The Response of Grapevines to Transient Soil Salinisation

by

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ABSTRACT

Colombard grapevines on Ramsey rootstocks were irrigated with saline water, with an electrical conductivity (EC) of 3.5 dS/m during any one of the four stages within the seasonal growth of mature grapevines. Saline water was produced by addition of a sodium chloride brine to River water (EC 0.6 dS/m). Periods of salinisation and treatment designation were as follows: the treatment salinised between bud-burst and full-bloom was designated BB-FB; that between full-bloom and veraison - FB-V; that between veraison and harvest - V-H; that between harvest and leaf-fall - H-LF. At other times these treatments were irrigated with river water. A control, designated CONT, was irrigated with river water throughout the season.

Over a single season, saline irrigation of immature grapevines in any period reduced shoot growth by an equivalent amount, 12% on average. During saline irrigation, leaf water potential (Ψ_l) was reduced by 0.15 MPa. Leaf Na and Cl concentrations rose in response to saline irrigation and remained elevated.

In mature field grapevines, saline irrigation over three consecutive seasons had no effect on either the pruning weights or the butt enlargement. Yield only declined in treatment FB-V, and then only in the second season. The decline of 6% was entirely due to a reduction in the weight of berries.

Measurements of Ψ_l made during the second consecutive season of saline irrigation showed that Ψ_l fell by between 0.05 and 0.15 MPa during saline irrigation. Leaf Cl concentrations rose with ECw. However, the rises in leaf Na did not necessarily bear any relationship with those in the ECw.

Saline irrigation affected the juice composition in all three seasons and by the second season it increased the concentrations of malate, tartrate and potassium, and increased the pH and titratable acidity of all treatments. Saline irrigation did not affect juice total soluble solids (°Brix).

It was concluded that during periods of high water salinity in the River Murray, vignerons would gain the most benefit from non-saline dilution flows released between mid-November and mid-January, and that the response of mature vines could not be predicted from the results of the experiment with immature vines.

SUMMARY

The response of Colombard grapevines on Ramsey rootstocks to transient soil salinisation was studied in immature potted grapevines for a single season and for three seasons in mature field grapevines growing under favourable productive conditions. Five treatments were applied; four consisted of irrigating with saline water during one of the four stages within the seasonal growth of mature grapevines. River water, with an electrical conductivity (EC) of about 0.6 dS/m, was salinised by the addition of a sodium chloride brine which increased the EC to 3.5 dS/m. Periods of salinisation and treatment designation were as follows: the treatment salinised between bud-burst and full-bloom was designated BB-FB; that between full-bloom and veraison - FB-V; that between veraison and harvest - V-H; that between harvest and leaf-fall - H-LF. At other times these treatments were irrigated with river water. A control, designated CONT, was irrigated with river water throughout the season.

In immature grapevines, saline irrigation in any period reduced shoot growth by an equivalent amount, 12% on average. Most of this reduction occurred during the application of saline irrigation. The fall in growth was equivalent to that reported in a study with Sultana on Ramsey rootstock where the same annual salt load was evenly distributed across the entire season.

During saline irrigation, leaf water potential (Ψ_l) was reduced by 0.15 MPa. This reduction bore a near one-to-one relationship with the fall in the osmotic potential of the irrigation water suggesting the electrical conductivity of the soil solution (ECsw) was equivalent to that of the irrigation water (ECw). Leaf Na and Cl concentrations rose in response to saline irrigation. The maximum concentrations were 228 and 280 mmol/kg for Na and Cl, respectively. Concentrations of Na and Cl remained elevated after saline irrigation ended.

In mature vines, the irrigation was scheduled to replace water as it was used by the grapevines. This schedule produced a variation in the volume of water

applied in each growth stage and a variation in the amount of salt applied per season in each treatments. Had the salt load, which was applied in a two month period, been evenly spread across the season then the ECw in treatments V-H, FB-V, H-LF, and BB-FB would have been 1.7, 1.6, 0.9, and 0.8 dS/m. After two months of saline irrigation, the electrical conductivity of the saturated soil paste extract (ECe) rose to about that of the irrigation water, 3.5 dS/m. Changes in the ECe lagged behind those in the ECw. Because of this lag the ECe of the rootzone displayed large variations with depth.

In the second consecutive season of saline irrigation, Ψ_1 fell by between 0.05 and 0.15 MPa during saline irrigation. The fall had a near one-to-one relationship with the fall in the osmotic potential of the saturated soil paste extract suggesting ECe was equivalent to ECsw. Leaf Cl concentrations rose with ECw. However, the rises in leaf Na did not necessarily bear any relationship with those in the ECw: in BB-FB, leaf Na did not rise until one month after the end of saline irrigation and in V-H it rose two months before the beginning of saline irrigation. The rise in the leaf Na of V-H occurred whilst its ECe was equivalent to that in the control treatment suggesting that Na was carried over within the vine from the previous season. The concentrations of Na and Cl in the March sample of the leaf lamina and grape berry juice were normalised to remove the effect of differences in the annual salt loads between treatments. This transformation showed that the greatest rate of Cl uptake per unit increment in annual salt load occurred in the leaf in the treatment BB-FB and in the grape in treatments BB-FB and FB-V. Uptake rates of Na into the leaf and grape were equivalent in the three treatments which received saline irrigation before harvest.

As the season advances the Cl uptake rate by the berry declines. In combination with a relatively constant Na uptake rate this caused an increase in the ratio of Na to Cl. As a result saline irrigation between full-bloom and veraison in the second season and between veraison and harvest in the second and third seasons produced juice where the excess of sodium over chloride ions was above that acceptable in wine destined for the EEC.

Over three consecutive seasons, saline irrigation had no effect on either the pruning weights or the butt enlargement. Yield only declined in treatment FB-V, and then only in the second season. The decline of 6% was entirely due to a reduction in the weight of berries, however a decline in berry weight did not necessarily lead to a reduction in yield. In the third season, berry weight declined in the three treatments which received saline irrigation before harvest. Normalisation of these data to remove the difference in the annual salt loads between treatments showed that the greatest reduction occurred in treatment BB-FB.

The yield data was conservatively adjusted to allow comparison with results reported in a study on the response of own-rooted Sultana to a saline irrigation regime where the annual salt load was evenly distributed across the season. The comparison showed that the yield savings gained by constraining the annual salt load to a two month period within the season were in the order of 10%. It was hypothesised that constraining saline irrigation to a two month period within the season created opportunities for the vine to avoid salt stress.

Saline irrigation affected the juice composition in all three seasons and by the second season it increased the concentrations of malate, tartrate and potassium, and increased the pH and titratable acidity of all treatments. Saline irrigation did not affect juice total soluble solids (°Brix). When the changes in composition were normalised to remove the difference in annual salt load between treatments the greatest increase in the concentrations of malate, tartrate and potassium, and in the titratable acidity, occurred in treatment BB-FB.

In models of the effect of salinity on the growth of grapevines it has been assumed that an equilibrium exists between the concentration of salt in the irrigation water and soil solution, and that under this condition the ratio in the pot between ECw and ECsw is 1:1 and in the field between 3:1 and 5:1. Therefore irrigation of a potted immature vine with water of ECw 3.5 dS/m should create conditions which equate to an ECsw in the field of between 0.7 and 1.2 dS/m. Given that ECsw in the field was threefold greater than 1.2 dS/m after two months of saline irrigation,

the growth loss in potted vines should have under-estimated the loss found in field vines. Instead it over-estimated the loss. In the present study, the rapid turnover of soil water in pots quickly established an equilibrium between the ratio of ECw:ECsw with a value of 1:1. In contrast, turnover of soil water in the field was slower and although the ratio of ECw:ECsw rose over the two months of saline irrigation it only just reached 1:1 at the end of this period. These results indicate that, with an irrigation regime which constrains saline irrigation to a two month period within the season, the assumption regarding the ratio of ECw:ECsw which is used in the modelling of grapevine response to salinity does not apply.

Up to 40% of the vine's annual irrigation requirement can be met with water of EC 3.5 dS/m without loss of yield. Saline irrigation between full-bloom and veraison reduces yield, however the loss is much less than that predicted had the same annual salt load been spread evenly across the season. During periods of high water salinity in the River Murray, vignerons would gain the most benefit from non-saline dilution flows released between mid-November and mid-January. Further the results suggest that in seasons with a high annual salt load, damage can be reduced by selecting a strategy which concentrates the annual salt load into a two-month period over a strategy which evenly spreads the annual salt load over the entire season. Timing of saline irrigations affects the levels of free sodium in the juice and this level rose above that acceptable in wine destined for export to the EEC. The sensitivity of juice composition to salinity was greater than that of yield or berry weight. Changes in composition were not secondary effects of salinity induced changes in maturity or berry volume. The response of mature vines could not be predicted from the results of the experiment with immature vines.

Abbreviations and Symbols

BB	Bud-burst
FB	full-bloom
V	veraison
H	harvest
LF	leaf-fall
CONT	control treatment
EC	electrical conductivity
ECe	EC of a saturated soil paste extract
RWECe	root-weighted **ECe**
ECi	EC of irrigation water
ECw	EC of water from irrigation and precipitation
ECsw	EC of water in the soil solution
Ψ	water potential
Ψ_s	potential of water in the soil
Ψ_l	potential of water in the leaf
Ψ_π	osmotic potential
$\Psi_{\pi l}$	osmotic potential in the leaf
$\Psi_{\pi s}$	osmotic potential of soil solution
$\Psi_{\pi w}$	osmotic potential of irrigation water
τ	matric potential
G	gravitational potential
P	pressure
P_l	pressure in the leaf
π	osmotic pressure
π_l	osmotic pressure in the leaf
RWF	root-weighting factor
RLD	root length density
ETo	reference crop evapotranspiration
RWC	relative water content
TSS	total soluble solids.

Declaration

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

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1. General Introduction

In South Australia, vineyards along the River Murray produce 23% of the Australian grape production (ABARE, 1989). The climate of this region is semi-arid and the River Murray is the sole source of irrigation water. Its salinity is highly variable. In some seasons it reaches an EC of 1 dS/m which is high enough to cause a yield decline in Sultana (Prior *et al.*, 1992a).

In field crops, a change in the irrigation strategy i.e. redistributing the annual salt load with most of it concentrated into one of the crop's annual growth stages, has been shown to alter the effects of salinity. Lai (1985), Maas *et al.* (1986), and Maas and Poss (1989) found the effect of saline irrigation on crop yield was dependent on the crop growth stage at which salinity was applied.

Irrigators in the Riverland can draw on only one water supply i.e. the River Murray. Its salinity is inversely proportional to its flow. Increasing flow from 89 to 630 GL per month reduces the salinity at Morgan from 1.0 to 0.6 dS/m (McKay *et al.*, 1988). Opportunities exist with the present River management to vary flow within the same season. Water storages in the Murray-Darling system filled with non-saline water diverted during periods of high river flows have a capacity of 9300 GL (B. Harper, pers. comm.). The release of water from storage bodies during periods of low river flow can temporarily lower salinity. The efficacy of this strategy for grapevine yield may depend on the sensitivity of the grapevine growth stage during the period of water release.

This study was undertaken to ascertain whether the response of the grapevine to saline irrigation was dependent on the stage within the seasonal growth cycle at which saline irrigation was applied. It consisted of two experiments. Most of the reports on grapevine response to salinity are based on experiments with immature grapevines and the first experiment investigated the growth response of immature grapevines to saline irrigation applied for two month periods corresponding with the different stages in the seasonal growth of a mature grapevine. This experiment was

conducted over a single season. Results from salinity experiments with immature grapevines have been used to predict the response of mature grapevines. The second experiment, conducted over three consecutive seasons, determined the response of mature grapevines to saline irrigation applied during the different stages within the seasonal growth cycle.

2. LITERATURE REVIEW

2.1 SALINITY AND GRAPEVINES

2.1.1 Definition of salinity and salinisation

Definition

Salinity is a term used to describe the deleterious conditions for plant growth that arise from exposure of the plant to excessive concentrations of soluble salts (Bernstein, 1975). In the United States of America, the major ions associated with salinity in the field are chloride, sulphate, bicarbonate, sodium, calcium and magnesium (Bernstein, 1975).

Salinisation

Plants may be exposed to salt via their roots or their foliage. Foliar exposure occurs near the sea when landward winds deposit salt of oceanic origin on leaves and when salt is deposited by over-canopy irrigation with saline water. This thesis will only consider the response of grapevines which have been mainly exposed to salt via their roots.

Rootzone soil salinisation is caused by the addition of soluble salts. These are carried into the rootzone by water infiltrating downward from irrigation or precipitation, and by water rising upward from the water table carrying with it dissolved salts. A build-up of salt can be reduced or prevented by the drainage of a sufficient volume of water, which carries salts from rootzone, a process referred to as leaching. In addition, the salt concentration may be increased and decreased by processes of dissolution and precipitation, respectively.

In the Riverland, where the climate is semi-arid and the topsoils well-weathered, precipitation was the major salt source before the introduction of irrigation. Precipitation annually delivered about 34 kg/ha of salt (Blackburn and McLeod, 1983) and in their native state the topsoils were not saline (Wetherby,

1973). Application of irrigation water drawn from the Murray River (at an electrical conductivity of, say, 0.5 dS/m) increased the annual salt load to 2020 kg/ha. Provided the leaching of salt was sufficient to prevent accumulation of salts then this salt load did not cause soil salinisation.

In the Murray River, elevated water salinity was due mainly to an increase in the concentrations of sodium and chloride ions (Gutteridge *et al.* 1970). The high solubility of sodium chloride and the low reactivity of the major precipitate in the soil, calcium carbonate, minimised the role that dissolution and precipitation have played in changing the soil solution salt content. Where drains and good irrigation management have maintained the water table below 2.5 m, the movement of water, and with it salt, from the watertable into the rootzone is minimal (Grismer and Gates, 1988). Under these conditions, which applied in the field trial described in this thesis, irrigation was the major source of salt addition to the rootzone and drainage was the major mechanism responsible for its loss.

Measurement

The most widely used specification of salinity in irrigation water and water in the soil is the measurement of electrical conductivity (EC), in dS/m at 25°C (Ayers and Westcot, 1985). Soil water is extracted from a saturated soil paste. These measurements of water and soil are abbreviated as ECw and ECe, respectively. The popularity of EC measurements is based on their low cost and rapidity.

Measurements of EC neither quantify the total concentration of ions nor identify the ion species. In the United States of America, an extensive survey of saline soils and waters showed that the ion concentration in mequiv./L could be approximated by multiplying the EC in dS/m by 10 (USDA, 1954).

Other measures of soil salinity include those based on the conductivity of extracts from soil:water solutions in ratios 1:1 or 1:5, and that based on the percent salt in dry soil. These measures may not faithfully reflect the concentration of ions

in the soil solution in situ. Ions which have been removed from the soil solution by precipitation may be redissolved in 1:1 and 1:5 extracts and this leads to an overestimation of the ions present in soil solution. Soils have a five-fold variation in their water holding capacity. Because of this variation, measurements of salt content expressed as a percent of soil dry weight cannot be readily expressed as a concentration of salts in soil solution without further information on the water holding capacity of the particular soil. In addition, specification based on dry weight does not distinguish between soluble and insoluble forms of ions (USDA, 1954; Bernstein, 1975).

Sampling soil salinity

The grapevine excludes salts from the transpirational stream at its roots and in many commercial vineyards, where complete leaching of the rootzone is rare, salts accumulate in the rootzone raising the salt concentration of soil solution. Within the rootzone of a single plant, the salt concentration in the soil varies with depth and distance from the dripper or sprinkler (Groot Obbink and Alexander, 1977; Stevens and Douglas, 1994). This variation reflects a variation in the amount of water extracted by the plant from different depths of soil and a variation in the amount of leaching, which may change with the distance from the dripper or sprinkler and depth. Olsson and Rose (1988) showed under well-watered conditions that water uptake was proportional to root length density. A sampling procedure which characterises the salt concentration of the water bathing the plants roots must account for the variation within the rootzone of water uptake by the grapevine and of ECe. Ayers and Westcot (1985) proposed that a value which characterises the salt concentration of the water bathing the plants roots could be obtained by summing measurements of soil salinity at various depths after each was weighted to reflect the relative root length density at the respective depth.

In potted grapevines, the free-draining rootzones allows irrigation well in excess of the soil water deficit without risk of waterlogging. Under these conditions salts do not accumulate in the rootzone and the concentration in the soil solution is similar to that in the irrigation water.

Inter-conversion between measurements of soil and water salinities

Plants respond to the concentration of salts in the soil solution rather than the concentration in the irrigation water. Labour costs generated by the preparation of a saturated soil paste make the measurement of ECe more expensive than that of ECw. In the field, the soil water content is usually below that at saturation and the salt concentration greater than that at saturation. Relative to the ease with which a solution can be extracted from a saturated paste the sampling of soil water *in situ* is difficult and expensive. For these reasons, a set of empirical determined conversion factors have been developed to estimate the values of soil salinity from the measurement of ECw.

Ayers and Westcot (1985) suggested the ECe could be approximated from the ECw by multiplying ECw by 1.5 and that the concentration of the salt in soil water at a soil water content representative of the range in the field (ECsw) could be approximated from ECe by multiplying ECe by 2.0. As the suggested inter-conversion factors were not qualified with a time dependent function it must be assumed that they apply after changes in soil water have stabilised i.e. an equilibrium has established between the salinity of the irrigation water and soil.

In the field, Prior *et al.* (1992c) observed that the change in the concentration of salts in the soil lagged that in the irrigation water. Over a six years period they found application of irrigation water with an EC of 3.5 dS/m caused the ratio of ECe:ECw to rise steadily from 0.4 to 2.0. At the end of this period, L.D. Prior (pers. comm.) found that the ratio of ECe:ECsw was 2.6 which gives an ECsw:ECw ratio of 5.2. This value is the same as that assumed by Blesing and Tuffley (1977) to be applicable in the Riverland, but double that predicted by USDA (1954). Prior *et al.* (1992c) found the ratio of ECe:ECw was still rising at the end of the six years and therefore the value of 5.2 for ECsw:ECw is presumed to be an underestimate for equilibrium conditions.

These conversion factors do not apply to potted grapevines subject to high frequency irrigation where it is assumed that the ECsw in the pot is equivalent to

the EC of the irrigation water. For example, Downton (1985) suggested that frequent irrigation of potted grapevines with solutions containing chloride concentrations ranging from 12 - 75 mM would establish chloride concentrations in soil solution equating to those established under field conditions following irrigation with water in which the chloride concentrations ranged from 2 - 15 mM i.e. ECsw is about six times ECw.

2.1.2 Osmotic, toxic and nutritional effects of salinity

Osmotic effect - Definition and measurement of the components of water potential in the soil and plant

The concentration of salts in the soil water solution may be increased through the addition of soluble salts or the removal of water from the solution. An increase in concentration causes a decline in the osmotic potential of the soil water solution and this fall may decrease the potential of water in the plant. The decline in soil osmotic potential is referred to as the osmotic effect of salinity. It is caused by all ions regardless of whether they are toxic or non-toxic. The effect occurs without the ions entering the plant.

The osmotic effect is caused by changes in the potential of water in the soil. The water potential of a solution can be expressed as the sum of its component potentials.

$$\Psi = P - \pi + \tau + G$$

Where **P** is the pressure, π is the osmotic pressure, τ is the matric potential, and **G** is the gravitational potential (Nobel, 1983; Begg and Turner, 1976). When water is held in the matrix of an unsaturated non-swelling soil (such as found under good irrigation management in highland vineyards of the Riverland S.A.) **P** is considered

to be negligible. G is redundant where all measurements are made at the same altitude. Therefore

$$\Psi_s = \tau_s - \pi_s$$

where subscript 's' indicates that the terms refer to water in the soil.

Soil water potential can be decreased by either the addition of solutes, which changes the osmotic potential, or the extraction of water, which changes the matric and osmotic potentials (provided the amount of soluble salts per unit soil volume remains constant).

