter was measured using a mobile pallet jack equipped with a scale. The vines were grown for one year under equivalent conditions while irrigated with water having low salinity (EC = 0.5 dS m^{-1}, Cl = 3.8 mM). In the winter of the second year, the vines were pruned, leaving each with four canes with eight buds, and four spurs with two buds. Salinity treatments were begun immediately after pruning. Irrigation water treatments included water with increasing Cl concentrations: 3.8, 31, 55, 82, 104, and 149 mM. Salinity was increased by adding 1:1 molar concentrations of NaCl and $CaCl_2$ to the low salinity (Cl 3.8) water. The salinity levels (0.5, 3, 5, 7, 9, and 12 dS m^{-1}) of irrigation water represent prefertilization values. Fertilizer additions to irrigation water varied with plant stage and raised EC by 0.5 to 1.0 dS m^{-1}. Electrical conductivity, concentrations of major chemical components, and the osmotic potential of the irrigation waters are found in Table 1. Osmotic pressure (π) was calculated based on the van't-Hoff equation, $\pi = iMRT$, where i is the van't Hoff factor (moles of particle in solution/moles of solute dissolved), M is molarity of the solute, R is the universal gas law constant, and T is temperature. Each set of three replicates had a target irrigation level equal to 120% of their actual evapotranspiration quantity. Daily water balance generated evapotranspiration (*ET*) data for each lysimeter (grapevine) were calculated using: $ET = I - Dr + \Delta W$, where *I* is irrigation, *Dr* is drainage, and ΔW is change in soil water determined from changes in lysimeter weight. No rainfall occurred during the relevant experimental period.

Fertilization and plant protection measures were conducted as recommended by the local vineyard extension service and as practiced by local commercial growers. Nitrogen-phosphorus-potassium (N-P-K) fertilizers were applied daily in irrigation water as ammonium nitrate, phosphoric acid, and potassium nitrate at rates that varied with vine growth stage over the season. Concentrations in water (g m^{-3}) of elemental N:P:K were pruning to budburst, 50:7:40; budburst to shoots of 3 cm, 80:8:60; shoots of 30 cm to flowering, 80:5:75; flowering to harvest, 40:2:2.5; and postharvest, 40:0:0. Vines were trellised on independent T-systems in each lysimeter. Biomass removed during pruning was collected for fresh and dry weights. Berry yields of harvested grapes were recorded. At the end of the harvest season the vines were removed and the fresh and dry biomass was measured for individual components. Leaf samples of 20 mature or 20 young leaves were collected, dried at 65°C, digested, and analyzed for sodium (Na), calcium (Ca), and K by atomic absorption spectrometry and

Table 1 Irrigation water composition including electrical conductivity (EC), major ions, and osmotic pressure (π).

	EC	Ion (mM)					π
	dS m^{-1}	Ca	Mg	Na	SO_4	Cl	MPa
Lysimeter	0.5	1.27	1.23	3.4	2.23	3.8	0.029
	3.0	3.87	1.23	23.4	2.23	31.3	0.154
	5.0	6.11	1.23	44.0	2.23	55.1	0.271
	7.0	9.16	1.23	64.0	2.23	81.7	0.399
	9.0	11.33	1.23	78.0	2.23	104.35	0.500
	12.0	16.32	1.23	108.0	2.23	149.0	0.712
Field	1.8	5.10	4.30	8.0	4.3	10.2	0.068
	3.5	7.35	5.25	17.5	11.15	20.4	0.125
	6.0	13.85	5.25	34.5	11.15	45.4	0.268
	9.0	21.85	5.25	56.5	11.15	75.4	0.421

for Cl by titration methods (Page et al. 1982). Soil in the lysimeters was periodically sampled at four depths (0 to 20 cm, 20 to 40 cm, 40 to 60 cm, and 60 to 80 cm) midway between the vine trunk and the lysimeter wall. Saturated paste extracts of oven-dry soil were analyzed for EC and Cl, according to Page et al. (1982). Direct measurements of EC in irrigation and drainage waters and in soil extracts were taken with a temperature-compensating conductivity meter (Cyberscan 500; Eutech Instruments, Singapore) and Cl was measured by a chloridometer (model 926; Corning, Medfield, MA).

Field study. In a separate five-year field study, grapevines (*Vitis vinifera* L. cv. Sugraone) were grown in Arava sandy loam soil at the Arava Research and Development Station. Irrigation waters of four salinity levels (EC 1.8, 3.5, 6, and 9 dS m^{-1}, and 10.2, 20.4, 45.4, and 75.4 mM Cl) replicated three times were applied. The Cl 10 treatment used desalinated water, while the Cl 20 treatment used commercial irrigation well water. For the more saline treatments (EC 6, 9 and Cl 45, Cl 75), a 1:1 molar ratio of NaCl and $CaCl_2$ was added to the Cl 20 water. Electrical conductivity, concentrations of the variable ions, and the osmotic pressure of irrigation water before addition of fertilizer are presented in Table 1. Replicates were 10-meter plots of single rows, with vines planted every two meters, randomly located within six, 24-meter rows of a larger vineyard. Row spacing was 3.5 meters. Vines were irrigated at 130% of potential evapotranspiration, which was calculated as class A pan evaporation multiplied by the percent canopy cover. Fertilization, plant protection measures, and trellising were conducted as recommended by the local vineyard extension service and as practiced by local commercial growers. Irrigation water was applied through drip-irrigation systems (Netafim) with injection pumps (Amiad, Kibbutz Amiad, Israel) for the introduction of salt and fertilizer. Nitrogen, P, and K were applied with irrigation water as ammonium nitrate, phosphoric acid, and potassium nitrate with seasonal plant stage variations as described for the lysimeter experiment. Irrigation water was periodically sampled and analyzed for EC and Cl. Soil was sampled twice annually, after budding in spring and immediately following harvest. Soil samples were taken every 20 cm to 1.2 m depth for each replicate in the vine row at the midpoint between two vines. The EC and Cl of the irrigation and drainage waters and the soil extract EC and Cl were measured as in the lysimeter study. Vines were trellised on four-wire Y-shaped systems. Pruning was conducted in December each year as recommended by the local extension service and as practiced in local commercial vineyards on the basis of leaving two long canes of 8 to 10 buds and four renewal spurs of 2 to 3 buds on each side of the trellising for each vine. After two years, 3-m deep trenches were dug between the rows to prohibit roots from traversing the treatments. Fruit biomass and Na, Ca, Cl, and K ion accumulation in leaves were measured each harvest season using analysis as described for the lysimeter study. Vine mortality was determined as number of individual vines failing to bud and grow after winter dormancy each season.

Results

Soil salinity and Cl levels. Near constant Cl concentrations were measured as a function of depth in the soil profile for each of the treatments in the lysimeter study, although there were some slight increases in depth for the Cl 55, 82, and 104 treatments (Figure 1). Irrigation water with prescribed salt concentration caused increased salinity of soil water solution. The high frequency of water application and a constant irrigation to transpiration ratio led to quasi-steady-state conditions in the soil profile and resulted in similar concentrations of chloride in the soil solution and leachate.

Irrigation water salinity (as EC or Cl) was highly correlated to root-zone salinity measured as leachate Cl concentration as well as to soil solution Cl from extract analysis. Correlation analysis of soil leachate solution Cl and irrigation water Cl resulted in the linear relationship: leachate Cl [mM] = 25.4 + 1.19* irrigation water Cl [mM], $r^2 = 0.99$, $\alpha = 0.01$. Similarly, correlation of irrigation water Cl with depth averaged Cl in soil solution based on sample extracts resulted in: soil solution Cl [mM] = 2.4 + 1.5 * irrigation water Cl [mM], $r^2 = 0.99$, $\alpha = 0.01$.