Matric potential is measured with a semi-permeable membrane, a tensiometer cup, to which a mercury manometer is attached (Slatyer, 1967). The osmotic pressure of a solution is calculated from measurements of the temperature at which it freezes or the vapour pressure of the atmosphere above it; both of these measurements of π_s require specialised equipment. It was found (USDA, 1954) that, in saturated soil paste extracts, and surface and well waters, the osmotic pressure could be approximated by the following equation:

$$\pi_s \text{ (MPa)} = 0.036 \text{ EC}$$

The osmotic effect of salinity is sometimes equated to the effect of soil drought. Both exert an effect on the plant without causing an increase in the plant content of specific ions and both have an identical effect on the Ψ_s, however Ψ_s is only one of the parameters which control the flux of water from the soil to the plant. Drought, but not salinity, also affects another parameter controlling this flux.

The flux of water from the soil to the plant is proportional to the difference in potential between the soil and plant and, the hydraulic conductivity of the soil (Gardner, 1964). A single order of magnitude change in τ equates to a change of four orders of magnitude in the hydraulic conductivity (Baver *et al.*, 1972), whereas

a single order of magnitude change in π has no effect on the hydraulic conductivity. Therefore based on a physical model of water movement into the plant, the salinisation of soil water does not equate to the depletion of soil water.

The flux of water from soil into the plant is proportional to the difference in potential between the soil and plant. A fall in Ψ_s reduces the magnitude of the difference and unless the plant compensates by also reducing its Ψ then the flux will fall. In plants, the general equation for the description of water potential is modified; τ is subsumed by measurements of π and **P** (Passioura, 1980; Nobel, 1983) and **G** is redundant where all measurements are made at the same height; the description for leaves is as follows:

$$\Psi_l = P_l - \pi_l$$

where subscript 'l' indicates that the terms refer to water in the leaf.

Leaf water potential is measured with a Scholander pressure chamber (Scholander *et al.*, 1965) which consists of a sealed chamber into which the leaf is inserted with its petiole protruding. Raising the pressure in the chamber until it is equal and opposite to Ψ_l causes sap to appear at the cut surface of the petiole. The Scholander pressure chamber can also be used to derive the osmotic potential of the leaf. A pressure-volume curve can be constructed by measuring the volume of sap exuded at each step in pressure above the balance pressure, and $\Psi_{\pi l}$ can be calculated from this curve assuming that the osmotic pressure of the xylem sap equals zero (Turner, 1981).

Osmotic effect of salinity in grapevines

After irrigating potted grapevines for one day with 25 mM NaCl, Downton and Loveys (1981) found the decline in Ψ_l was equivalent to the decline in the osmotic potential of the irrigation solution ($\Psi_{\pi w}$). Both Downton and Loveys (1981) and Walker *et al.* (1981) observed the response of the osmotic potential to salinity had stabilised within 10 days of salinising the substrate. The rapidity of stabilisation and the near one-to-one relationship between the change in Ψ_l and that in $\Psi_{\pi w}$ were

not unique. Downton and Millhouse (1983) found after 21 days of salinisation the ratio was two-to-one and by 45 days it was three-to-one. Differences between the studies may have arisen due to differences in the amount of leaching, and hence the concentration of salt within the rootzone or because of decreases in root hydraulic conductivity.

Prior *et al.* (1992b) observation that Ψ_l in mature grapevines was not affected by salinity contrasts with observations in immature grapevines. These grapevines had been irrigated with saline water (ECw 3.5 dS/m) for six years and the difference between the ECsw of the control and the salinised treatment was about 17 dS/m which is equivalent to a fall of about 0.5 MPa in the soil solution osmotic potential. With regard to the equation of Gardner (1964) describing the flux of water from the soil to the plant and from the plant to the atmosphere, if the conductances to the flow of water in these two sub-systems remain constant then flow within and between these sub systems is proportional to differences between the potential of water in the soil, plant or atmosphere. If the difference between the Ψ_{plant} and Ψ_s increase due to a fall in Ψ_s then unless Ψ_{plant} also falls by a similar amount the flux of water will be increased. The absence of such a fall in Ψ_{plant} suggests that the fall in the potential of water in the soil coincided with a fall in the flux which was probably due to a reduction in stomatal conductance and leaf area. Further its absence suggests that the long term adjustment of grapevines to constant salinity may not involve a response of cell growth to changes in Ψ_{plant}.

Cell expansion requires a positive P_l and as P_l falls so too does cell expansion (Bradford and Hsiao, 1982). A decrease in Ψ_l must be due to either a fall in P_l or an increase in π_l. A reduction in growth can be prevented by a increasing π_l by such an amount as to restore P_l. This process is known as osmotic adjustment and occurs rapidly in potted grapevines. Downton and Loveys (1981) showed within a few days of irrigation with 100 mM solution of chloride salts that the increase in π_l was equal to that in Ψ_l, and P_l recovered to that in the non-salinised treatments.

Saline conditions increase the uptake of Na and Cl by the grapevine. Both ions are highly soluble and therefore remain osmotically active once inside the grapevine. Downton and Loveys (1981) observed that the increase in **P** following salinisation could be accounted for by the osmotic contribution of increases in the leaf concentrations of Na and Cl. This contribution was in excess of that necessary to counter the fall in substrate osmotic potential and they suggested that salinisation of the substrate caused a decrease in other unidentified osmotically active solutes. Walker *et al.* (1981) found that irrigation with saline water caused a 1.3 MPa decline in Ψ_l and a 0.9 MPa fall in $\Psi_{\pi l}$. The fall in $\Psi_{\pi l}$ was insufficient to fully restore **P**. They also observed that the osmotic contribution of increases in the leaf concentrations of Na and Cl was more than sufficient to account for the change in turgor pressure. Both results suggest that uptake of Na and Cl was an adaptation to higher substrate salinity.

Toxic effect - definition

The rise in concentration of soil salts eventually overwhelms the plant's exclusion mechanism and ions enter the plant where they may reach a concentration that is toxic to the plant metabolism. The negative effect that the increase in tissue concentrations of such ions has on plant metabolism is referred to as the toxic effect of salinity. In contrast to the osmotic effect, the toxic effect only occurs after these ions enter the plant. Chloride ions is considered to be toxic for fruit crops at low tissue concentrations i.e. above 85 mmol/kg dry weight in the leaf (Ayers and Westcot, 1985).

There are different perspectives on the action of salinity on the plant. Greenway and Munns (1980) questioned the occurrence of toxicity caused by a specific ion and suggested that the toxic response was due to an excess of ions independent of the ion species. They described the effect as a 'ion excess'. They suggested the occurrence of ion excess explained the decline in growth of plants growing in solutions with excessive concentrations of soluble salts relative to that of those in solutions with iso-osmotic concentrations of inert osmotica. Bernstein (1975) supported an alternative view that specific ions are toxic to the plant

metabolism. He argued that experiments with inert osmotica cannot distinguish osmotic effects from specific ion effects because inert osmotica has been found to both stimulate and suppress growth relative to iso-osmotic solutions of soluble salts i.e. inert osmotica was not inert. The divergence of views may have been due to the use of different experimental material by the two proponents. Bernstein (1964) studied fruit crops and found that they had a specific sensitivity to chloride and sodium ions which distinguished them from vegetable, forage and field crops. Greenway and Munns (1980) studied annual crops which they concluded did not exhibit specific ion toxicity. In agreement with Bernstein (1975) they acknowledge that an ion excess in fruit crops may be due to the toxic effects of sodium and chloride.

Toxic effect - Uptake of Na and Cl by the grapevine

When grapevines are exposed to a saline substrate the tissue concentrations of ions associated with salinity increase. The nature of the relationship between the ion concentration in the grapevine and that in the substrate has been investigated over substrate concentrations of NaCl ranging from 0 to 150 mM. The investigations show the relationship between tissue concentrations of Na and Cl and concentrations in the substrate follows an asymptotic form. In the first third of this range, the increase in leaf lamina, petiole, cane and juice concentrations of sodium and chloride is directly proportional to increases in substrate concentration. At higher levels of salinity, increases in tissue concentration diminishes with increasing substrate concentration until they reach zero which coincides with the death of the organ (Prior *et al.* 1992b; Joolka *et al.* 1977; Taha *et al.* 1972; Thomas, 1934).

Alexander and Woodham (1968) reported that root chloride concentration underwent the greatest increase between the 0 and 25 mM substrate concentrations, whereas the greatest increase in leaf levels occurred between the 50 and 100 mM step. This suggests that Cl must reach a threshold concentration in the roots before it moves to the shoot.

The above studies analysed tissue concentrations at harvest after a sustained period of exposure to salinity. They do not provide direct information on the dynamics of Na and Cl accumulation.

In a short term experiment on immature Cabernet Sauvignon grapevines, Downton (1977b) found that the sap bleeding from decapitated grapevines only rose above 4 mM when the NaCl concentration in the irrigation water was above 25 mM. Shoot growth declined when the NaCl concentration in the sap was greater than 4 mM. These results suggest that below a threshold in substrate concentration of NaCl the grapevine can prevent NaCl moving into the shoot.

The roles of passive and active transport in the movement of Na and Cl within the grapevine are unclear. The reduced rates of accumulation of Na and Cl in the grapevine as substrate Na and Cl concentrations rise into the high end of the range may be due to an associated decrease in transpiration caused by the soil osmotic effect i.e. soil drought. This association suggests that Cl is passively transported in the xylem. If so then the rate of chloride accumulation should accelerate as transpiration increases. In practice the opposite occurs with the rate of increase in the sodium and chloride content of the petiole and lamina declining as the season progresses from spring to late summer i.e. with increasing atmospheric evaporative demand and hence transpiration (Prior *et al.* 1992b; Woodham, 1956). Chloride accumulation in the leaf is not due solely to passive deposition at the end of the xylem pathway.

The temporal pattern of change in the concentration of chloride in the berry contrasts with that of the leaf. In fruiting grapevine rootlings, Downton and Loveys (1978) reported that the rate of increase in chloride concentration was much greater in the latter half of summer (after veraison) than in spring and early summer. Berry transpiration falls after veraison (Düring and Oggionni, 1986). If chloride accumulation was due to passive deposition then the fall in transpiration combined with a continuing increase in berry volume should slow the rate of increase in Cl concentration in the berry. The rate of increase in Cl concentration accelerates after

veraison which suggests that, as for the leaf, Cl accumulation is not due solely to passive deposition at the end of the xylem pathway.

Lee (1990) suggests that one of the causes of higher Cl in Australian wines relative to those of northern Europe was the greater water use by the grapevine in Australia's hotter climate. This suggestion does not align with the observation that the major accumulation of Cl in the berry occurs whilst berry transpiration is reduced.

In grapevines grown on substrates where sodium and chloride were present in equi-molar concentrations the tissue concentrations of these ions were not equi-molar. In mature grapevines, Prior *et al.* (1992b) found concentration (mmol/kg) of chloride in leaf lamina and petiole was 1.5 fold that of sodium. In immature grapevines, Ehlig (1960) showed that the chloride concentration of the lamina was 4-10 fold that of sodium. In general, tissue chloride concentration was greater than that of sodium. Boland *et al.* (in press) thoroughly investigated the Na to Cl ratio in salinised peach trees. They also found that the ratio of Na to Cl was below unity in all tissue, except in wood of the trunk where it was greater than ten.

Downton (1977b) found that the ratio of Na and Cl in grapevine tissue changed with the length of exposure to salinity. He found that petiole and lamina sodium concentrations did not increase until the chloride concentrations had reached, respectively, 570 and 230 mmol/kg d.w.. A similar finding in mature plums prompted Hoffmann *et al.* (1989) to propose that the ability of tissues to exclude sodium was destroyed at high tissue concentrations of chloride.

Neither chloride nor sodium accumulation is due solely to passive transport with the transpiration stream. Rates of accumulation do not correlate with transpiration. More chloride is transported to the leaf than sodium. With short exposures the grapevine has a buffering capacity that can prevent a rise in the chloride level of metabolically active tissue such as the leaf. These differences

suggest that chloride and sodium accumulation are under different control mechanisms.

The tissue concentrations of ions associated with salinity have a potential diagnostic value. Before establishing the critical concentration, which indicates the onset of damage, other sources of variation in concentrations had to be removed. Within a single grapevine the concentration of sodium and chloride varies with the type and physiological age of the organ (Woodham, 1956). Workers dealing with grapevine nutrition faced a similar dilemma and they identified the petiole opposite the adaxial bunch sampled at full-bloom as exhibiting nutrient levels which were representative of vineyard nutritional status (Christensen, 1969; Robinson *et al.* 1982). Prior *et al.* (1992b) found the sodium and chloride concentration in this sampling unit accounted for the variation in yield of grapevines salinised in the field. In petioles sampled in November (at full-bloom) from own-rooted Sultana they concluded that concentrations of Na and Cl greater than 217 and 423 mmol/kg, respectively, were associated with poorer growth.

Distribution of Na and Cl amongst organs of the grapevine

In mature grapevines, petiole chloride and sodium concentrations, expressed on a dry weight basis, were two times those in the lamina and 10-15 times those in the cane (Woodham, 1956; Prior *et al.* 1992b). In immature grapevines, the petiole sodium and chloride concentration was equivalent to that in the roots. The petiole chloride was 1.5-3 times that in the lamina, and 3-10 times that in the stem. The petiole sodium concentration was 2-10 times that in the lamina, and 4-10 times that in the stem (Downton, 1977a; Downton, 1985; West and Taylor, 1984). The apparent differences amongst organs may depend on the mode used to express the concentrations of elements.

In immature grapevines, the ratio of root:stem:lamina chloride concentrations expressed on a fresh weight basis was 1:1.1:1.3. This compares to a ratio of 3.2:1:1.4 expressed on a dry weight basis (Downton and Hawker, 1980).

Differences between organs in the concentration of elements has led to the formation of propositions regarding the role organs play in controlling the movement of ions. In grapevines grown under non-saline conditions, Downton (1977c) found that the concentration of Cl in the leaf petiole, expressed on a dry weight basis, was greater than that in the leaf lamina. Based on this observation, he proposed that the petiole acts as a reservoir for surplus ions permitting the lamina to maintain lower levels of chloride. With grapevines grown under saline conditions, Prior *et al.* (1992b) also reported that the petiole concentration of chloride was much higher than that of the lamina when expressed on a dry weight basis, but when expressed on a fresh weight basis the concentration was slightly less. This finding did not support Downton's (1977c) proposition, but it is possible that the proposed mechanism only operates under non-saline conditions where the chloride load is low.

Toxic effect - effects of cultivar and rootstock

Comparison amongst own-rooted cultivars shows that the chloride concentrations in juice, leaf lamina and petiole and cane, and the sodium concentrations in leaf petiole and cane may vary two-fold across cultivars growing on substrates with equivalent salt concentrations (Ravikovitch and Bidner, 1937; West and Taylor, 1984; Ehlig, 1960).

In Sultana scions, Downton (1985) showed that amongst four rootstocks and own-rooted grapevines, sodium and chloride concentrations of the Sultana scion underwent a 4, 2 and 1.5 fold variation in, respectively, lamina, petiole and canes. He found that Ramsey, the rootstock used in the present study, was a good excluder of chloride.

In field grapevines growing under non-saline conditions, Downton (1977c) reported that the petiole sodium concentration in Shiraz on its own roots was higher than in Shiraz on Harmony rootstock, but in Cabernet Sauvignon the converse prevailed. These results suggest that the petiole concentrations of Na and Cl are affected by interactions between cultivar and rootstock.

The response of grapevine growth under saline conditions was also modified by cultivar and rootstock, but growth was not necessarily proportional to tissue Cl concentration e.g. Downton (1985).

Chloride or sodium?

In grapevines growing in a sand culture, Ehlig (1960) investigated the association between appearance of leaf damage and the presence of chloride and sodium in the leaf and substrate. The treatments consisted of irrigation with iso-osmotic solutions of $CaCl_2$, NaCl, Na_2SO_4 and mixed salt solution consisting of $CaCl_2$ and NaCl. Leaf damage and yield were measured. Based on an association between chloride in the substrate and leaf damage Ehlig (1960) concluded that chloride was the toxic ion, however he made no conclusions regarding the effect of salinity on yield.

In salinity studies on mature field grown grapevines, the tissue chloride concentrations have been measured more often than tissue sodium concentrations. In studies where only the tissue concentration of Cl was measured, within the same cultivar-rootstock combination the vigour ratings based on yield and vegetative growth were negatively associated with chloride concentration (mmol/kg d.w.) of the leaf, annual wood and fruit (Thomas, 1934; Woodham, 1956). In studies where both tissue Na and Cl have been measured, increases in both were associated with decline in vigour rating (Ravikovitch and Bidner, 1937; Prior *et al.*, 1992b).

In addition to the use of substrates with iso-osmotic concentrations of different ion species, the tissue concentrations of Na and Cl can also be separately manipulated by the use of rootstock with differing ion exclusion characteristics. Downton (1985) salinised Sultana scions on a range of such rootstocks. The differences in the growth amongst rootstocks could not be accounted for as a function of either leaf sodium or chloride concentrations.

In grapevines, it is still unclear whether the loss of growth is due to the action of Na or Cl or of both Na and Cl.

Nutritional effects

Salinity may also cause an imbalance in plant nutrition when an excess of specific ions in either the soil or the plant cause a change in the availability or distribution of nutrients. Whilst there are many reports associating a decline in the growth of plants with osmotic and toxic effects of salinity, reports associating a decline in growth with salinity induced nutrient imbalances are fewer in number. The most commonly mentioned nutrients are potassium, nitrate and phosphorus (Bernstein and Hayward, 1958; Bernstein, 1975; Gorham *et al.* 1985; Marschner, 1986).

In grapevines, reports on the effects of salinity on the tissue concentrations of macronutrients are conflicting. In immature glasshouse grown grapevines, leaf macronutrient concentrations responded as follows: phosphorus and potassium either increased or decreased; calcium increased or did not respond; magnesium increased, decreased or did not respond and nitrogen decreased or did not respond (Downton, 1985; Joolka *et al.*, 1977; Sourail *et al.*, 1985; Taha *et al.*, 1972). Downton (1985) found the effect of salinity on nutrient levels was the same for lamina and petiole. These reports did not attribute changes in metabolism or growth to changes in tissue concentrations of macronutrients.

In the sole study on mature grapevines, Prior *et al.* (1992b) observed that the effects of salinity on the leaf concentrations of macronutrients were not consistent from year to year. Salinity caused a decline in potassium levels in the petiole in all years but only in two of four years in the lamina; decreased petiole phosphorus in three of four years but did not affect that in the lamina; increased magnesium in the lamina, but in the petiole it was either unaffected, increased or decreased; calcium in the lamina and petiole was, in different years, either decreased, increased or unaffected.

Robinson *et al.* (1982) related vineyard performance to petiole concentration of nutrients at full-bloom. The nutritional status of vineyards was classified as deficient, adequate or excessive/toxic with regard to each nutrient. Prior *et al.*

(1992b) reported that saline irrigation (ECw 3.5 dS/m) lowered the concentration of phosphorus in the petiole into the deficient range, but did not affect the concentration in the lamina. The contention that the effect of salinity on petiole phosphorus indicates a nutritional deficiency can be countered by the absence of an effect on the phosphorus levels of the metabolically more active tissue, the lamina. Prior *et al.* (1992b) did not attribute any of the changes in growth or metabolism to changes in tissue concentrations of macronutrients. The response of mature grapevines to salinity is probably not due to nutrient deficiency.

Salinity - Toxic or osmotic effect?

In mature grapevines fruit production ceased at petiole chloride levels of 705 mmol/kg d.w., and at cane levels of 186 mmol/kg d.w. the grapevines were dead (Woodham, 1956; Thomas, 1934). In contrast, growth has been reported from immature grapevines growing in a glasshouse with petiole chloride levels at 1185 mmol/kg d.w. and cane levels of 423 mmol/kg d.w. (Alexander and Groot Obbink, 1971). Immature grapevines grown in glasshouse can continue to grow at chloride concentrations which kill grapevines growing in the field. The differences in response may be due to differences in climate. The observations in the field were made in a semi-arid climate with high temperatures and low humidity, whereas in the glasshouse temperature was generally controlled to remain below 30°C. Bernstein (1961) demonstrated that in a moderate climate the plant can tolerate a higher salinity in irrigation water and Bernstein (1964) put forward the general observation that for a given substrate concentration salinity damage was worse the hotter and more arid the climate. This suggests that the grapevine should be less sensitive to salinity when grown in the glasshouse.

Prior *et al.* (1992b) noted that the onset of leaf necrosis was not associated with a particular tissue concentration of chloride, rather it was associated with the onset of hot dry weather with the maximum temperatures reaching above 35°C.

Greenway and Munns (1980) see the increase in sensitivity of plant growth to salinity with decreasing relative humidity as evidence that water relations are involved in the plant response to salt stress.

Walker *et al.* (1981) and Downton and Loveys (1981) showed that whilst the initial decline in grapevine photosynthesis was associated with a fall in Ψ_l and increases in leaf chloride concentration, the continuing decline was associated with increasing chloride concentration but no change in Ψ_l. Following irrigation with non-saline water, Walker *et al.* (1981) observed that the recovery of photosynthesis followed recovery of Ψ_l and occurred even though tissue chloride levels remained high. These results show that rise in toxic ions and fall in Ψ_l were associated with the onset of the effect of salinity, whereas recovery from salinity proceeded without a large fall in the toxic ion levels in tissue.

In contrast to findings in immature potted grapevines, Prior *et al.* (1992b) observed in field grapevines, which had received saline irrigation for six years, that leaf photosynthesis declined with increasing chloride concentration even though Ψ_l was unaffected.

There is insufficient knowledge to apportion the relative contributions of both effects to the decline in growth. Salinity produces a change in soil and tissue levels of salt and tissue nutrients. As the absence of a reduction in Ψ_l does not indicate an absence of change in Ψ_s nor does the presence of high levels of Cl necessarily indicate Cl toxicity.

2.1.3 Effects of salinity on the grapevine growth

Visual

The visual symptoms of grapevine decline associated with high levels of total soluble salts in the soil have been thoroughly described by Thomas (1934), Ravikovitch and Bidner (1937) and Woodham (1956) and include reduced leaf size, necrosis and abscission of leaves, desiccation of fruit, and failure of fruit and annual

wood to mature. Their occurrence was associated with an increase in the tissue or soil level of chloride and sodium. These observations were made after the symptoms presented. As a consequence the reports were not accompanied by information on either the length of exposure to salinity prior to appearance of the symptoms or the level of salinity. Subsequent experiments have shown that salinity had the least effect on growth of organs in which the symptoms were the most obvious.

Reports of an association in grapevines between leaf necrosis and chloride have been based on chloride concentrations measured in the whole leaf. Initially necrosis occurs first at the leaf margins. In strawberries, Bernstein (1975) divided the leaves of salt affected strawberries into necrotic and non-necrotic regions. He found that the chloride concentrations of both regions were similar.

Photosynthesis

In both immature glasshouse grown and mature field grown grapevines, leaf photosynthesis was negatively correlated with the concentration of chloride in the leaf lamina. In both types of grapevine the slopes of the regression equations describing these relationships were similar (Prior *et al.* 1992b; Downton, 1977a).

Downton (1977a) proposed that the decline in photosynthesis observed in salinised grapevines was caused by reductions in both leaf stomatal and mesophyll conductances. Walker *et al.* (1981) ascribed the decrease in mesophyll conductance to an increase in photorespiration on the basis of a comparison between the photosynthetic rates in atmospheres with 2% and 20% oxygen. Downton *et al.* (1990) showed that an apparent decrease in the mesophyll conductance may also be generated by patchy stomatal closure and explained the observations of Walker *et al.* (1981) with regard to the effect of salinity on photorespiration as a consequence of patchy stomatal closure.

At leaf chloride concentrations below 150 mM (about 600 mmol/kg d.w. with a fresh weight to dry weight ratio of 4:1), Walker *et al.* (1981) and Downton

et al. (1990) observed that the effect of saline irrigation on photosynthesis was due entirely to decreases in stomatal conductance.

After raising the NaCl concentration in irrigation water from 0 to 90 mM over a four day period, Walker *et al.* (1981) observed a fall in both stomatal conductance and photosynthesis. When the salinity of the irrigation water was only raised to 25 mM Downton and Loveys (1981) found that 25 days had to elapse before stomatal conductance fell. Walker *et al.* (1981) demonstrated that photosynthesis could fully recovered if saline irrigation was replaced with non-saline at leaf chloride levels below 550 mmol/kg d.w.. At leaf chloride concentrations less than 225 mmol/kg recovery occurred after five days of non-saline irrigation, whereas at a level of 425 mmol/kg it took 25 days. The greater the change in substrate salinity the faster the decline in leaf photosynthesis and the lower the leaf chloride the more rapid the recovery following application of saline irrigation. This suggests that grapevines on chloride excluding rootstocks may recover from transient salinisation quicker than those on rootstocks which do not exclude chloride or on their own roots.

Prior *et al.* (1992b) claimed that the primary reason for yield reduction in salinised field grapevines is the decline in leaf photosynthetic rates. They observed that leaf photosynthesis fell as lamina chloride concentration increased and that the relationships between photosynthesis and lamina Cl were similar in field and glasshouse grown vines. If the decline in photosynthesis is the major cause of growth loss then in field and glasshouse grown vines with comparable levels of tissue Cl the growth losses should be similar. Observations on growth and tissue Cl levels shows that this is not the case. For example, field grown vines were dead at cane Cl concentration of 186 mmol/kg d.w., whereas in glasshouse grown vines growth continued at a cane Cl concentration of 423 mmol/kg d.w.. The disparity between the insensitivity of photosynthetic rates to growth conditions and the sensitivity of growth to these conditions suggests it is unlikely that the effects of salinity on growth can be explained by changes in leaf photosynthetic rates.

In immature vines, Downton (1977a) observed that salinity caused a fall in the total leaf carbohydrate. Similarly, Prior *et al.* (1992b) showed that salinity reduced the levels of starch and total carbohydrates in canes of mature grapevines. In both tissues, the level of reducing sugars increased suggesting a change in carbohydrate metabolism.

Vegetative growth

In immature grapevines, Alexander and Woodham (1968) found with four cultivars that the total grapevine mass declined linearly with increasing irrigation water salinity (range 0 - 125 mM). In six cultivars, West and Taylor (1984) observed that the rate of decline in shoot length slowed with increasing salinity (0 - 90 mM). With four different rootstocks, Downton (1985) showed that the rate of decline in cane mass was either constant or slowed with increasing salinity (0 - 75 mM).

Alexander and Woodham (1968) found that the rate of decline in the shoot growth was much greater after 4 weeks exposure than after only two. Over a 40 day period, Downton (1977b) found that the decline in shoot growth only occurred when the sap chloride concentration rose above 4 mM and that a period of 40 days exposure to 25 mM NaCl was insufficient to cause sap chloride to rise above 4 mM. Results from short term experiments support the existence of a threshold in growth response to salinity.

In immature grapevines irrigated with 90 mM NaCl, Walker *et al.* (1981) demonstrated that shoot growth rate could be restored to that in the non-saline control grapevines provided non-saline water was applied within 28 days after commencing saline irrigation. This finding suggest that vegetative growth can fully recover from a moderate duration of exposure to salinity.

In mature field grapevines, Prior *et al.* (1992a, 1992b) found pruning weights declined with increasing irrigation water salinity (0.4 - 3.5 dS/m). The decline was not linear: in light textured soils it was greater at high salinities and in

heavy textured soils it was greater at low salinities. Whilst there was no evidence for the existence of a threshold ECw below which growth did not respond, the decline in growth did not occur until the second year of exposure. This lag in response may equate to a concentration threshold. It may be due to the buffering effect that non-saline water in the soil of the rootzone has on changes in irrigation water salinity. Until most of the rootzone is salinised the grapevine can avoid salinity by preferentially extracting water from zones of low salinity (Shani *et al.*, 1993).

Within the grapevine, organs display differences in the sensitivity of growth to salinisation of the rootzone. In Sultana receiving saline irrigation water (ECw 3.5 dS/m), Prior *et al.* (1992b, 1992c) found the proportions of the mass of fruit, prunings (stem) and roots was 54, 40 and 25% respectively of the mass in the non-salinised control. Observations in immature glasshouse grown grapevines contrast with that in the field. In a collection of four grapevine cultivars, Alexander and Woodham (1968) found at a salt concentration of 50 mM the masses of leaf, stem and root were 71, 35 and 76 percent of the control. In Cabernet Sauvignon, Downton and Hawker (1980) found at the same concentration the masses of leaf, stem and root were 48, 63 and 58 per cent of the control. In the glasshouse the most sensitive organ was the shoot, whereas in the field it was the root.

In mature grapevines, each organ grows for only a particular period(s) within the season. The apparent differences in the sensitivity of organs may reflect differences in the opportunities available for the grapevine to avoid salt stress during particular periods within the season. In the Riverland, for example, the season often opens with the soil profile partially filled by non-saline winter rains. This soil store provides grapevines receiving saline irrigation with an opportunity to draw water from a non-saline reservoir. As this reservoir is drawn down the opportunity for the grapevine to avoid salinity diminishes. This stress avoidance opportunity is likely to be most favourable to organs which grow early rather than late in the season e.g. primary shoots compared with fruit.

Alexander and Woodham (1968) investigated the between-cultivar differences in the growth of immature grapevines irrigated with 75 mM NaCl. The growth of Gordo, the least tolerant variety, declined by 55%, whereas the growth of Currants, the most tolerant variety only declined by 25%.

With immature Sultana scions on four rootstocks and own-roots, irrigated with a 75 mM solution of mixed chloride salts, Downton (1985) found the cane dry weight was reduced to 36% and 23% of the control in the most (Ramsey) and least (1613) tolerant rootstocks, respectively. The response of vegetative growth to salinity is modified by rootstock and cultivar.

Fruit Growth and Composition

Over a six year period, Prior *et al.* (1992a) investigated the yield response of own-rooted Sultana grapevines to irrigation with waters in which the salt concentrations ranged from 0.4 to 3.5 dS/m. In each treatment the salinity was kept constant for the entire duration of the experiment. They found yield declined with increases in ECw above 0.4 dS/m, with increases in the soil between depths of 60 and 90 cm above 19% silt plus clay and with increasing length of exposure to salinity.

Yield per grapevine is the product of the number of grape bunches per grapevine, berries per bunch, and berry weight. Prior *et al.* (1992a) found that the reduction in yield caused by salinity was due mainly to a reduction in bunch number. This was due primarily to a reduction, in the season preceding yield expression, in the number of shoots suitable for retention as canes. The yield was directly dependent on the vegetative growth of the grapevine.

In small fruiting grapevine rootlings, Hawker and Walker (1978) found that the effects of salinity on number of berries per bunch and the berry weight was dependent on the timing of saline irrigation. Commencing irrigation with saline water (50 mM NaCl) 10 days prior to full-bloom significantly reduced berry set and

weight, to 66% and 33% of that in the non-salinised control, whereas commencing it 10 days after full-bloom had no effect.

Salinity also affected the composition of the fruit. In Sultana grapevines, Prior *et al.* (1992a) found the TSS of grape juice was unaffected in the first four years of a six year trial and declined in the last two years. Juice titratable acidity was unaffected by salinity in the 6 years of the trial, excepting those grapevines on the heaviest soils (silt plus clay fraction of 28% or more). On these soils, acidity was increased by salinity in 5 out of 6 years.

In fruiting rootlings of Cabernet Sauvignon, Downton and Loveys (1978) found that salinity advanced grape maturity. A comparison between berries with the same concentrations of reducing sugars showed that salinity had no effect on the grape juice titratable acidity content. With similar material, Hawker and Walker (1978) found the response of berry reducing sugars concentration to salinity depended on when saline irrigation (20-50 mM NaCl) commenced; if it began 10 days before full-bloom then the concentration was reduced, but if it began 10 days after full-bloom there was no effect. Based on these observations, the sensitivity of two of the three yield components and berry composition to salinity was greater before full-bloom.

After four years of saline irrigation using water with an EC greater than or equal to 2.7 dS/m, Prior *et al.* (1992a) found the concentration of chloride in grape juice exceeded 17.5 mM. It is likely that wine made from such grapes will also have a high concentration of Cl. Wine with a chloride concentration, expressed as sodium chloride, greater than 17.5 mM cannot be sold in some overseas markets (Lee, 1993).

2.1.4 Modelling Yield Response to Salinity

Maas and Hoffmann (1977) modelled grapevine yield decline in response to salinity as a bent stick model (Figure 1). The model has two important

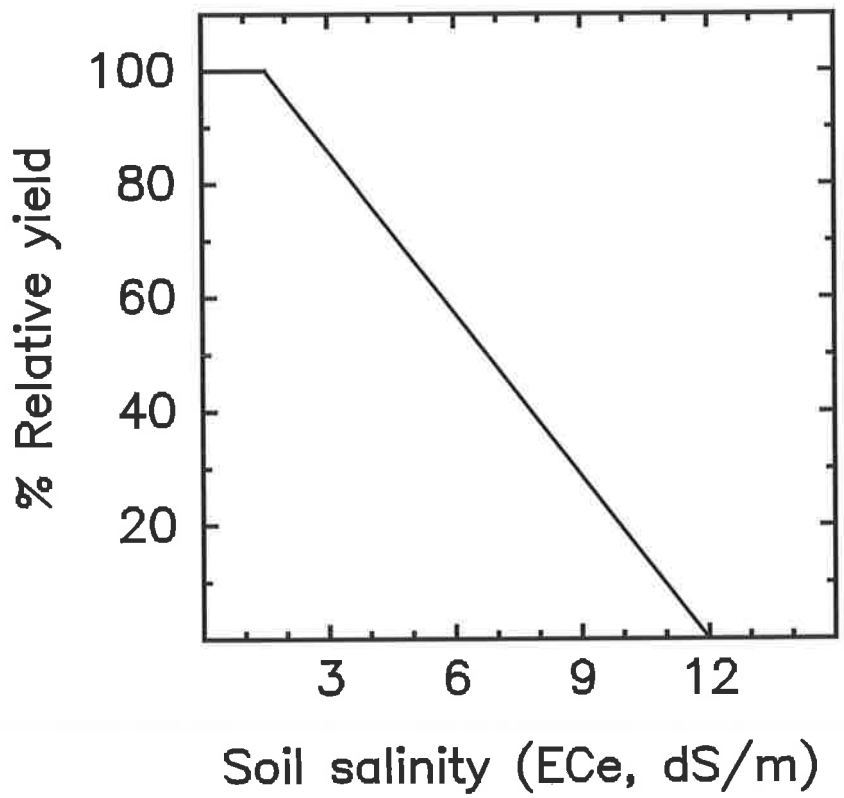

Figure 1. Bent stick model of grapevine yield response to soil salinity [after Maas and Hoffmann (1977)].

characteristics, a threshold and a slope. The threshold was the ECe below which no yield loss would occur. For grapes this was set at an ECe of 1.5 dS/m. The slope specified the rate of decline in yield for increased in ECe above the threshold. For grapes yield declined at 9.6% per dS/m increase in ECe.

The model was derived from reports of Nauriyal and Gupta (1967), Taha *et al.* (1972) and Groot Obbink and Alexander (1973) on short term studies of the response of the vegetative growth of immature potted grapevines to salinity, and from unpublished reports. None of the published works report values of ECe. It is likely that Maas and Hoffmann (1977) assumed that the ECe of potting mix was equivalent to the EC of irrigation water (ECi). The threshold value was probably based on the work of Taha *et al.* (1972) or unpublished work, as the increments of salt addition in Groot Obbink and Alexander (1973) were too great to establish a threshold, and Nauriyal and Gupta (1967) reported salt concentrations as a percent dry weight of soil. Taha *et al.* (1972) found the vegetative growth declined when the irrigation water salt content was greater than 1000 ppm (ECi about 1.6 dS/m). The nature of the relationship between published works and the slope is unclear.

Ayers and Westcot (1985) restate the model in terms of ECi by assuming the ratio ECi:ECe was 1.5:1. They predict the yield of grapevines on chloride excluding rootstocks will not decline until ECi rises above 1 dS/m. Above 1 dS/m, they predict a 10% yield loss will be sustained for every 0.7 dS/m rise in ECi. They did not consider how to integrate the effective rainfall received during the growing season into their model.

Both models were presented in reports which drew heavily on work conducted by the United States Department of Agriculture Salinity Laboratory. This laboratory based their investigation of crop response to salinity on growth of plants in a sand culture e.g. Ehlig (1960). In sand culture, the salinity of the substrate is brought rapidly into equilibrium with that of the irrigation water. The models applied to conditions where the soil has come to equilibrium with the salinity of irrigation water. Neither report considered the dynamics of the growth response

whilst an equilibrium was developing between the salt concentrations in the soil and water, and, therefore, they did not predict a time lag between the salinisation of irrigation water and a decline in yield.

Two assumption are implicit when these models are used to estimate the yield response of mature grapevines to salinity. It is assumed that the salt concentration in the soil and irrigation water have reached an equilibrium and that the sensitivities of vegetative and fruit growth to salinity are equivalent.

Over six seasons, Prior *et al.* (1992a) investigated the yield response of mature Sultana grapevines to irrigation water in which the ECi ranged from 0.4 to 3.5 dS/m. They found yield decline could be described as a logistic function of ECi and soil texture. In lighter soils (19% silt plus clay), the rate of yield decline increased with increasing ECi - a response similar to that found in systems which do not respond below a certain threshold. In heavier soils (28% silt plus clay), the rate of yield decline slowed with increasing ECi - a response which suggests that the system had no threshold or that the threshold was below the treatment with the lowest ECi i.e. below an ECi of 0.4 dS/m.

Prior *et al.* (1992a) found the decline in yield produced by irrigation water with an ECi of 2.2 dS/m increased from 10% in the second year of treatment to 30% in sixth year. Over the same period irrigation with saline water of ECi 3.5 dS/m increased the ECe from 2.5 to 7.0 dS/m (Prior *et al.*, 1992c). After six years, an equilibrium between the soil and water salinities had not been reached.

Prior *et al.* (1992a) compared their results for the second,fourth and sixth seasons of saline irrigation with the loss estimates of Ayers and Westcot (1985). They found that Ayers and Westcot (1985) underestimated the losses and that the divergence between their results and the estimated losses increased with successive seasons of saline irrigation. These results were unexpected for two reasons. The estimates of Ayers and Westcot (1985) were based on vegetative growth which Prior *et al.* (1992a) found to be more sensitive to salinity than fruit growth, and,

therefore, the Ayers and Westcot (1985) model should have over-estimated rather than under-estimated losses. Ayers and Westcot (1985) had described the response for an equilibrium situation. With successive seasons of saline irrigation, it would be expected that the salinity of the soil would advance toward an equilibrium with that in the irrigation water, and the yield response would converge with the estimates developed for an equilibrium situation, rather than diverge.

Ayers and Westcot (1985) nominate either ECi or ECe as inputs to their model. Prior *et al.* (1992a) used ECi as the input to the model of Ayers and Westcot (1985). Prior *et al.* (1992c) found ECe increased with length of exposure and had they used ECe as the input to the model then the divergence between estimates and their results would not have increased with successive years of exposure. It is unlikely that Ayers and Westcot (1985) envisaged an input of ECe as acting to account for the cumulative effects of long exposures. They nominated the inter-conversion between ECe and ECi as fixed which suggests that they envisaged their model as applying to conditions where an equilibrium existed between the salt concentration in the soil solution and in the irrigation water. Prior *et al.* (1992c) found that over a period of six years the ratio of ECe to ECi was not fixed and increased with time.

Prior *et al.* (1992a) findings demonstrate that the two assumptions underlying application of the model of Ayers and Westcot (1985) to the prediction of the response of mature grapevines were not met after six years of saline irrigation. In addition, their findings also confirm those in other studies on immature grapevines, e.g. Downton (1985), that the response of grapevine growth to the salt concentration in soil or irrigation water could be described as a continuous function with no clear threshold. However, Prior *et al.* (1992a) did observe a lag in the response of growth to saline irrigation.

Prior *et al.* (1992a) found that the yield and pruning weights of the treatments irrigated with 3.2 and 1.2 dS/m water did not decline in the first year. This suggests that the threshold for yield response lies above the salt load

represented by one year of irrigation with 3.2 dS/m water which is equivalent to about three years irrigation with 1.2 dS/m water. However, in the second season, saline irrigation with 1.2 dS/m caused yield and pruning weights to decline. These results suggest that loss of growth to salinity could not be explained by specifying the threshold as a particular salt load i.e. a function of ECi and time. This specification of threshold ignores other factors which may ameliorate the effects of saline irrigation.