Vine evapotranspiration. Salinity reduced the cumulative evapotranspiration (ET) (Figure 2). Vine water uptake was a function of climate and canopy cover, with relatively low ET during the winter and in early spring when the vines budded and began vegetative growth and much greater ET in the late spring and summer with full canopy

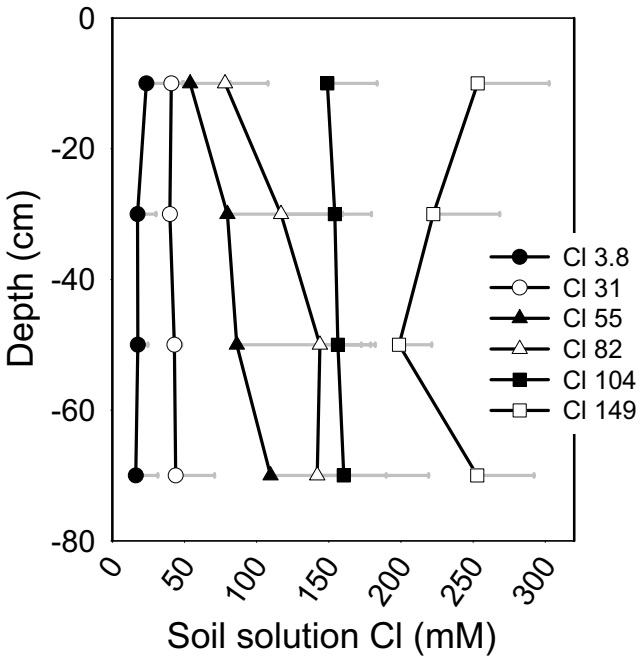

Figure 1 Soil solution Cl concentration profiles in lysimeters. Soil sampled in 20-cm intervals from 0 to 80 cm. Horizontal bars represent 95% confidence values.

coverage. Differences in ET measurements corresponding to salinity treatments became evident 30 to 40 days after budding (March 30 to April 10) and increased as vine shoot growth advanced. Linear regression analysis for the seasonal, cumulative ET data measured over 113 days for treatments Cl 3.8 through Cl 104 showed a 358.5 L reduction of water consumption for every increase of 10 $mM \cdot L^{-1}$ Cl in irrigation water (ET [L] = 4585.7 - 37.68·irrigation water Cl [mM], $r^2 = 0.95$, $\alpha \leq 0.01$). The highest levels of salinity resulted in vine death, and the mortality of vines is evident where negligible ET rates are seen in Figure 2. The Cl 149 treatment stopped biomass production and vines had insignificant water uptake after 45 days (April 15). The Cl 149 vines had little flowering and no fruit production. The Cl 104 vines maintained low, but measurable, ET for approximately 100 days (June 6), at which point water uptake also became negligible. In addition to causing vine mortality, salinity stress was observed visually as resulting in smaller vines and chlorosis and necrosis of leaves.

Vine biomass, fruit yield, and mortality. Yield responses to increases in EC_e were manifested in the lysimeter experiment as both decreased leaf and stem weight and decreased fresh berry weight (Figure 3). Threshold response values to salinity were not evident. The linear regression analysis was performed on the treatments up to Cl 104 and did not include the Cl 149 vines. Leaf and stem biomass (dry weight basis) declined 13% with every increase of 1.0 dS m^{-1} in EC_e. Fresh fruit biomass decreased 14.4% for each dS m^{-1} in EC_e. Total aboveground dry biomass declined 13.2% for each dS m^{-1} in EC_e.

Relative fruit yields ($Y \cdot Y_{max}^{-1}$) from the lysimeter experiment and the fourth year of the field experiment are shown in Figure 4 as a function of irrigation water Cl concentration. The response of fruit yield to irrigation water salinity was remarkably similar. These data suggest that the threshold for economic yield reductions was 20 mM Cl, after which yield decreased by 13.3% with each additional 10 mM Cl.