The lag in the response of growth to saline irrigation could also be envisaged as evidence of a threshold below which the rate of an unidentified process is insufficient to affect growth. Storage tissue within the grapevine may act as a buffer between the rise of salt in the grapevine roots and its rise in metabolically active tissue, with the process being the uptake of ions at a rate sufficient to saturate the pools within metabolically inactive tissue into which toxic ions are sequestered. The soil may buffer changes in ECi, with the process being the addition of salt to the rootzone at a rate sufficient to entirely salinise it under the prevailing rainfall and evaporation regime.

West (1986) suggests that toxic ions may accumulate in metabolically inactive storage and structural organs prior to movement into metabolically active organs. In immature grapevines, at bud-burst the mass of the potential storage tissue, cane and roots, is only 20% of the mass that is accrued by the subsequent season's growth (Stevens, unpublished data). In contrast, at bud-burst in fruiting grapevines grown in sand culture the mass of potential storage tissue, root, trunk, arms and canes, is about 50% of the vegetative mass at harvest (Conradie, 1980). Grapevines with greater proportions of storage tissue could be expected to have the greater lag in their response.

With Ramsey rootstocks the depth of the rootzone may reach 2 metres (Stevens and Douglas, 1994). At field capacity, 2 m of rootzone soil holds 480 mm of water. This volume is about half of the grapevine's seasonal water requirement. In the major irrigation area of Australia, the Murray River, the salinity of irrigation

water varies across the season. The season often opens with the soil profile replenished by winter rains. Once irrigation commences, the rate of change in the salinity of rootzone soil solution is dependent on the ratio of the accumulated volume of saline irrigations to the volume of soil water. This relationship is further modified whenever irrigation is replaced by rainfall. The effectiveness of a large rootzone acting as a buffer to saline irrigation depends on how frequently it is renewed by flushing rains or a cyclic reduction in ECi.

If the process responsible for the lag was based on sequestration of toxic ions in metabolically inactive tissue then as this tissue is perennating the process could be expected to be limited by the size of the pool. In contrast, if the process responsible for the lag was based on a large rootzone buffering the changes in ECi then where rains are sufficiently frequent and the oscillation in ECi sufficiently regular the regeneration of the capacity of the buffer is likely to be limitless.

Modelling of the response of grapevine growth to salinity has only addressed situations where the salinity of the irrigation water has remained constant across the entire season. These models probably do not apply where the salinity of the irrigation water varies across the season; for instance, yield sensitivity to salinity in field crops was strongly dependent on the crop growth stage at which the saline water was applied e.g. Lai (1985).

2.2 GRAPEVINE GROWTH AND DEVELOPMENT

2.2.1 Definition of growth

Morphogenesis, the development of the grapevine and its constituent organs, involves the processes of differentiation and growth. Differentiation refers to a change from the simple to the complex and it is most evident at the process of cell division when the undifferentiated cells of meristematic tissue divide and differentiate into the cells of the different tissues found in mature organs. Following division, cells undergo growth which is an increase in mass and linear dimensions (Salisbury and Ross, 1969).

The grapevine is a deciduous plant which in temperate climates grows between spring and autumn. The growth of mature grapevines is determinate. Annual growth represents the sum of the growth of the grapevine's constituent organs. Each organ is a distinct and visibly differentiated part of the grapevine. The grapevine consists of the following organs: roots, trunk, arms, shoots (which consist of stem, leaves and inflorescences which develop into grape bunches [synonymous with clusters]) and canes (synonymous with mature shoots) (Winkler, 1962; Pongracz, 1978).

Each organ grows during a distinct period(s) within the season. Stress causes a decline in growth. Where the stress is not constant its consequence for grapevine growth will depend on which organs are undergoing growth during the period of stress.

In mature grapevines, the growing season can be divided into four phases based on readily observed changes in the canopy and fruit. They are: (1) pre-anthesis, between bud-burst and full-bloom, (2) berry development, between full-bloom and veraison, (3) berry maturation, between veraison and harvest, (4) post-harvest, between harvest and leaf-fall. The growth of shoots commences at bud-burst and berry growth first becomes visible two to three weeks after full-

bloom. Shoot growth generally ceases at veraison when berries begin maturation. Berries are harvested at ripeness. Shoots mature between harvest and leaf-fall (Winkler, 1962). The growth of grapevine organs other than canopy and fruit is also discontinuous and limited to certain periods within the season.

Cultivars, location and season are sources of variation in the dates at which vegetative and fruit growth are initiated and berry maturation ceases. Differences in the climate between various locations and between seasons are a probable source of this variation. In an attempt to explain this variation, the timing of these events has been analysed as a function of growing degree days e.g. Gutierrez *et al.* (1985). Due *et al.* (1993) lists numerous examples of the failure of growth models based on degree day to predict phenological events beyond the locations at which they were determined. Across the wine growing districts of Australia, they found that most of the variation in date of both flowering and harvest were accounted for by non-weather terms in their model i.e. cultivar, year and district. These results suggest that, in Australia, the current models of grapevine phenology based on weather data are unlikely to account for the variation across district or year.

2.2.2 Roots

In mature Sultana grapevines, on their own roots or on Ramsey rootstock, McKenry (1984) found the major increase in the length of flushing roots occurred in a two week period commencing just before full-bloom. In Colombar on 99R rootstock, Van Zyl (1984) found the highest number of actively growing new root tips occurred at full-bloom. Post-harvest, the increase in the length of roots in Sultana was minor. In contrast, the post-harvest increase in the number of actively growing root tips in Colombar on 99R was similar to that at full-bloom. It is not clear whether differences in the importance of the second flush between Colombar, and Sultana are due to location or cultivar. These studies were undertaken on field grown grapevines and on-balance they show that the major increase in new root growth occurs at around full-bloom.

In potted fruiting Chenin Blanc on 99R rootstock, Conradie (1980) found the greatest gain in root mass occurred post-harvest with a minor gain occurring one month after full-bloom. In Waltham Cross on Jacquez rootstock grown in a lysimeter, Van Rooyen *et al.* (1980) found the greatest increase in roots length also occurred post-harvest with a minor increase at around full-bloom. In Shiraz, growing in a lysimeter, Freeman and Smart (1976) found the highest number of new roots occurred one month after full-bloom.

In both grapevines grown in the field and those grown in pots or lysimeters, root growth was bi-phasic occurring at full-bloom and harvest. Comparison between the two types of growing conditions suggests that constraining the rootzone volume changes the timing of the major increase in root length and mass.

In apples, Atkinson (1983) found that root shedding during winter dormancy reduced the root length by 50%. The effect of root shedding on grapevine root length is unknown.

2.2.3 Trunk

In field grown Colombar on 99R rootstock, Van Zyl (1984) found a major increase in the trunk circumference occurred between full-bloom and veraison. In one of the three years of observation, a minor increase occurred post-harvest. During berry maturation, the trunk shrunk. In potted fruiting Chenin Blanc on 99R, Conradie (1980) found trunk mass underwent two major increases and one minor increase in a season. The major increases occurred just after full-bloom and after harvest. The minor increase occurred in the two weeks following bud-burst. These results suggest that constraining the rootzone volume may add another phase to the annual cycle of trunk growth.

2.2.4 Shoot and leaves

Shoots can be divided into primary shoots, lateral and water shoots. Primary shoots arise directly from one year old wood; lateral shoots arise from the primary shoots of the current season; water shoots arise from mature wood.

The most common measurement of shoot growth is the weight of prunings (stem) removed in winter. The growth of leaves, whether measured as a change in linear dimension or in mass, can be inferred from that of stems as the growth of these two organs is temporally coincident and their gains in mass are highly positively correlated with each other (de La Harpe and Visser, 1985; Wermelinger and Koblet, 1990).

Shoots and leaves are initiated in the season preceding their emergence and growth. Initiation begins two weeks prior to full-bloom and at least three weeks prior to floral initiation. Three weeks after initiation, between three and eight leaf primordia are present and a further five may differentiate before the bud enters dormancy (Srinivasan and Mullins, 1981).

Primary shoots grow between bud-burst and veraison. During this period Freeman and Smart (1976) found the shoot elongation rate in Shiraz growing in a lysimeter was constant. In contrast, with field grown grapevines Van Zyl (1984) found the rate in Colombar on 99R rootstock was greatest in the month prior to full-bloom, and Van Zyl and Weber (1977) and de la Harpe and Visser (1985), found, in Chenin Blanc and Cape Riesling, it was greatest at full-bloom. It is not clear whether the differences in timing of growth maxima were due to cultivar or climate or constraint of the rootzone volume.

Wermelinger and Koblet (1990) found lateral shoot growth in Pinot Noir was initiated at full-bloom and, where grapevines were topped, it may continue up until harvest. In the study of Williams (1987), where there was no report of topping, he found that the lateral and primary shoots of Sultana developed coincidentally with

the increase in the number and area of leaves on both shoot types, ceasing just after veraison.

Leaf abscission began in Chenin Blanc on 99R one month before harvest and continued for two months (Conradie, 1980). In Pinot Noir on 5C rootstock leaf abscission began just before harvest (Wermelinger and Koblet, 1990).

2.2.5 Inflorescence and fruit

Reproductive organs pass through many stages of development. The first is initiation of Anlagen and transition to inflorescence primordia; this occurs in the season preceding emergence of the inflorescence. Anlagen may differentiate into inflorescence primordia or tendril primordia, a differentiation which takes 3-4 weeks and is under hormonal control. In the basal bud, anlage formation occurs after production of 3-8 leaf primordia at about 2 weeks before full-bloom. Buds develop in acropetal succession and each bud is out of phase with the previous bud by 2 days (Srinivasan and Mullins, 1981; Buttrose, 1974). Where a second and third inflorescence primordium form, entry to dormancy is delayed until harvest of the current seasons fruit crop (Swanepoel and Archer, 1988; Pratt, 1971).

In the subsequent season, individual flowers begin differentiation just before bud-burst and complete it about a month after bud-burst (Srinivasan and Mullins, 1981). Cell division in the ovary wall begins 3-4 weeks before full-bloom and ceases in the berry pericarp about a month after full-bloom (Pratt, 1971). At full-bloom the pericarp contains between a third and a half of its final cell number (Harris *et al.* 1968). In the 20 days following full-bloom, the berries in which pollination has not occurred or in which the embryo has degenerated undergo abscission; those which remain attached and undergo growth are referred to as having set. Abscission rate is variety dependent; Muscat loses about 95% of flowers, whereas Concord Seedless loses only 50% (Nitsch *et al.*, 1960; Coombe, 1973).

Various patterns of berry growth following fruit set have been proposed. Staudt *et al.* (1986) divided the growth into two phases of rapid growth. Coombe and Bishop (1980) divided into two phases of rapid growth separated by a lag phase; and Nitsch *et al.* (1960) divided it into two cycles each consisting of lag phase followed by a growth phase. Each observation was made on a different cultivar and under different climatic conditions. Coombe and Bishop (1980) were the only authors to statistically validate their claims. They discerned three phases. In the first phase, referred to as berry development, growth is due to cell division and enlargement. Cessation of cell enlargement marks the end of the first phase and the beginning of the lag phase. The length of this phase is dependent on variety, number of seeds and growth environment (Harris *et al.* 1968; Nitsch *et al.* 1960; Coombe, 1976). The end of the lag phase is coincident with veraison and the recommencement of growth in berry diameter. In the second phase, referred to as berry maturation, growth is due solely to cell enlargement (Harris *et al.* 1968). The second phase is complete when the berry reaches maturity.

2.2.6 Fruit composition

At maturity the major constituents of the berry, in addition to water, are glucose fructose, malate, tartrate and potassium (Coombe, 1976). Sugars and acid are synthesised from exogenous sucrose (Ruffner, 1982a; Bollard, 1970). Glucose and fructose account for 99% of the sugars and malic and tartaric acid for 90% of the acids (Whiting, 1970; Peynaud and Ribereau-Gayon, 1971). The composition of the berry undergoes major changes during its growth.

Sugar accumulation begins at veraison and is continuous throughout maturation (Coombe, 1992).

Synthesis of malic and tartaric acid occurs throughout berry development and ceases at veraison. After veraison the berry acid content declines. Malate is degraded by the processes of gluconeogenesis or respiration (Ruffner, 1982b;

Possner and Kliewer, 1985). Cell enlargement during maturation dilutes the remaining malate and tartrate.

Potassium accumulation is continuous throughout berry growth. On a per berry basis, the amount accumulated after veraison is double that accumulated before veraison (Harris *et al.* 1968; Possner and Kliewer, 1985).

The pH is dependent on the total acidity, the proportion of malic to tartaric acid and the degree of proton exchange for potassium (Iland, 1984). The total acidity is the proton equivalent of the organic acid anions (Boulton, 1980). Tartaric acid (H2T) is stronger than malic acid (H2M). The rise in pH after veraison is caused by changes in all three of these parameters. Malate degradation and continued berry expansion without further acid synthesis cause a fall in the total acidity after veraison. Post-veraison the proportion of malic to tartaric acid is modified by processes of malate degradation and conversion of tartaric acid to tartrate salts. At maturity all of the malate anion is present in the acid form, whereas the tartrate anion is present both in acid form and as salts. Tartrate may be present as potassium bi-tartrate (KHT) or di-potassium tartrate (K2T) or as tartaric acid. In the conversion of tartaric acid to its salts protons are exchanged for potassium. The exchange of protons for potassium raises the juice pH (Iland, 1984).

3. General Materials and Methods

3.1 MATERIAL AND TREATMENTS

The experiments were conducted between 1986 and 1989 on Colombard grapevines on Ramsey rootstocks at the South Australian Department of Agriculture Loxton Research Centre (34°38'S 140°38'E). Treatments were applied to immature non-fruiting potted grapevines growing in the glasshouse and mature grapevines growing in the field.

Five treatments were applied; four consisted of irrigation with saline water during one of the four physiologically distinct periods in the seasonal growth of mature grapevines. Periods of salinisation and treatment designation were as follows: the treatment salinised between bud-burst and full-bloom was designated BB-FB; that between full-bloom and veraison - FB-V; that between veraison and harvest - V-H; that between harvest and leaf-fall - H-LF. At other times these treatments were irrigated with river water. A control, designated CONT, was irrigated with river water throughout the season. The timing of treatment applications in the glasshouse corresponded to growth stages of mature grapevines in the field.

The electrical conductivity of irrigation water (ECi) water was about 0.5 dS/m at 25°C and addition of sodium chloride brine to this produced a saline irrigation water with an ECi of 3.5 dS/m.

3.2 IRRIGATION WATER MEASUREMENTS

Each week, the volume of irrigation water was measured by an in-line flow meter and the salinity of irrigation was measured with an EC meter. Salinity was measured on a sample collected by continuously bleeding the supply line through a micro-capillary tube into a 4 L jar.

For each growth stage and for the entire season, the EC of water received by the grapevines (ECw) was expressed as a 'volume-weighted average'. This was calculated for k consecutive irrigations as the sum of the products of the ECi and the volume of irrigation at each irrigation (IV) divided by the sum of the volumes of k irrigations.

$$ECw = \frac{\sum_{n=1}^{k} (ECi)_n . IV_n}{\sum_{n=1}^{k} IV_n}$$

In the glasshouse experiment, Chapter 4, ECw equated to the volume-weighted ECi. In the field experiment, Chapter 5, precipitation was also included in this calculation whenever the rate was greater than 5 mm in a 24 h period and for this reason ECw was a volume weighted function of the ECi and the EC of precipitation. The EC of precipitation was set at 0.044 dS/m (Blackburn and McLeod, 1983).

3.3 GRAPEVINE WATER RELATIONS

Leaf water potential (Ψ_l) and stomatal conductance were measured once a month. The sampling dates and position of leaves within the canopy are detailed in the Material and Methods sections of Chapters 4 and 5. Ψ_l was measured with a Scholander pressure chamber (Scholander *et al.*,1965). Measurements were made from before dawn till after sunset. Leaves were enclosed in aluminium coated plastic bags just prior to excision (Turner and Long, 1980). Measurements began within 30 s of excision.

Stomatal resistance was measured with a Delta-T (Mark 3) transit-time porometer. Measurements commenced mid-morning and ceased mid-afternoon. Before each measurement the porometer cup was brought to ambient conditions by clamping it on an exposed leaf for ten minutes. The instrument was calibrated at each measurement period and the dependence of resistance on transit time was

described as a cubic polynomial of the natural log of the transit time (Gay, 1983). Stomatal conductance was calculated as the inverse of stomatal resistance.

Leaf lamina wet to dry weight ratio and leaf osmotic potential ($\Psi_{\pi l}$) were measured at the end of treatment periods BB-FB, FB-V and V-H. Prior to excision the leaf was enclosed within a aluminium coated plastic bag. Immediately following excision the base of the petiole was placed in water. Measurements began after two hours of re-hydration which raised Ψ_l to above -0.1 MPa.

After measurement of the leaf lamina wet weight and area, it was dried to a constant weight at 70°C. Leaf area was measured on a Delta-T area meter which was regularly calibrated with a set of leaves fabricated from cardboard.

Leaf osmotic potential was determined from the pressure volume curve which describes the dependence of the inverse of Ψ_l on the leaf relative water content (RWC). The leaf was weighed immediately after removal from the plastic bag to establish the weight at a RWC of 100%. It was then placed on a bench where it was allowed to dehydrate at room temperature (22°C). Periodically the leaf Ψ_l and weight were measured as it underwent dehydration. The curve assumes a linear form when leaf turgor pressure reaches zero (Turner, 1981). A regression equation was fitted to the linear region of the curve and $\Psi_{\pi l}$ at full turgor was calculated by substituting a %RWC value of 100 into the equation. Measurements were repeated whenever the significance of the regression was greater than 0.01.

3.4 TISSUE ION CONTENT

The sodium and chloride concentrations of leaves were determined, respectively, by atomic absorption spectroscopy and with a Buchler chloridometer. Samples were prepared for analysis by drying at 70°C and grinding to pass a 0.2 mm mesh. Sodium was determined on a hot nitric acid digestion or on ash redissolved in hot hydrochloric acid (Leece and Short, 1967). Standards were

included to ensure that element recovery was similar with both methods of preparation. Chloride was determined on a cold water extract.

The leaf lamina concentrations of Na and Cl on a tissue fresh weight basis were calculated, as required, from the measurements of leaf wet:dry weight ratio and Na and Cl concentrations expressed on a dry weight basis.

3.5 STATISTICAL ANALYSIS

The significance of differences was tested by an analysis of variance. Validity of assumptions concerning normal distribution and non-additivity were assessed with the approximate Wilks Shapiro statistic (Shapiro and Francia, 1972) and Tukeys test (Snedecor and Cochran, 1980), respectively. The least significant difference was only calculated when the F value was significant (Chew, 1976).

4. THE RESPONSE OF POTTED IMMATURE GRAPEVINES TO TRANSIENT SALINISATION

4.1 INTRODUCTION

In many viticultural regions, the irrigator can draw on more than one source of water. Generally, the sources have different salinities and the supply of that with the lower salinity is insufficient to meet the seasonal water requirements of the grapevine. In these circumstances, the irrigation or water authority manager may choose to reduce the maximum concentration of salt in the irrigation water by mixing water from both sources to maintain a constant salt concentration over the entire season or to reduce the duration of salt stress by applying water with the higher salt concentration for only part of the season.

Maas and Hoffmann (1977) and Ayers and Westcot (1985) modelled the response of grapevine yield to salinity based on studies of the response of immature potted grapevines to a range of saline irrigation treatments. In all of these studies, the salt concentration in irrigation water was maintained at a constant level over the entire season.

This experiment measures the growth responses of immature grapevines to irrigation with saline water for two month periods and relates the response to changes in the grapevine tissue ion concentration and water relations.

4.2 EXPERIMENTAL PROCEDURE

4.2.1 Material, Culture and Irrigation

The grapevines were bench grafted in November 1987 and potted in four litre pots which contained a steam-sterilised potting mix consisting of composted pine bark, washed river sand and peat moss 45:45:10 by volume that held 860 mL of water at field capacity. They grew for the remainder of the season in a shadehouse. In August 1988, they were trimmed to single three-bud spurs and moved to a seventy per cent shaded glasshouse where the temperature was maintained between 15 and 30°C. After a single shoot of six leaves had established, the remaining buds were rubbed off. The shoot was trellised to a string suspended between the bench base and a mesh 2 m above it. By November, the grapevines had grown beyond the trellis. Subsequently, growth above the trellis and lateral shoots greater than two nodes in length were trimmed monthly and retained for measurement of dry weight. On the rare occasions when inflorescences emerged they were promptly removed and discarded.

The grapevines were irrigated with a commercial hydroponic mix (Top Hydroponic mixture) diluted to one-tenth strength with river water. The concentrations of N, P, K, Ca, Mg, S, Na and Cl in the irrigation water were, respectively, 1.5, 0.1, 0.6, 0.8, 0.7, 0.6, 2.7, 2.7 mM. FeEDTA was added to irrigation water at the rate of 6.1 g/kL. Peristaltic pumps were used to dose the nutrient concentrate into the irrigation water. Periodically 2.5 mL of panoctine was added to the nutrient concentrate to suppress wild yeast growth. Irrigation was applied between three and five times daily through 2 L/h drippers. The volume of irrigation was monitored by an in-line meter and between bud-burst and mid-season it was gradually increased from 0.4 to 1.0 L/d. Pots were flushed with one litre of irrigation solution before bud-burst.

Periodic measurement of the drainage volume showed that it accounted for at least 50% of the water applied i.e. 50% leaching. At this rate of application, the maximum time required for the complete turnover of soil water was two days.

4.2.2 Treatments

A saline solution was produced by addition of a sodium and calcium chloride brine to the irrigation solution. The resulting solution had a sodium to calcium ratio of 17:1 (Greenway and Munns, 1980) and a sodium chloride concentration of 33 mM.

Treatment periods were delineated by events occurring in mature field grown grapevines. In 1988-89 season, the events and dates of their occurrence were as follows: bud-burst - 2 September; full-bloom - 10 November; veraison - 17 January; harvest - 15 March; leaf-fall - 11 May.

4.2.3 Measurements

The diurnal patterns of Ψ_l and stomatal conductance were measured on the following dates in the 1988-89 season: 18 October, 9 November, 13 December, 4 January, 10 February, 8 March and 13 April. Measurements were made without regard to cloud cover conditions.

The water potential was measured on leaves inserted between the first and eighth node. On any one day, the leaves were sampled so that their average insertion point was at the fourth node. After measurement of Ψ_l, the leaves were retained for determination of lamina sodium and chloride content. Stomatal conductance was measured on leaves inserted at the tenth node in October and on those at the fifteenth node in the following months. Measurements of leaf succulence and osmotic potential were made on leaves inserted at the sixth and eighth nodes, respectively. Leaf turgor pressure was calculated by subtraction of leaf osmotic potential from pre-dawn Ψ_l.

At termination of the trial, the above ground seasonal growth was divided into leaves and stems which were dried and weighed. The seasonal growth was the sum of the weights of tissue removed during the season and at harvest.

4.2.4 Experimental Design

The experiment was a completely randomised design replicated four times. Each replicate consisted of eight grapevines. Each replicate occupied a bench and a single row of barrier grapevines was placed around the perimeter of each bench.

4.3 RESULTS

4.3.1 Water relations

In every set of diurnal measurements, the effects of salt stress on Ψ_l and stomatal conductance were independent of the time of day at which these parameters were measured. Accordingly, only the daily means of these two parameters are considered.

The leaf water potential remained relatively constant over the season except during periods of saline irrigation when it was reduced by between 0.10 and 0.16 MPa (Figure 2). Leaf water potential recovered following release from salt stress. Small but significant differences between the Ψ_l in the control and those in treatments BB-FB and H-LF occurred in March and January. They were independent of salt stress and were probably caused by the rapid changes in cloud cover which occurred on these days (Jones, 1990).

Leaf water potential changed as a linear function of the osmotic potential of the irrigation water, $\Psi_{\pi w}$ (estimated by assuming a solution with an EC of 3.0 dS/m has an osmotic potential of -0.1 MPa). The relationship between pre-dawn values of Ψ_l and $\Psi_{\pi w}$ (MPa) is described by

$$\Psi_l = 0.99\ \Psi_{\pi w} - 0.09$$

The relationship is highly significant ($p < 0.001$) and the near one-to-one relationship between Ψ_l and $\Psi_{\pi w}$ indicates that the osmotic effect of salinity on pre-dawn Ψ_l was a direct function of the osmotic potential of irrigation water.

Salt stress only caused a reduction in stomatal conductance in November and March (Figure 3). Stomatal conductance completely recovered following release from salt stress. It declined as the leaves aged.

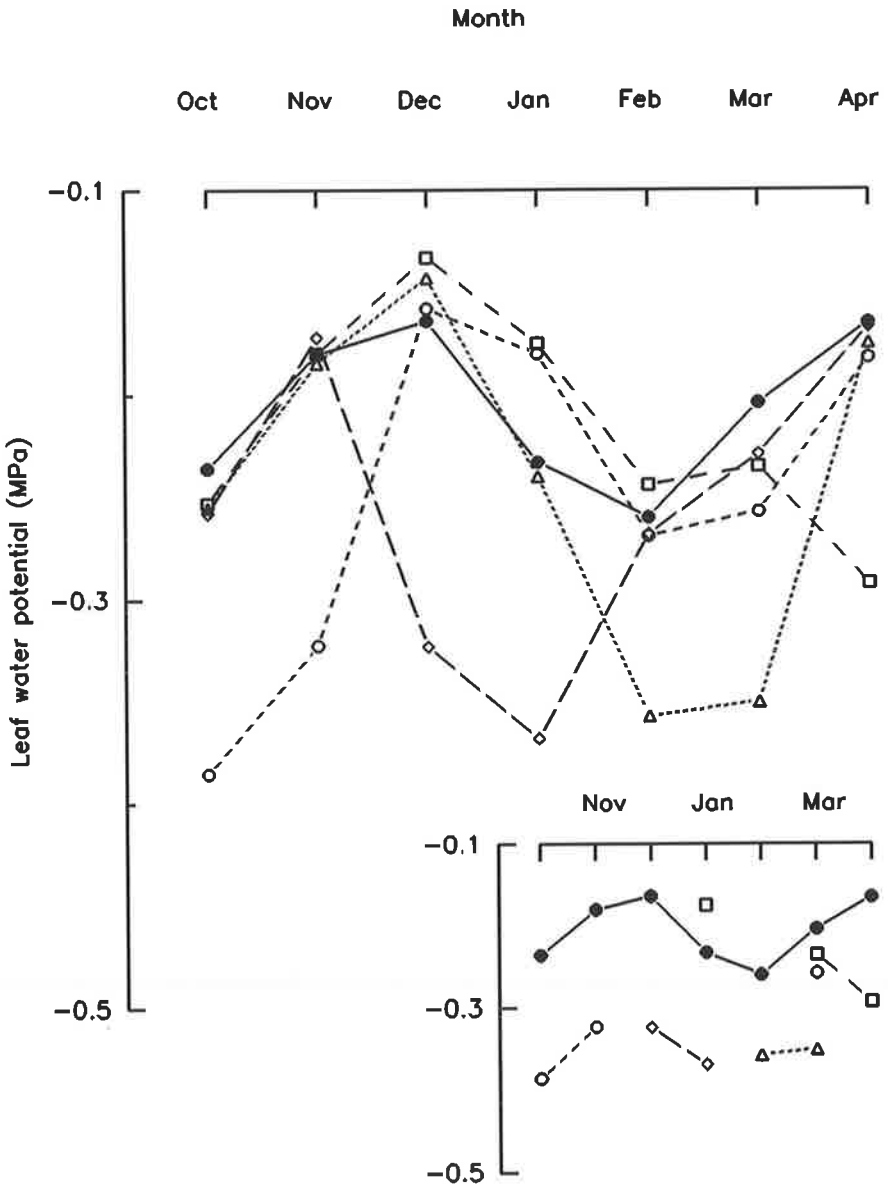

Figure. 2. Treatment effects on the daily mean of diurnal measurements of leaf water potential. Inset indicates treatments which significantly differed ($p < 0.05$) from the control. BB-FB(○), FB-V(◇), V-H(△), H-LF(□) and CONT(•).

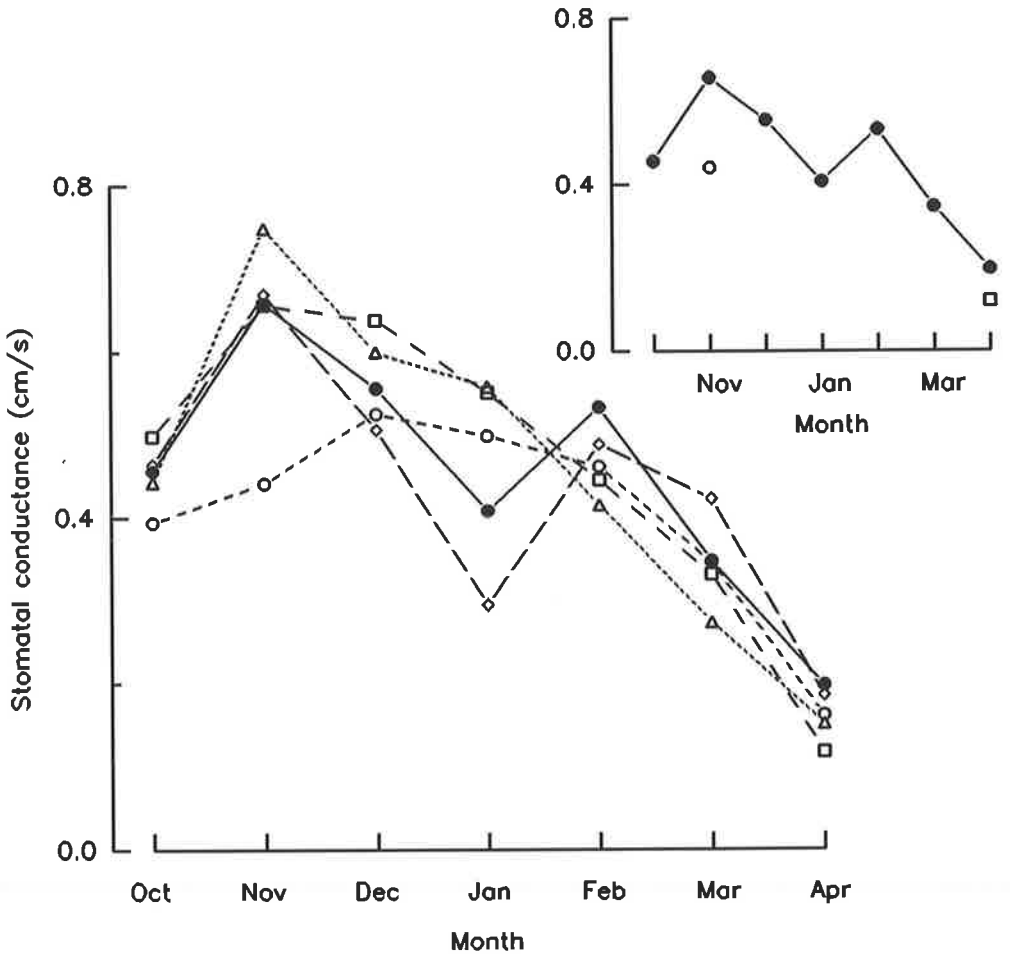

Figure 3. Treatment effects on the daily mean of diurnal measurements of stomatal conductance. Inset indicates treatments which significantly differed ($p < 0.05$) from the control. BB-FB(○), FB-V(◇), V-H(△), H-LF(□) and CONT(•).

Saline irrigation caused a fall in leaf osmotic potential which although not significant was sufficient to prevent any loss of leaf turgor (Figure 4). There was a trend for turgor pressure to remain elevated following release from salt stress. $\Psi_{\pi l}$ declined with leaf age with values for November, January and March of -0.9, -1.3 and -1.5 MPa, respectively.

In the second and third quarters of the season, salt stress significantly reduced the wet to dry weight ratio of leaves (Figure 5). Following release from salt stress at the end of the second quarter, the wet:dry ratio of leaves in treatment FB-V increased to above that in the control. The ratio also fell as the leaves aged past five months, i.e. the March sample. These changes were due solely to variation in the dry weight per cm^2 of leaf which rose during salinisation and fell following it, and rose in all treatments in March (data not presented).

4.3.2 Ionic composition

In the first half of the season, saline irrigation caused large increases in lamina sodium and chloride concentrations (Figure 6). In treatment BB-FB, the concentrations rose rapidly following commencement of saline irrigation and fell slowly following its cessation. Once elevated, the concentration of these ions in treatment FB-V remained static. In the second half of the season, saline irrigation caused small increases in the concentration of these ions in treatment V-H. Expression of the concentrations of these ions on a fresh weight basis (data not shown) showed a similar time course.

Salinisation caused the concentration of Na and Cl to rise by similar amounts e.g. in treatment FB-V salinisation had increased the Na and Cl concentration by 211 and 229 mmol/kg above the concentrations in the control by March. Similar rates of increase in Na and Cl caused the Na:Cl ratio to move toward unity from 0.3 in CONT to 0.8 in FB-V.

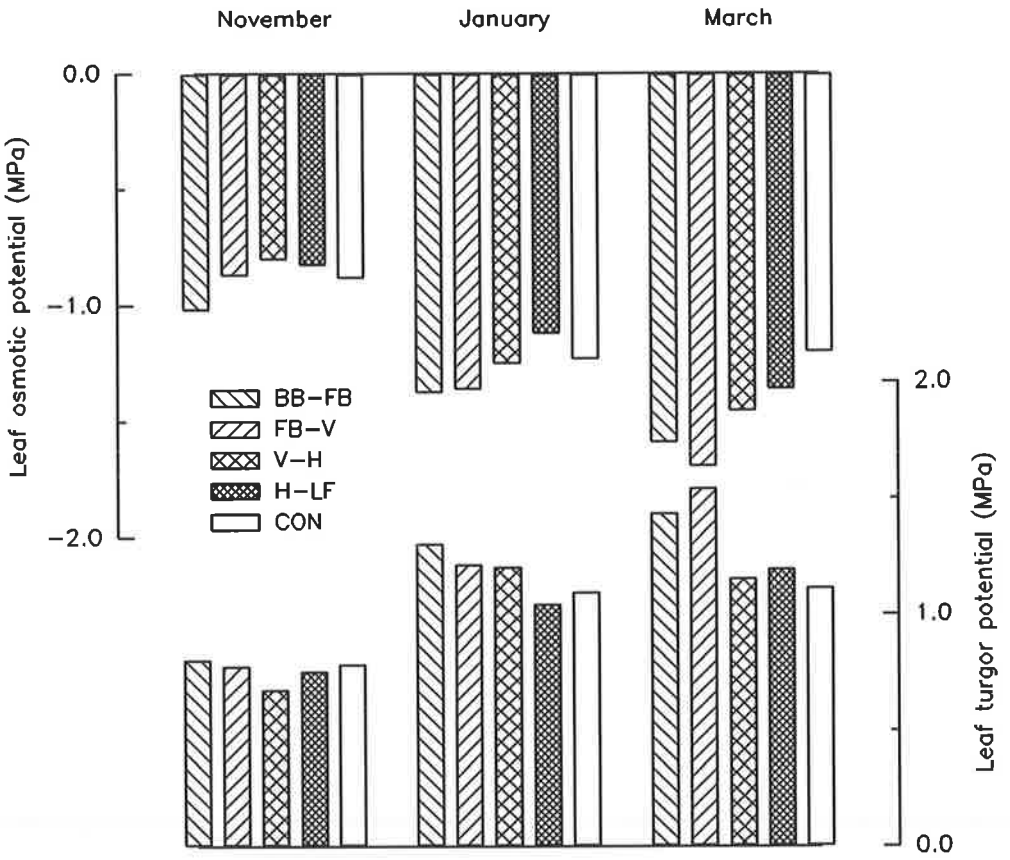

Figure 4. The effect of treatment on the pre-dawn leaf osmotic and turgor potentials at the end of salinisation of treatments BB-FB (November), FB-V (January) and V-H (March). Treatment effects were not significant.

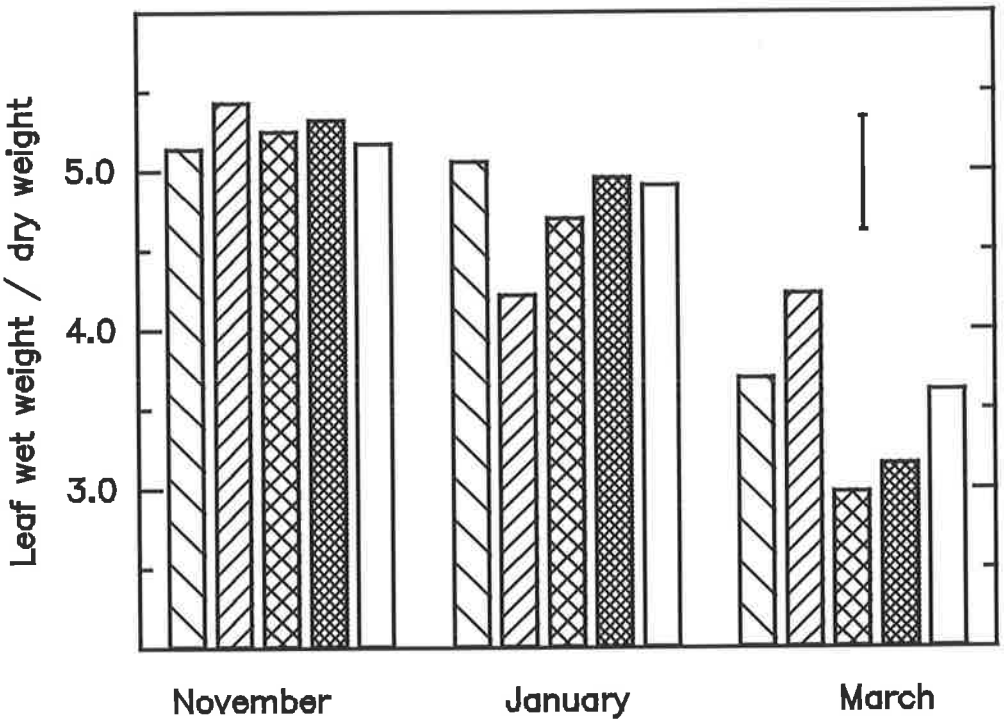

Figure 5. The effect of treatment on the ratio of leaf wet to dry weight at the end of salinisation of treatments BB-FB (November), FB-V (January) and V-H (March). Bar indicates l.s.d. ($p = 0.05$). Legend as designated for Figure 3.

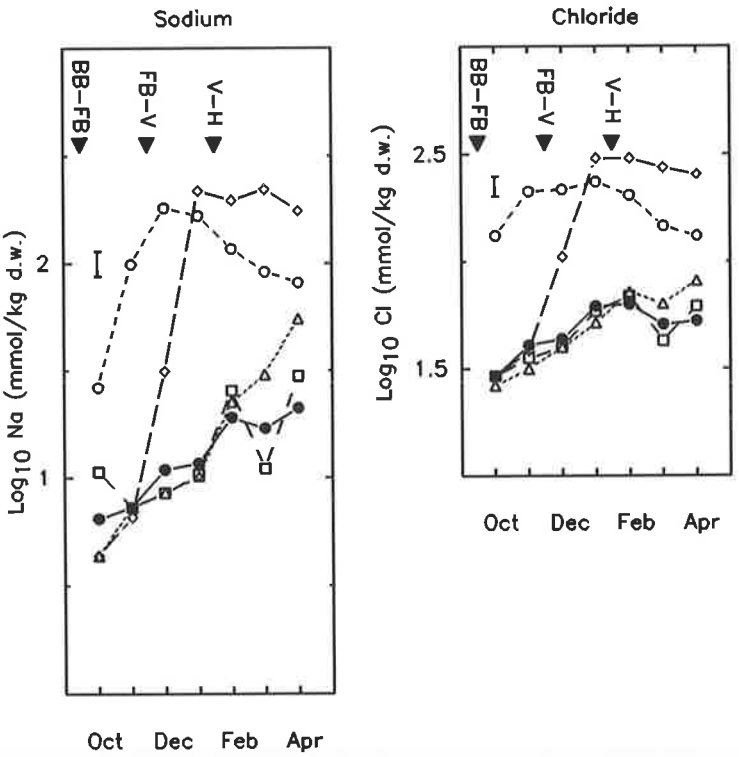

Figure 6. The effect of treatment on the leaf lamina Na and Cl concentration between October and April. Bar indicates l.s.d. ($p = 0.05$) BB-FB(○), FB-V(◇), V-H(△), H-LF(□) and CONT(•).