Both water uptake and yield were reduced as salinity increased. Final total aboveground, dry biomass of the grapevines is shown as a function of cumulative ET in

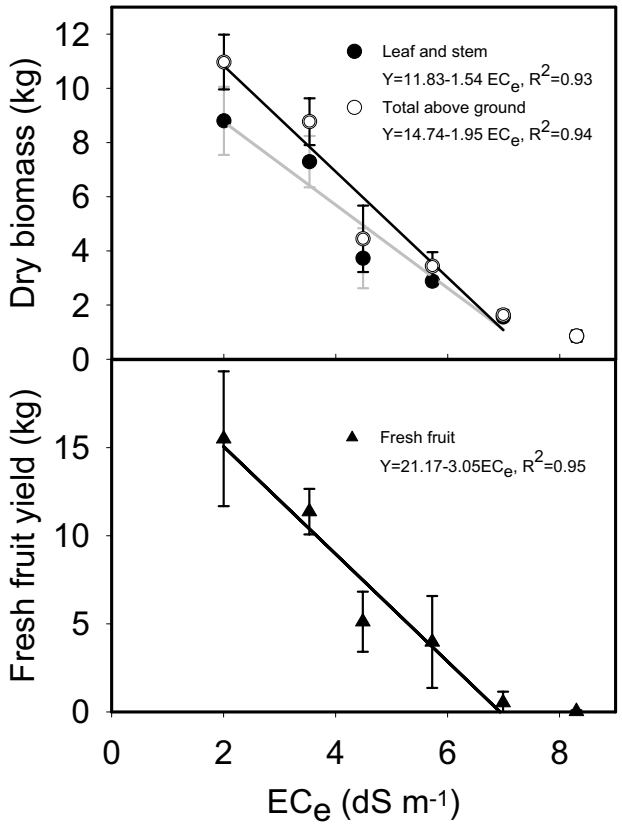

Figure 3 Yield response of lysimeter-grown grapevines to saturated paste soil salinity. Yield shown as total dry biomass and fresh fruit yield. Shown are means ± standard deviation; lines are linear fits for all treatments excluding those of irrigation water of Cl = 149 mM.

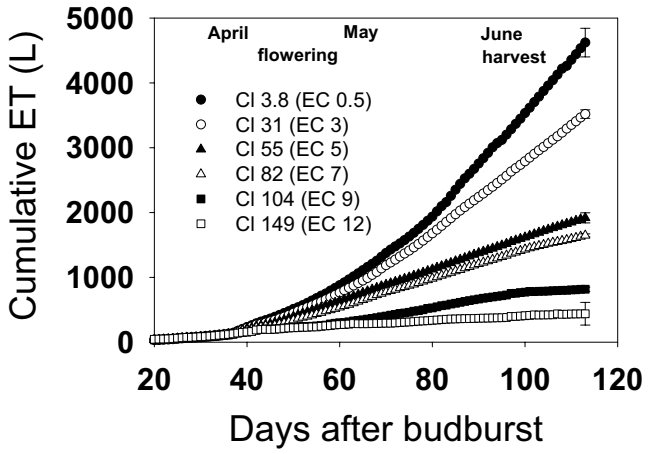

Figure 2 Cumulative evapotranspiration for grapevines in lysimeters with variable salinity of applied irrigation water. Symbols are mean daily water balance results. Vertical bars on final data are standard deviations.

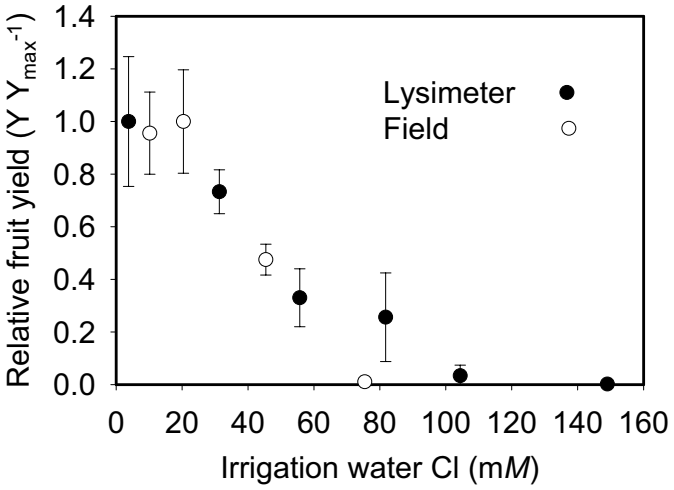

Figure 4 Relative fruit yield from lysimeter and field experiments as function of Cl concentration in irrigation water. Means ± standard deviation; n = 3.