The sodium and chloride concentrations in the petioles sampled in November and March are shown in Table 1. With reference to the measurements made in March, exposure to salinity in the first 6 months of leaf development significantly increased the sodium concentration. In March concentrations in treatments BB-FB, FB-V and V-H were at least double that in the control. Concentration of sodium was sensitive to the leaf age at exposure. After two months salinisation, the concentration in 2 months old petioles (BB-FB) had increased 1510 mmol/kg above that in the control, whereas in 6 months old petioles (V-H) the concentration had only increased 197 mmol/kg above that in the control. Exposure to salinity only increased the chloride concentration in the first four months of leaf development. Exposure during the fifth and sixth month did not significantly increase chloride concentrations.

In March, treatment BB-FB had been irrigated with river water for 4 months; sodium concentrations had fallen to a third of that in November, whereas chloride concentrations remained constant. Petiole sodium was more mobile than chloride.

4.3.3 Growth

Salt stress significantly reduced above ground seasonal growth in all treatments with the reduction in all being equivalent. The average decline was twelve per cent with a range between eight to fifteen per cent for treatment BB-FB and FB-V, respectively (Figure 7).

The weight of trimmings removed during saline irrigation was significantly depressed (Figure 8). In the first half of the season, growth recovered following release from salt stress, however at the end of the season, when growth had slowed, this recovery underwent a slight deterioration with the weight of trimmings removed from treatments BB-FB, FB-V and V-H falling in April.

Table 1. The effect of treatment on sodium† and chloride concentration in November and March petiole samples. (mmol/kg d.w.) (for the glasshouse)

Treatment		BB-FB	FB-V	V-H	H-LF	CONT	l.s.d. ($p = 0.05$)
November	Sodium	3.21 (1620)	1.85 (73)	1.85 (72)	1.87 (75)	2.03 (110)	0.13
	Chloride	500	183	162	175	211	52
March	Sodium	2.74 (567)	2.77 (595)	2.61 (410)	2.31 (206)	2.33 (213)	0.13
	Chloride	494	709	288	226	287	66

† Sodium data was transformed to $\log_{10}$ values for analysis - data in parenthesis are untransformed values

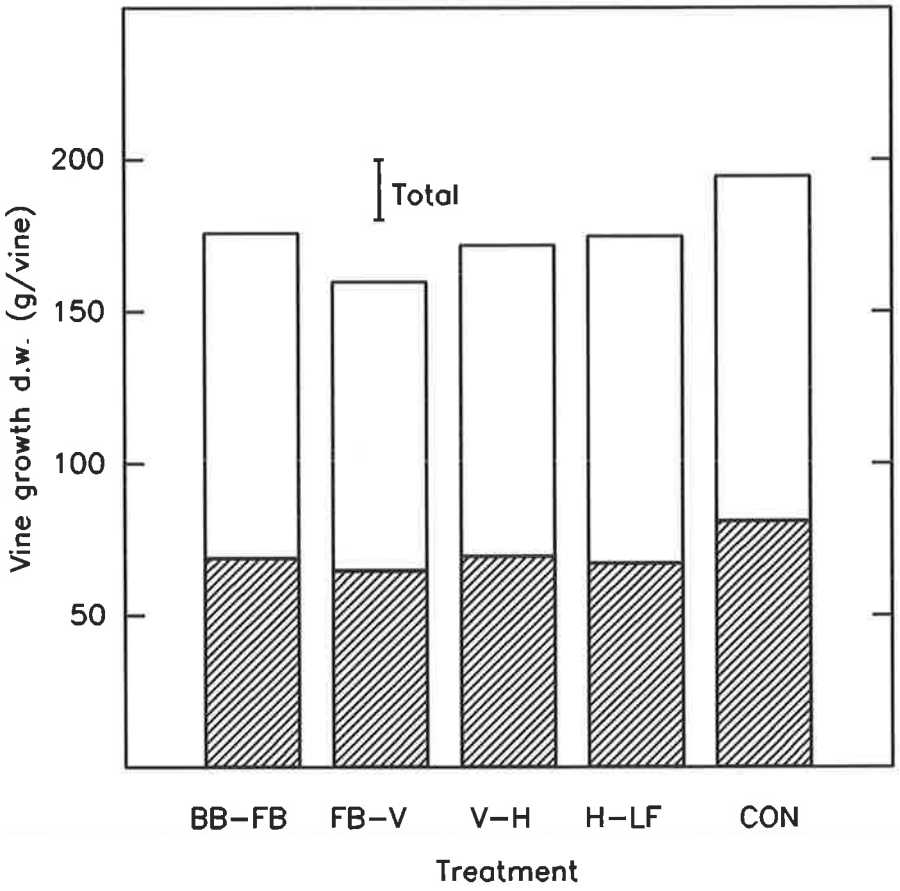

Figure 7. Effect of treatment on the growth of leaves (hatched bar) and stems (clear bar). Bar indicates the l.s.d. for combined stem and leaf growth (p = 0.05).

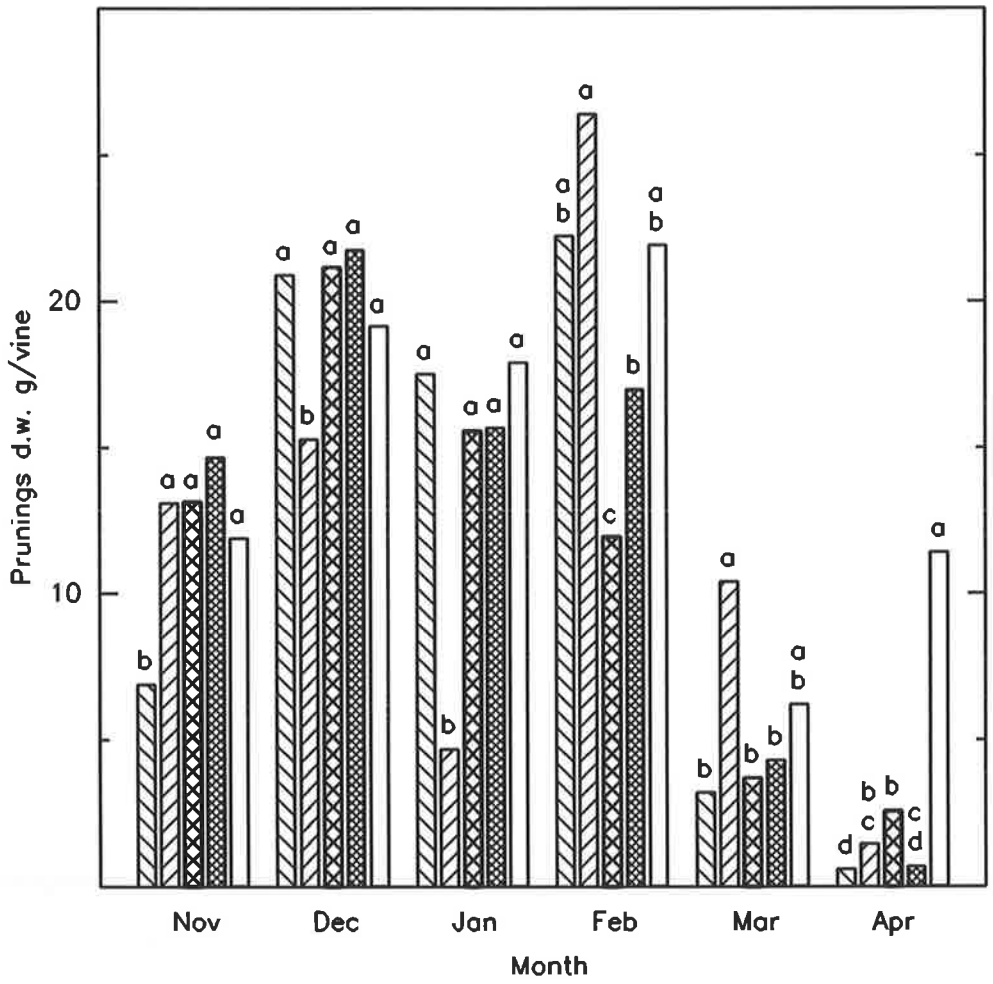

Figure 8. The weights of stems and leaves removed by monthly trimming. Legend as designated for Figure 3. Within each month, the total weights of trimmings from treatments labelled with the same letters were not significantly different ($p = 0.05$).

4.4 DISCUSSION

The growth reductions caused by saline irrigation in any of the four two-month periods were equivalent. This result indicates that indeterminate shoot growth was insensitive to the timing of saline irrigation.

Downton (1985) found irrigation with 12.5 mM chloride salts for the entire season caused a growth loss of thirteen per cent in Sultana on Ramsey rootstock. The growth loss reported by Downton (1985) falls within the range found in the present experiment i.e. between eight and fifteen per cent. The annual salt loads in the present experiment and Downton (1985) were similar i.e. 35 mM for one quarter of the season and 3 mM for three quarters equates to 10 mM for all four quarters. The similarity in decline between Downton (1985) with Sultana on Ramsey and the present experiment with Colombard on Ramsey suggest that the vegetative growth of these two scions have similar sensitivities to salt.

If spread evenly throughout the season, the annual salt load in the present experiment would cause a rise in ECw of about 1 dS/m. Ayers and Westcot (1985) predicted zero growth decline with this increase in ECi. They based their prediction on reports on the growth of immature own-rooted grapevines and suggest that for a salt excluding rootstock such a Ramsey the prediction over-estimates the growth decline i.e. the threshold for growth loss in grapevines on such rootstocks should be greater than ECw of 1.0 dS/m. The results of both the present study and those of Downton (1985) and Prior *et al.* (1992a) suggest that the prediction of Ayers and Westcot (1985) under-estimates grapevine growth sensitivity to salinity.

In the saline irrigation treatments, 69% of the loss of growth was due to a reduction in the weight of material removed by trimming during the season. The major loss in the weight of trimmings occurred during saline irrigation and was coincident with depressions of Ψ_l and stomatal conductance and a rise in tissue concentrations of Na and Cl.

Loss of growth during saline irrigation has been attributed to a lowering of the substrate osmotic potential, a raising of tissue concentrations of sodium and chloride to above toxic levels, and an imbalance in plant nutrition (Marschner, 1986). In the present experiment, the reduced Ψ_l was an example of the osmotic effect. The elevated concentrations of Na and Cl provided the potential for a toxic effect. Previous studies on salinised grapevines have not attributed growth loss to nutrient imbalance.

The falls in Ψ_l caused by saline irrigation in any of the four two-month periods were equivalent. Stomatal conductance only fell when saline irrigation was applied within a month of leaf emergence and the fall was not accompanied by a fall in P_l. Stomatal conductance and Ψ_l completely recovered following cessation of saline irrigation and this indicates that the leaching was sufficient to reverse the osmotic effect.

Leaf lamina Na and Cl concentrations rose immediately following the commencement of saline irrigation, however the rates of increase were dependent on the timing of saline irrigations. In the first, second and third quarter, saline irrigation increased the sodium concentration at 13, 63 and 3 times the rate of increase in the control treatment and increased chloride concentration at 6, 16 and 3 the rate of increase in the control. Uptake of Na and Cl by leaves was greatest between the 10th and 19th weeks after their emergence.

In treatment BB-FB, the lamina Na and Cl concentration began to decline two months after cessation of saline irrigation. The decline could be caused by re-transport or by growth dilution. The leaves were fully expanded before the decline commenced. A decline in content per cm^2 of leaf would be evidence of re-transport. Measurements of d.w./cm^2 of leaf (data not presented) made during the determination of leaf succulence were used to calculate the ion content per unit leaf area. The values for sodium in January and March were equivalent at 1066 and 1128 nanomoles/cm^2, respectively. In January and March, the values for chloride were equivalent at 1449 and 1409 nanomoles/cm^2, respectively. Leaf dry weight

per cm^2 increased between January and March and, it is likely that this increase reduced the Na and Cl concentrations when they were expressed on a d.w. per cm^2 basis.

In March, the average of the ratios of Na:Cl concentrations for treatments BB-FB, FB-V and V-H was 0.6 in the leaf lamina, 1.1 in the leaf petiole and 1.8 in the base of the stem (data not presented). In salinised peaches, Boland *et al.* (in press) also found a low Na:Cl ratio in the leaf and a high ratio in the metabolically less active tissue, butt wood. They proposed that sodium was sequestered in pools located in metabolically less active tissue and did not move to the leaf until high Cl concentrations in the leaf damaged the leaf.

After saline irrigation had ceased the changes in leaf sodium concentration were dependent on the timing of saline irrigation. Sodium rose after saline irrigation had ended in treatments BB-FB and V-H, but not in treatment FB-V. At the end of saline irrigation period treatment FB-V had a higher concentration of sodium than treatments BB-FB and V-H. The absence of a rise in treatment FB-V suggests that re-transport of sodium to the leaf following cessation of saline irrigation may be controlled by the leaf Na concentration. As the leaves were healthy at the end of saline irrigation, this control cannot be equated to that exerted by the death of leaves. These results suggest that if, in grapevines, sodium is sequestered into pools residing in metabolically less active tissue then its movement past or out of any such pool is neither a direct function of the substrate salinity nor of leaf health.

Further support for the effect of concentration on transport in the grapevine comes from observations of re-transport of chloride following cessation of saline irrigation. In fully expanded leaves, Walker *et al.* (1981) found that 40 per cent of Cl was transported out of leaves in a basipetal direction following cessation of saline irrigation. In the present experiment, the reduction in leaf Cl concentration at the end of saline irrigation was much smaller. It was due to dilution caused by an increase in the specific leaf dry weight rather than to export. In the present

experiment the leaf tissue chloride concentration reached a maximum value of 73 mM (estimated from leaf wet:dry weight ratio and Cl concentration expressed on a dry weight basis) which was much less than the 200 mM of Walker at al. (1981). This suggests export of Cl from the leaf may be concentration dependent.

Between November and January, saline irrigation increased the lamina chloride concentration by 260 mmol/kg, whereas between January and March it only increased it by 10 mmol/kg. The similarity in growth decline contrasts with the dissimilarity in leaf concentrations of Na and Cl. The growth loss in treatment BB-FB was similar to that in V-H even though the petiole chloride concentration in BB-FB was both eight fold greater than that in V-H and more than three times the level considered toxic by Prior *et al.* (1992b). The lack of a correlation between growth decline and tissue chloride concentrations is supported by the study of Downton (1985). He applied saline irrigation to Sultana scions on their own roots and on four rootstocks which varied in their degree of chloride exclusion. The greatest growth occurred on Dogridge which did not have the lowest tissue chloride and the least growth occurred on 1613 which did not have the highest tissue chloride. Between scion variation in growth was not proportional to leaf chloride concentration.

The recovery of Ψ_l, stomatal conductance and grapevine growth (trimming weights) following cessation of saline irrigation contrasts with the continuing elevation of leaf Na and Cl concentrations. This finding agrees with Walker *et al.* (1981) who also found the depression of shoot elongation was limited to periods when grapevines were irrigated with 90 mM NaCl. This level of salinity is nearly three times that in the present study and two findings of Walker *et al.* (1981) contrast with the present study. They found the loss of growth was accompanied by a loss of leaf turgor and the recovery of growth was accompanied by a re-transport of chloride from the leaf following cessation of saline irrigation. The absence of these two characteristics from the present study suggest that turgor loss is not a pre-requisite for growth decline and a fall in leaf Cl concentration is not a pre-requisite for recovery of growth. The dynamics of this recovery suggest that if

Na and Cl had a negative effect on growth then it was only manifest when these ions were present at osmotically significant concentrations in the substrate. Recent work (Stevens *et al.* in press) shows that wetting the foliage with 25 mM NaCl whilst the roots were irrigated with non-saline solution caused a 16% decline in growth which indicates that Na and Cl do have a negative effect on growth that can be demonstrated independent of a change in the osmotic potential of the substrate.

4.5 CONCLUSION

In potted immature Colombard grapevines on Ramsey rootstock the response of indeterminate vegetative growth to salinity was similar in all of the four two-month periods of the growth season i.e. it was insensitive to the timing of saline irrigation. Most of the depression of growth occurred during saline irrigation. The loss of growth was similar to that found by Downton (1985) when he applied an identical salt load which was evenly spread across the season. The similarity of the present results with those obtained with Sultana suggests the two cultivars have a similar sensitivity to saline irrigation. The results of both studies suggest that Ayers and Westcot (1985) model of grapevine response to salinity under-estimates growth losses.

Saline irrigation depressed Ψ_l by a similar amount in all treatments, however its effect on the leaf concentrations of Na and Cl was dependent on the timing of saline irrigation. The greatest rises in these ions occurred in those treatments where the saline irrigation was applied early in the season. Large differences between treatments in the leaf concentrations of Na and Cl did not translate into differences in growth.

Following cessation of saline irrigation, growth recovered. This recovery was associated with a recovery of Ψ_l, but not with a change in leaf concentrations of Na and Cl. The dynamics of this recovery suggest that if Na and Cl had a negative effect on growth then it was only manifest when these ions were present at osmotically significant concentrations in the substrate.

5. THE RESPONSE OF MATURE FIELD GRAPEVINES TO TRANSIENT SOIL SALINISATION

5.1 INTRODUCTION

Ayers and Westcot (1985) estimated the response of grapevine yield to saline irrigation from reports of salinity experiments on immature grapevines. They assumed that the response of yield would be similar to that of vegetative growth. In the present work, the results of the experiment on potted immature grapevines combined with those of Downton (1985) showed that vegetative growth was insensitive to the irrigation strategy i.e it was a function of the annual salt load regardless of the temporal course of its delivery. Continuing with the assumption of Ayers and Westcot (1985), it could be hypothesised that the response of yield to salinity is also insensitive to the irrigation strategy.

Hawker and Walker (1978) working with fruiting grapevine rootlings varied the salinity of irrigation across the season and found that the response of fruit growth to salinity was dependent on the growth stage at which saline irrigation was applied.

Prior *et al.* (1992a) found that models of grapevine yield response to salinity which were based on observations of the response of immature grapevines failed to predict the response of mature grapevines.

In this study, I investigated the effects of transient salinisation on the growth and physiology of mature field grapevines over three consecutive seasons. Saline irrigation ECw of 3.5 dS/m was applied for one quarter of the season presenting an annual salt load equivalent to irrigating throughout the season with water of up to ECw 1.7 dS/m. The investigation had two components. One consisting of a routine set of measurements of ECw, ECe, vegetative and fruit growth made regularly in each season. The other consisting of more intensive measurements of ECe, tissue ion content, grapevine water relations, vegetative growth, and fruit growth made in the second season of the trial.

5.2 EXPERIMENTAL PROCEDURE

5.2.1 Culture and irrigation

The vineyard was planted in 1977. By 1986, the annual yield was greater than 50 t/ha. which was more than twice the average yield of the district. The grapevines were spaced at 3.5 m between rows and 2.5 m within rows, cane pruned and trained on a wide-T trellis. The vineyard soil type was a Nookamka Sandy Loam (Blackburn and Wright, 1972). The textures within the profile were: 0-30 cm sand or sandy loam or sandy clay loam, 30-150 cm sandy clay loam or clay loam. A compact, class 3b, lime layer (Wetherby and Oades, 1975) was found between 85-90 cm.

Application of nutrients and weed control followed local farm practices. Nitrogen was applied as urea and phosphorus as phosphoric acid. Both were applied in the irrigation water at annual rates of 103 kg N/ha and 11 kg P/ha. A full cover herbicide program was applied throughout the growing season.