Figure 5. A linear relationship between relative yield and relative ET is evident.

Although a portion of the biomass (stem and trunk weights) existed previously to the imposition of salinity treatments, measured ET corresponded only to the period after treatments began, which explains why positive biomass is shown for zero transpiration. In the third and fourth years of the field experiment, vine mortality showed a progressive increase (Figure 6). Greater than 90% of vines receiving irrigation water of Cl 75 died by the third year, and vine loss in the Cl 45 treatment increased from 5% in the third year to >30% in the fourth year. Similarly, vine death in the Cl 20 treatment increased from 5% to >10% between years three and four. No mortality was found for vines irrigated with Cl 10 water.

Leaf tissue ion content. Chloride and NA in leaf tissue from both field and lysimeter environments increased as irrigation water salinity increased (Figure 7). The concentration of these ions increased at a relatively moderate level as the irrigation water salinity increased from 3.0 to 82 mM Cl in the lysimeters and 10 to 45 mM in the field, but Na and Cl accumulation increased dramatically as the irrigation water reached 100 mM Cl in the lysimeters and 75 mM Cl in the field. This steep increase of Cl and Na in leaf tissue occurred in the treatments where vine mortality was most significantly encountered. Ion contents in composite leaf samples taken just before harvest during the second season of the field experiment were consistent with those from the lysimeter experiment. The only noticeable difference was that in the field, the dramatic Cl and Na accumulation was found at lower salinities. Potassium and Ca in leaf dry matter was similar for lysimeter and field samples and did not correspond to irrigation water salinity. Potassium content of leaves averaged 0.25 M·kg^{-1} (± 0.04) for mature leaves and 0.34 M·kg^{-1} (± 0.07) for young leaves, and Ca content for mature and young leaves was 0.43 M·kg^{-1} (± 0.1) and 0.21 M·kg^{-1} (± 0.06), respectively. Trend lines were created using the best-fit logistic curve of data from mature leaves (field and lysimeter) plotted in the figures. The lines represent:

$$I = I_0 + \frac{a}{1 + e^{-\left(\frac{Cl - Cl_0}{b}\right)}} \qquad [1]$$

where I is ion concentration in the leaves and Cl is irriga-

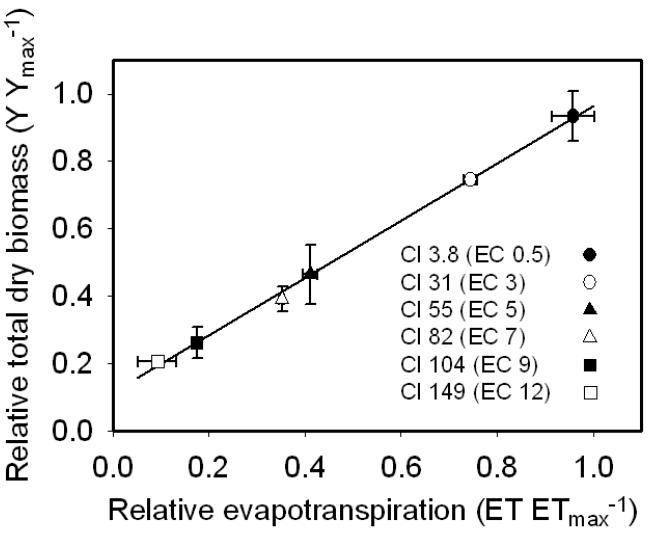

Figure 5 Biomass-evapotranspiration relationships for grapevines grown under six irrigation water salinity treatments in lysimeters. Shown are means ± standard deviation, and the line is the best fit linear relationship: (Y·Y$_{max}^{-1}$) = 0.11 + 0.87 (ET·ET$_{max}^{-1}$), R^2 = 0.98.