Irrigation was applied between one and six times per week for up to eight hours a day at a rate of 1.25 mm/h by drippers. The irrigation depth was calculated from climatic data (Doorenbos and Pruitt, 1977). Depth applied in a week was the sum of daily product of reference crop evapotranspiration (ETo) in the previous week and the monthly crop factor. This depth was increased by 5% to provide for leaching of salts. The crop factors were determined from tensiometer and testwell records obtained in previous years when these grapevines were irrigated with microjets; they were 0.1, 0.3, 0.5, 0.7, 0.8, 1.0, 1.0, 0.9 for September to April, respectively (Stevens and Harvey, unpublished data). When the depth of precipitation was greater than 5 mm/d the amount was deducted from that to be replaced by irrigation. Measurements used in the calculation of ETo were made at a Commonwealth Meteorological Bureau station 100 m east of the experimental site.

Treatments are described in section 3.1.

Twice weekly measurements of soil matric potential, in the top 120 cm of soil, and perched watertable height showed that the irrigation schedule maintained root-weighted matric potential (similar to RWECe except that matric potential measurements were substituted for measurements of ECe) above -20 kPa and the perched water table depth below 2.5 m.

5.2.2 Design

The experiment was conducted on 11 rows of 31 grapevines each. It was a randomised block design which was replicated 16 times with each replicate consisting of two two-vine panels. Measurements were made on the middle 2 grapevines and the exterior grapevines acted as within row barriers. A 1.5 m deep plastic sheet was inserted vertically between rows to act as a soil barrier to the movement of salt between rows.

5.2.3 Measurements - routine and intensive

Treatments commenced in September 1986. Between 1986 and 1989 pruning weights, butt circumference, yield and fruit composition were annually measured in all replicates. An intensive program of measurements was undertaken in the 1987-88 season; leaf water relations, tissue ion content, and root length were measured in replicate numbers 2, 11 and 15; shoot growth, canopy interception of solar radiation, the numbers of set and unset flowers, and the numbers of nodes, shoots and bunches on spurs and canes were measured in replicate numbers 2, 11, 12 and 15.

5.2.4 Soil measurements

Soil salinity was monitored by measuring ECe at depths of 5, 35, 60, 90, and 120 cm in replicates 2,11 and 15. In 1987-88, measurements were made on a monthly basis during the season. In 1986-87 and 1988-89, measurements were made at the opening of the season and at the end of each treatment period.

In order to aid the interpretation of soil salinity, for each sample time a single root-weighted value was calculated for each sample location. Measurements of root length density (RLD), which were made in the second season of the experiment, were used to derive a root-weighting factor (RWF) for a depth increment n as follows:

$$RWF_n = \frac{RLD_n}{\sum_{n=0}^{120} RLD_n}$$

The root-weighted ECe (RWECe) for depth 0 - 120 cm is calculated as the sum of the products of ECe and RWF for each depth

$$RWECe = \sum_{n=0}^{120} RWF_n.(ECe)_n$$

5.2.5 Measurements of water relations and ion content

The diurnal patterns of Ψ_l and stomatal conductance were measured on the following dates in the 1987-88 season: 26 October, 12 November, 17 December, 16 January, 16 February, 17 March and 21 April.

Measurements of Ψ_l and $\Psi_{\pi l}$, leaf succulence and stomatal conductance were made on exposed primary leaves inserted at about the seventh node on shoots arising from canes. After measurement of Ψ_l, leaves were retained for ion analysis.

The petiole sample taken in November was inadvertently destroyed. The concentrations of Na and Cl in November sample were estimated by linear interpolation between the concentrations of samples taken in October and December (data not presented).

5.2.6 Measurements of vegetative growth

Each year in August, the butt circumference at 30 cm above ground level and pruning weights were measured.

The length of shoots, and number, width and length of leaves were measured on four shoots arising from canes once every ten days from mid October to harvest. Leaves on the primary and lateral shoots were measured separately. Leaves, sampled from barrier grapevines, were used to develop a calibration equation which predicted leaf area from the product of width and length measurements (Smith and Kliewer, 1984). Area was measured with a Delta-T area measurement system.

The interception of solar radiation by the canopy was measured between 1030 and 1430 h at full-bloom, veraison and harvest. The solar radiation (wavelength 300 to 2100 nm) transmitted by the canopy was measured with tube solarimeters 1 m in length. They were positioned on a 1 m by 2 m rectangular box. Five measurements were made at equidistant locations along the top of the box. The box was moved twice so that 15 measurements were made in an area of 3 m by 2 m which had its long axis aligned at right angles to the vine row and with its midpoint lying beneath the grapevine. The box was supported on an array of level pegs. Readings from another solarimeter placed above the canopy were used in the derivation of the percentage solar radiation intercepted by the canopy.

After leaf-fall in August 1988, root length density (RLD) was measured at sites midway between grapevines within the vine rows. Soil cores, 180 cm deep by 9 cm wide, were removed by auger in 20 cm increments. Soil was washed from the roots on a 2 mm sieve. White roots attributed to weeds were removed and the remainder stored at 0°C. Root length was measured on a Delta-T area measurement system operating in length measurement mode. The system was calibrated against a set of grapevine roots which had their length measured manually.

5.2.7 Measurement of fruit growth and composition

The grapevines were harvested in late March (the exact dates were set by the winery which purchased the crop). In each season, the fruit yield per plot, the number of bunches and the weight of a random sample of a 100 berries were measured at harvest. A bunch was defined as a structure arising from a shoot and bearing more than 5 berries. The number of berries per grapevine was calculated by dividing yield by berry weight, and the number of berries per bunch was calculated by dividing the number of berries per grapevine by the number of bunches per grapevine.

A comprehensive analysis of yield components was based on measurements of the number of nodes, shoots, inflorescences, flowers and percentage fruit set. These measurements were used to analyse yield following the suggestion of May (1987) i.e. yield as a product of its components: node/vine, shoots/node, inflorescence/shoot, flowers/inflorescence, berries/flower and berry weight.

Flower numbers and fruit set were measured by enclosing six bunches per replicate in muslin bags from a week before full-bloom till after fruit set had finished (four weeks after full-bloom). At the end of this period, the number of flowers and percentage set were calculated by counting the contents after they had been divided into berries which set and flowers which failed to set. Bunches which lost branches due to wind abrasion were not measured.

Grape composition was determined on juice extracted by crushing a 100-berry sample with a tomato juicer. The extraction was complete within 3 h of sampling. The juice was clarified by centrifuging at 7000 rpm for 8 minutes. A 1 in 50 diluted sample was pasteurised and frozen for subsequent determination of malate, tartrate, potassium and sodium. The remainder was used for measurements of TSS (^{o}Brix, refractometer reading corrected to 20^{oC}) titratable acidity, pH and chloride. Titratable acidity was determined on an auto-endpoint titration system by titrating against 0.133 N NaOH to pH 8.3. This machine also read the pH.

Chloride was measured by silver ion titration. Malate and tartrate were measured by ion exchange chromatography using n-butyric acid as the eluting solution. Sodium and potassium were determined by flame photometry.

5.3 RESULTS

5.3.1 Irrigation Water and Soil Salinity

The volume-weighted ECw, depths of irrigation and effective precipitation, and reference crop evapotranspiration are shown for the 1987-88 season in Table 2. Treatments differed in the percentage of the seasonal irrigation depth which was met with saline water; treatments FB-V and V-H received 40%, whereas treatments BB-FB and H-LF only received 10%. As a consequence, the annual salt loads, i.e. the volume weighted ECw between bud-burst and leaf-fall, of treatments FB-V and V-H were twice those of treatments BB-FB and H-LF which, in turn, were twice that of the control, CONT. Values in the 1986-87 and 1988-89 were similar to those in 1987-88.

Changes in soil salinity lagged behind those in the salinity of irrigation water. The seasonal course of the root weighted ECe for the 1987-88 season is shown in Figure 9. Precipitation during winter was insufficient to leach all of the salt applied in the preceding season and at bud-burst the soil salt concentration in treatment H-LF was higher than that in the control. The highest values were reached at the end of the two month periods of irrigation with saline water. Minima were reached after four months of irrigation with non-saline water. The maxima of treatments with high annual salt loads, FB-V and V-H, were greater than those with low annual salt loads, BB-FB and H-LF. Values in the 1986-87 and 1988-89 were similar to those in the second season. Comparison of root weighted ECe within any treatment over the three seasons at the same phenological time showed no increase in value excepting that between the first and second season in the measurements made before bud-burst.

Changes in ECw did not cause a uniform change in ECe down the soil profile. Figure 10 shows sequential samples of ECe by depth. In January, treatment FB-V had been irrigated with saline water for 2 months. The ECe varied with depth. Above 90 cm it was greater than 3.5 dS/m, but below 90 cm it was

Table 2. The volume-weighted electrical conductivity of applied water (EC_w, dS/m), the depth of irrigation and precipitation (I&P mm) and the depth of the reference crop evapotranspiration (ETo mm) for each vine growth period in the 1987-88 season

Growth period	Treatment					I&P	ETo
	BB-FB	FB-V	V-H	H-LF	CONT		
Bud-burst - full-bloom (18/9 - 12/11/1987)	3.34	0.45	0.45	0.45	0.45	92	305
Full-bloom - veraison (13/11/87 - 18/1/1988)	0.52	3.23	0.52	0.52	0.52	397	519
Veraison - harvest (19/1 - 22/3/1988)	0.58	0.58	3.49	0.58	0.58	415	439
Harvest - leaf-fall (22/3 - 10/5/1988)	0.61	0.61	0.61	3.16	0.61	140	154
Bud-burst - leaf-fall (18/9/1987 - 10/5/1988)	0.80	1.58	1.70	0.89	0.55	1043	1417

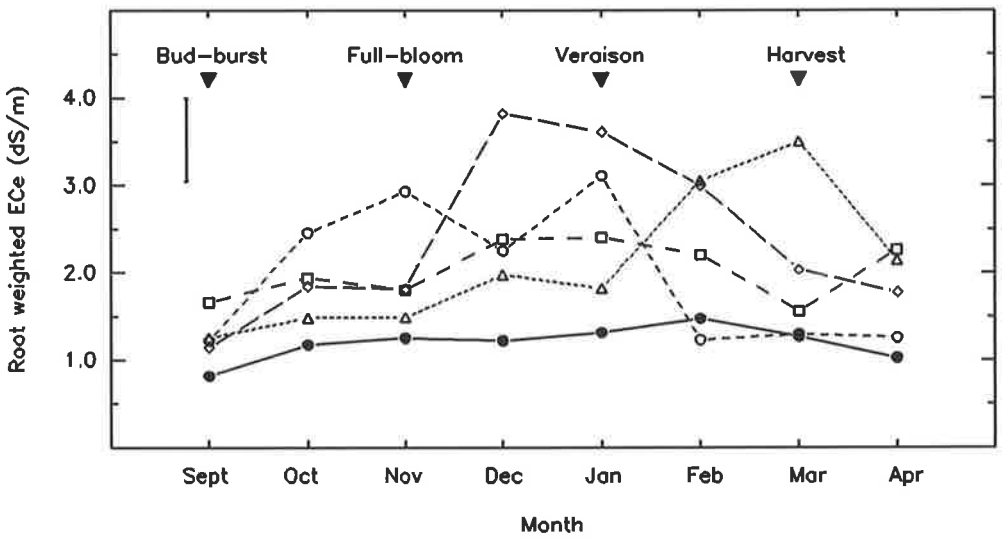

Figure 9. The effect of treatment on the ECe over the 1987-88 season. Bar indicates l.s.d. at $p < 0.05$. BB-FB(o), FB-V(◇), V-H(△), H-LF(□) and CONT(•).

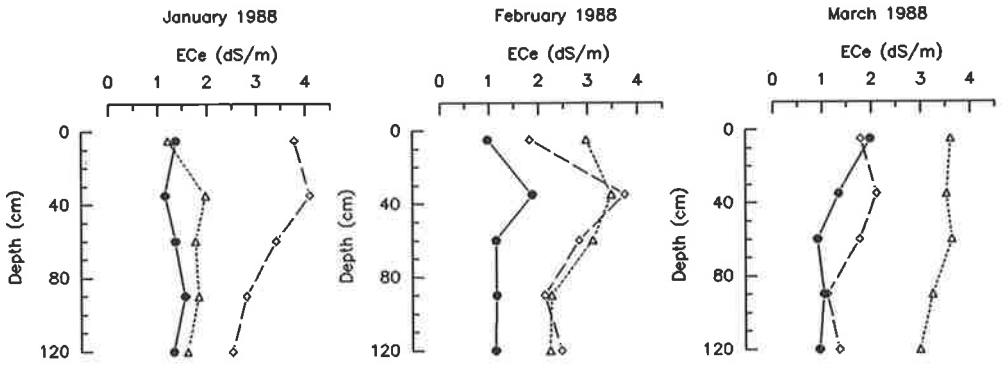

Figure 10. The ECe profile for treatments FB-V, V-H and CONT in January, February and March 1988. FB-V(◇), V-H(△) and CONT(•).

less than 3.0 dS/m. At least 25% of the grapevine roots lay below 90 cm. In February, after 1 month of irrigation with river water the ECe above 20 cm, where 22% of grapevine root length was located, had fallen to less than 2.0 dS/m. In March, after 2 months of irrigation with river water the salt had been leached from the entire rootzone. Following the January sampling, treatment V-H began receiving saline irrigation. In February, after one month of saline irrigation the ECe at 60 cm and above had risen from less than 2.0 dS/m to above 3.0 dS/m, but below 60 cm, where 40% of the root length is located, it had only risen from 1.5 to just above 2.0 dS/m. The irrigation volume applied within the first month of a two month period of saline irrigation was insufficient to change the salinity of the entire rootzone.

After two months of saline irrigation the mean of the ratios of ECw to RWECe in treatments BB-FB, FB-V and V-H was 1:1.

The root weighted values of the chloride and sodium concentrations in the saturated paste extract (data not presented) were highly correlated ($p < 0.001$, $R^2 > 0.88$) with RWECe.

5.3.2 Water Relations

For measurements of Ψ_l and stomatal conductance, the interaction between treatment and sampling time over the course of a day were not significant, and therefore only the daily means are presented for consideration.

Leaf water potential was reduced during and following saline irrigation (Figure 11). The greater reduction occurred during saline irrigation with a fall of between 0.05 and 0.15 MPa. After two months irrigation with fresh water, the Ψ_l of treatments BB-FB and FB-V had fully recovered. In contrast, the Ψ_l in treatment V-H had a trend to remain depressed from October until December which suggests that it had not recovered from saline irrigation which had ceased ten months before in the previous season.

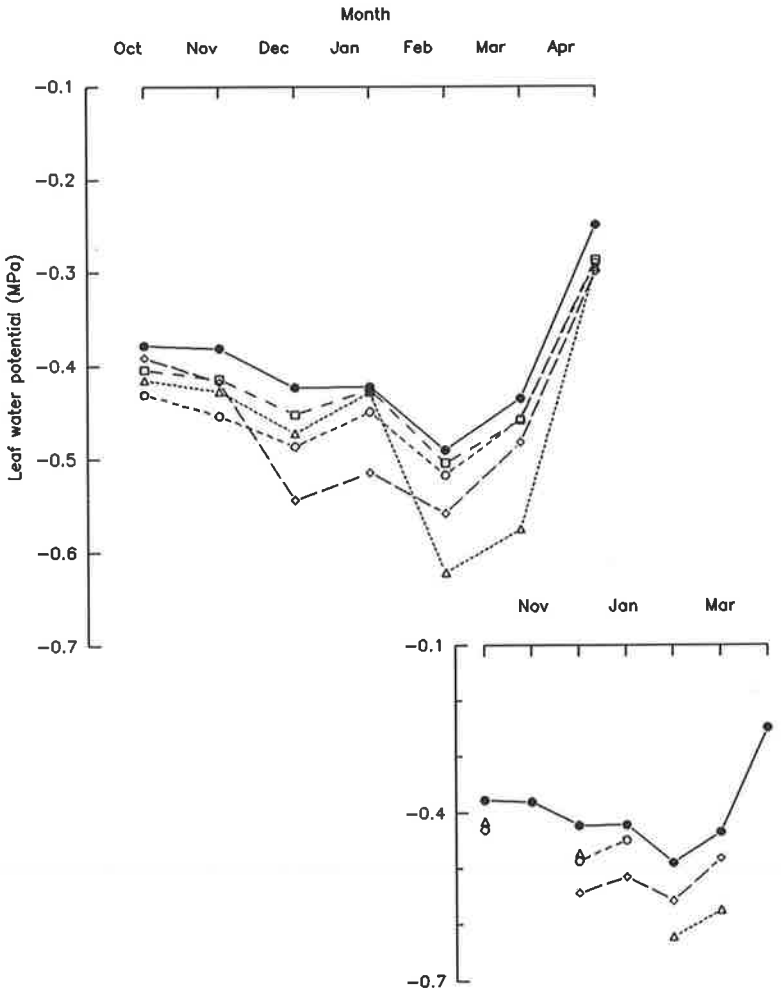

Figure 11. The effect of treatment on the daily mean of measurements of leaf water potential. Inset indicates treatments which significantly differed ($p < 0.05$) from the control. BB-FB(o), FB-V(◇), V-H(△), H-LF(□) and CONT(•).

The changes in pre-dawn Ψ_l were correlated with the changes in the osmotic potential of the saturated soil paste solution (estimated from root weighted measurements of its EC). The dependence is described by the equation

$$(\Psi_l - \Psi_{l\,CONT}) = 1.12(\Psi_{\pi s} - \Psi_{\pi s\,CONT}) - 0.015 \qquad (R = 0.76,\ p = 0.01)$$

where Ψ_l and $\Psi_{\pi s}$ are the values (MPa) of the Ψ_l and the osmotic potential of the saturated soil solution in salinised treatments. Addition of subscript CONT indicates the values in the control treatment.

The reduction in Ψ_l did not lead to a significant fall in leaf osmotic potential nor to a rise in pre-dawn leaf turgor potential (Figure 12). The former decreased and the latter increased with leaf age.

Stomatal conductance was not affected by irrigation with saline water (Figure 13). It declined as leaves aged.

Leaf wet to dry weight ratio did not respond to saline irrigation (Table 3). As leaves aged the ratio declined with values in March lower than those in November and January. The decline was due to a significant decrease in the water per cm^2 of leaf as the dry weight per cm^2 in March was similar to that in January (data not shown).

5.3.3 Ionic Composition

The seasonal courses of the chloride and sodium concentrations in the leaf lamina are shown in Figure 14. Chloride concentration rose most rapidly in the first month of saline irrigation e.g. during November in treatment FB-V. It also rose, albeit at a slower rate, in treatments where the last saline irrigation had been applied in the preceding season e.g. treatment V-H rose in December. At harvest, the mean chloride concentrations in treatments BB-FB, FB-V and V-H, 117 mmol/kg, were 1.5 times that in treatments H-LF and CONT, 72 mmol/kg.