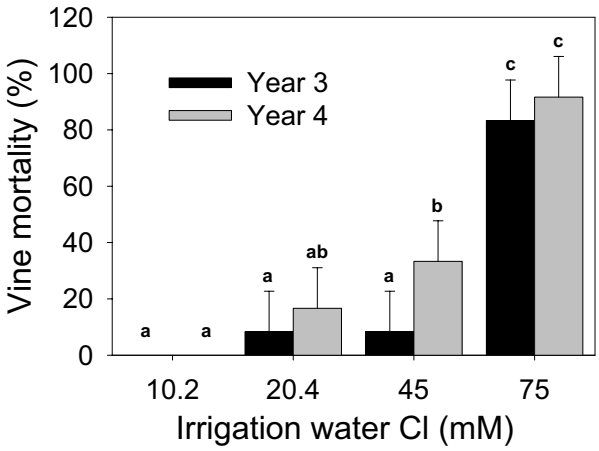

Figure 6 Rate of vine fatality for two years of field-grown grapevines as a function of irrigation water salinity. Shown are means ± standard deviation. Letters give grouping according to multiple analysis of variance significant at $p < 0.05$.

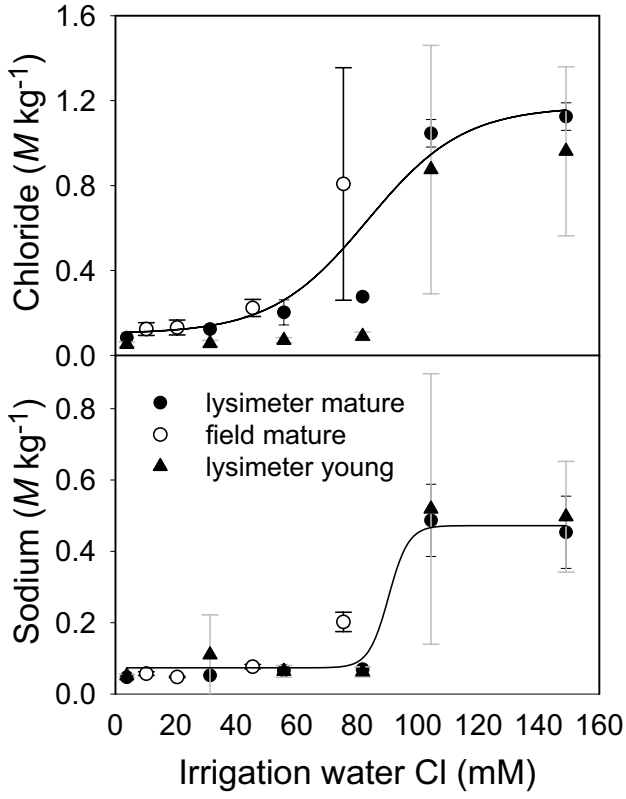

Figure 7 Chloride and sodium content in leaf dry matter as a function of irrigation water salinity. Symbols are means, and bars represent 95% confidence limits. Lines are best fit four-parameter logistic regression curves.

tion water ion concentration. The regression in Figure 7 for mature leaf Cl contents resulted in the following parameters: $a = 1.07$, $b = 15.86$, $I_0 = 83.3{,}9$ and $Cl_0 = 0.856$, $r^2 = 0.86$. Values for the regression line for Na in mature leaves were $a = 0.40$, $b = 3.29$, $I_0 = 0.90$, and $Cl_0 = 0.073$, $r^2 = 0.93$.

Discussion

Salinity reduced biomass production and water uptake in Sugarone grapevines. Reporting of linear relationships between stress-produced variations in yield and ET, although novel for grapevines, is well established for other crops (de Wit 1958, Childs and Hanks 1975, Shani and Dudley 2001). The strong correlation between declines in biomass production and ET (Figure 5) and the onset of declining ET as a function of increasing salinity early in the season (Figure 2) indicate that osmotic effects played an important role in response of the grapevines to salinity stress.

The responses of yield and ET to salinity were linear and began at the lowest levels tested in the study. Yield responses to salinity are commonly expressed using a piecewise linear curve defined by the threshold EC_e and by the subsequent slope of the line relating yield to EC_e above the threshold value (Maas and Hoffman 1977). The 13% decrease in biomass production per unit dS m^{-1} increase in EC_e and the 14.4% fruit yield reduction per unit EC_e increase are slightly greater than responses found for greenhouse-grown, young Sultana vines (Walker 2002, Downton 1985). While the difference may be explained by differences in variety, soil media, or growing conditions such as climate, the responses all fall within the range of "moderately sensitive" (Maas 1990) for grapevines where 50% loss is expected at an EC_e value of ~4.5 dS m^{-1}. A threshold level of biomass production response to salinity is commonly accepted and reported (Maas 1990, Walker 2002). Its absence in this study agrees with findings of Downton (1985), who measured yield decreases beginning from the lowest two levels (0 chlorides added to half-strength Hoagland compared to 12.5 mM Cl added as Na, Ca, and Mg salts at 6:2:2 ratio), and Fisarakis et al. (2001), who found linear decreases beginning from their lowest level of EC_e (1.9 dS m^{-1}) after 60 days of salinity treatments.

At the lower levels of salinity, Cl and Na accumulation in leaves agrees with that found by Downton (1985) for Sultana grapevines on Ramsey rootstock and by Fisarakis et al. (2001) for Sultana on a variety of rootstocks. Our data do not support Na-K antagonism as reported by Garcia and Charbaji (1993), since leaf matter K levels were not decreased by conditions of increased salinity and Na content either in the soil or in the leaves. The drastically higher concentrations of Cl and Na in leaf matter that corresponded with mortality suggest a breakdown in salt tolerance mechanisms. Greenway and Munns (1980), Munns (2002), and Storey et al. (2003) have proposed that the sequestration of ions in roots, and the prevention of their transport to the shoot in the xylem, is a mechanism for salinity tolerance. Fisarakis et al. (2001) found consistently higher accumulations of Cl and Na in roots as compared to the leaves of Sultana vines and suggested that capability to store Na in roots is a tolerance characteristic of rootstocks. Careful analysis of the results of Garcia and Charbaji (1993) for Cabernet Sauvignon grapes reveals similar phenomena of dramatic increased Na in leaves at the higher salinity levels with corresponding vine mortality. While soil solution ion levels in the current study increased linearly with salinity (Figure 4), shoot tissue Na and Cl levels show breakthrough-type curves with dramatic increases at higher salinities (Figure 7). Inadequate regulation of mechanisms that prevent ion transport to shoots is a reasonable explanation for these relationships between soil and leaf Na and Cl content. Eventually, complete or partial regulatory losses are responsible for subsequent mortality.

Conclusion

In a lysimeter experiment, salinity-induced reductions in transpiration in Sugraone grapevines appeared as early as 30 days after budburst. Biomass production and evapotranspiration were found to be linearly related. Total dry biomass production declined 13.2% per unit (dS m^{-1}) increase in EC_e and fresh fruit yields decreased 14.4% per unit (dS m^{-1}) increase. Our results from the lysimeter study and a parallel multiyear field experiment support the hypothesis that grapevine response to salinity involves two mechanisms. The first mechanism is reduced transpiration and biomass production with increasing salinity, resulting from decreases in soil solution osmotic potential. This general, osmotic effect on transpiration and growth begins almost as soon as salinity is experienced. The second mechanism involves vine mortality and is seen to be correlated with salinity level, breakthrough of Na and Cl into the leaves, and the duration of exposure to salinity whereby onset of mortality is observed later for lower salinities.

The last observation suggests that the two processes, production loss and mortality, are not dependent. After three years of salinity treatments in the field, while some of the vines irrigated with slightly saline water (Cl 20) failed to arise from dormancy, the remaining vines were found to be relatively productive. Overall, salinity was found to reduce transpiration and biomass production and to eventually cause vine mortality, with vine death being a function of both salinity level and exposure duration.

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