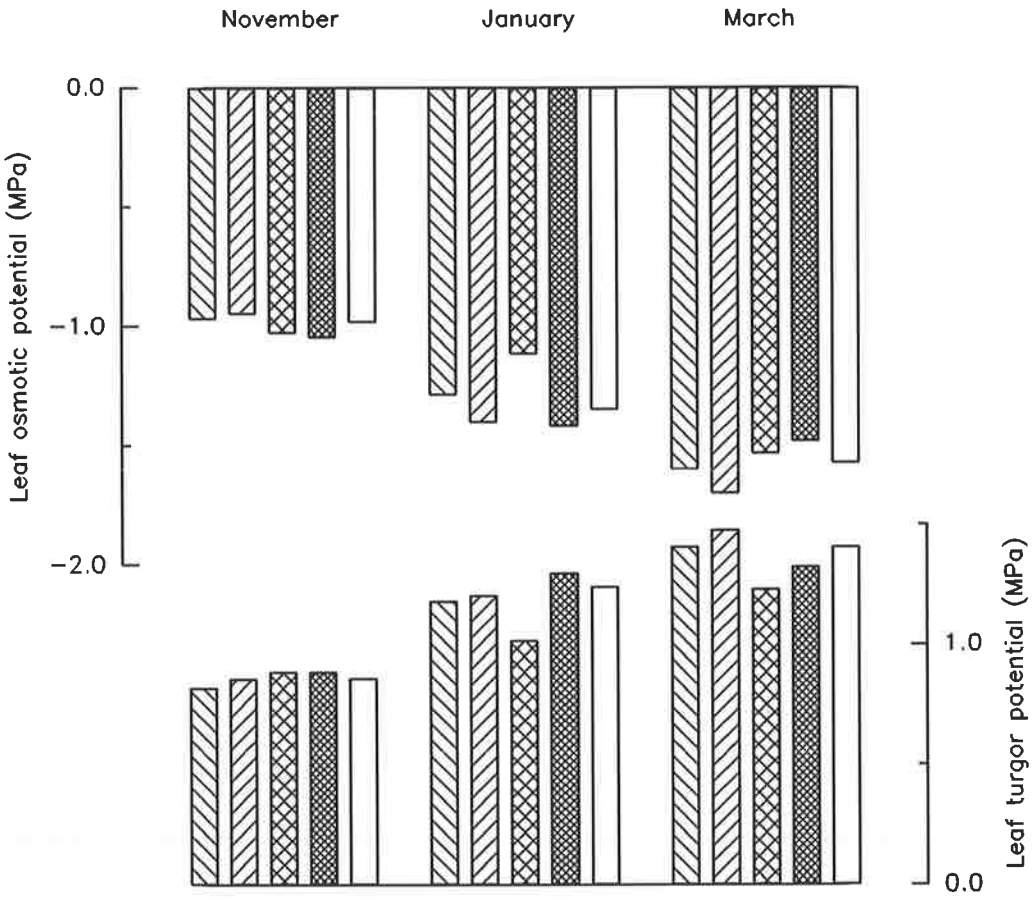

Figure 12. The effect of treatment on the pre-dawn leaf osmotic and turgor potentials at full bloom (November), veraison (January) and harvest (March). Legend as designated for Figure 3.

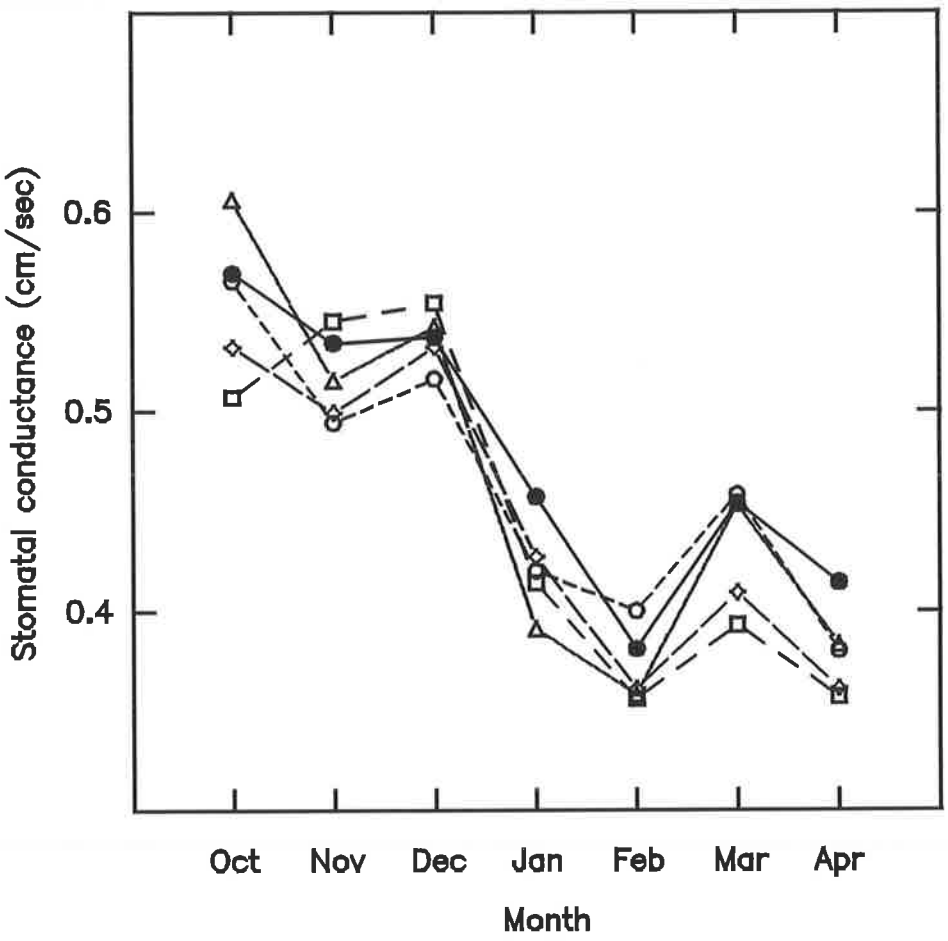

Figure 13. The daily means of measurements of stomatal conductance. Differences amongst treatments were not significant. BB-FB(○), FB-V(◇), V-H(△), H-LF(□) and CONT(•).

Table 3. The ratio of wet to dry weight in the leaf lamina at full-bloom (November), veraison (January) and harvest (March).

Time	Treatment					
	BB-FB	FB-V	V-H	H-LF	CONT	Mean
Full-bloom	3.53	3.52	3.68	3.47	3.63	3.57
Veraison	3.36	3.59	3.62	3.47	3.55	3.52
Harvest	3.22	3.04	3.27	3.15	3.17	3.17

l.s.d. for comparison between the mean of treatments at different times 0.12 ($p = 0.05$)

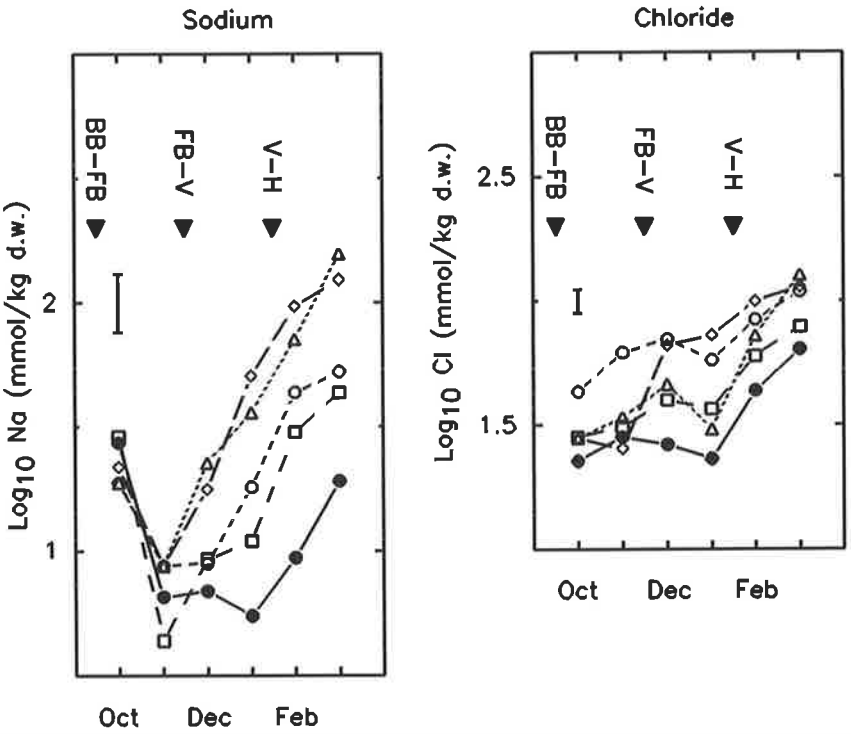

Figure 14. Treatment effects on the leaf lamina Na and Cl concentrations. Arrows indicate when saline irrigation commenced. BB-FB(○), FB-V(◇), V-H(△), H-LF(□) and CONT(•). Bar indicates l.s.d. ($p = 0.05$)

The rate of rise in sodium concentration could not be related to the time that had elapsed since the beginning of saline irrigation. In November, the concentrations in treatments FB-V and V-H increased at a similar rate; saline irrigation of treatment FB-V had just commenced, but that of V-H had ceased eight months before. In January, the sodium concentrations of treatments BB-FB and H-LF both rose above that in the control in January. In BB-FB, the rise in sodium commenced one month after cessation of saline irrigation, but in H-LF it commenced eight months after salinisation. At harvest, the mean sodium concentration of treatments FB-V and V-H, 144 mmol/kg, was seven times that in the control, 20 mmol/kg. The mean of treatments BB-FB and H-LF, 51 mmol/kg, was 2.5 times that in treatment CONT.

The sodium and chloride concentrations in the leaf petiole were up to ten times those in the lamina. Table 4 shows the concentration of these ions in petioles in November and March. In November, treatment BB-FB, which had been irrigated with saline water since bud-burst, had the highest chloride concentration. Chloride concentrations were also higher than the control in all other treatments. These had all received saline irrigation in the preceding season. In November, saline irrigation in either the 1987-88 or the preceding season did not affect the sodium concentrations. At harvest, the difference amongst treatments in the petiole sodium concentration had a pattern similar to that in the leaf lamina. Unlike the leaf lamina, the concentration of chloride in the petiole was not affected by the irrigation salinity.

5.3.4 Vegetative Growth

Neither pruning weights nor the annual growth in the trunk diameter responded to salinity. Both measures are shown for the 1987-88 season in Table 5. Data from the 1986-87 and 1988-89 seasons (data not shown) confirmed the absence of a response to salinity.

Table 4. The concentration of sodium and chloride (mmol/kg d.w.) in the November and March petiole sample from the 1987-88 seasons

Element	Treatment					l.s.d.
	BB-FB	FB-V	V-H	H-LF	CONT	(p=0.05)
November						
Sodium	117	195	190	110	143	n.s.
Chloride	258	212	187	190	127	32
March						
Sodium	500	861	1000	531	287	174
Chloride	508	482	403	415	381	n.s.

Table 5. The effect of treatment on the weight of prunings (kg/vine) and the annual increase in butt circumference (mm/vine) in the 1987-88 season.

	Treatment				
	BB-FB	FB-V	V-H	H-LF	CONT
Weight of prunings	3.1	3.0	3.2	3.0	3.1
Annual increase in butt circumference	12.4	13.6	10.4	9.5	12.3

In 1987-88, saline irrigation did not significantly reduce the rate of shoot elongation or the rates of primary and lateral leaf area expansion (Figure 15). Differences between rates were analysed separately at each sampling. Shoot growth began prior to commencement of sampling and finished 2 weeks after full-bloom. Expansion of primary leaf area followed a similar pattern but ceased two weeks later than shoot growth. Expansion of lateral leaf area was bi-phasic with the first phase coinciding with expansion of primary leaf area and the second phase commencing six weeks after veraison and lasting till harvest. By early March, the small differences in growth rate during the season had significantly reduced the mean area of primary leaves in treatment BB-FB (Table 6). A trend towards shorter shoots and less lateral leaves was present in those treatments salinised prior to harvest.

Saline irrigation did not affect light interception by the canopy (Table 7). The percent of radiation intercepted by the canopy increased between November and January and fell between January and March. The fall was probably due to the reduction in projected area caused by shoots dropping from a horizontal to a vertical alignment as the fruit gained weight.

Figure 16 shows the root length density profile for each treatment. Saline irrigation did not effect the root length density. The absence of an effect on the root length suggests that there was also no effect on root mass. Root length density declined with depth. The pruning weight of the two grapevines, one each side of the root sample, was correlated with the total root length in the 180 cm deep core ($R = 0.51$, $p = 0.05$).

5.3.5 Fruit Growth

The yield, berry weight, bunches per grapevine and berries per bunch for all replicates are shown in Table 8. In 1986-87 and 1988-89 the yield was not affected by salinity. In 1987-88, saline irrigation between full-bloom and veraison significantly reduced yield. This reduction was caused by a decrease in berry

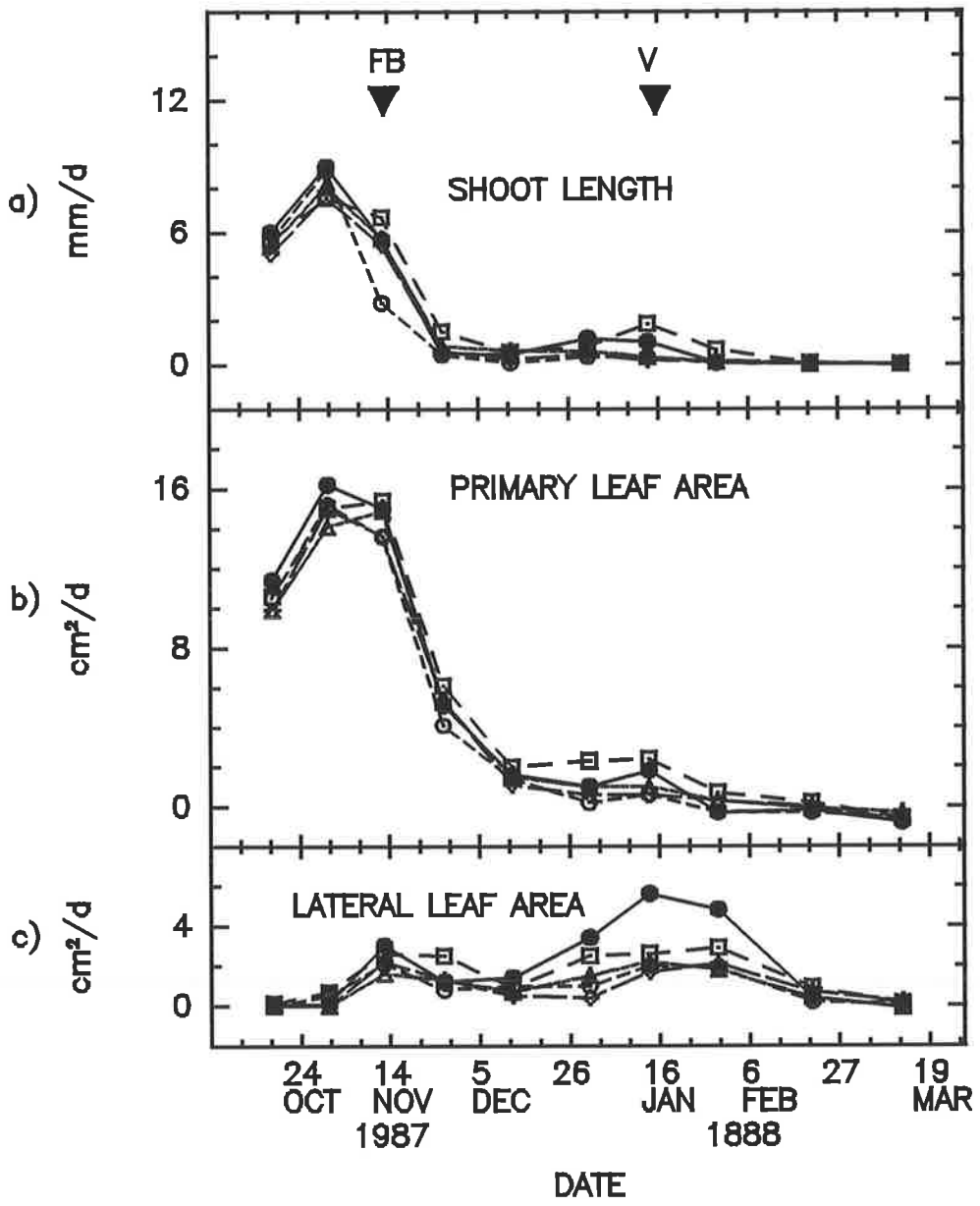

Figure 15. The rates of shoot elongation and leaf area expansion, on a per shoot basis. Arrows indicate full bloom and veraison. Differences between treatments were not significant. BB-FB(○), FB-V(◇), V-H(△), H-LF(□) and CONT(•).

Table 6. Shoot length, area and number of leaves per shoot and area of individual leaves on 4 March 1988.

Treatment	Shoot length mm	Number of primary leaves	Number of lateral leaves	Mean primary leaf area cm^2	Mean lateral leaf area cm^2
BB-FB	439	14.1	6.9	53.6	20.8
FB-V	437	14.7	7.7	54.4	20.4
V-H	445	14.5	7.3	54.7	16.2
H-LF	512	16.8	12.0	54.2	20.3
CONT	493	14.7	11.5	58.9	19.0
l.s.d. ($p<0.05$)	n.s.	n.s.	n.s.	5.1	n.s.

Table 7. The percent of solar radiation (300 -2100 nm) intercepted by the canopy between 1000 and 1400 h at full-bloom (November), veraison (January) and harvest (March).

Time	Treatment					
	BB-FB	FB-V	V-H	H-LF	CONT	Mean
Full-bloom	56.4	59.2	59.8	61.8	59.4	59.3
Veraison	38.2	41.9	44.2	51.1	46.4	44.3
Harvest	49.2	48.0	47.0	51.2	50.0	49.2

l.s.d. for comparison between the means of treatments at different times 3.6 ($p = 0.05$)

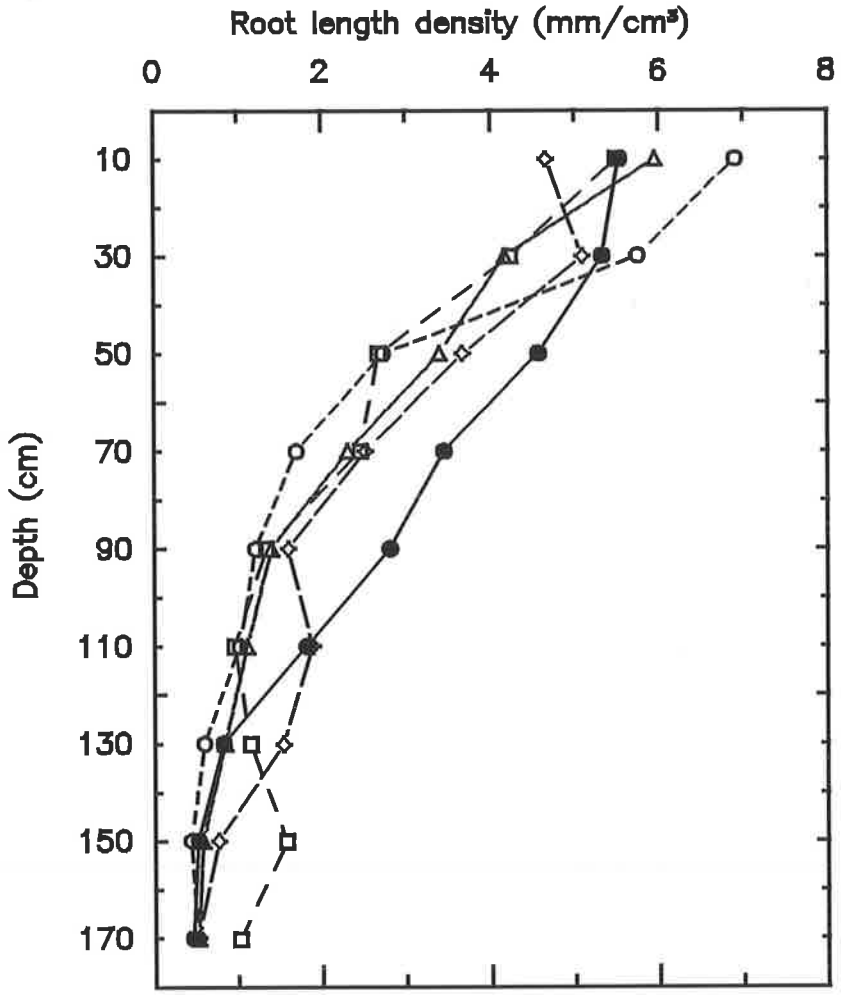

Figure 16. The root length density under the berm in August 1988. Differences between treatments were not significant. BB-FB(○), FB-V(◇), V-H(△), H-LF(□) and CONT(•).

Table 8. The effect of treatment on yield and its components in the three seasons between 1986 and 1989.

Component	Year of harvest	Treatment					l.s.d. ($p = 0.05$)
		BB-FB	FB-V	V-H	H-LF	CONT	
Yield per vine (kg)	1987	65.1	62.8	65.6	64.7	64.5	n.s.
	1988	47.7	43.5	45.8	45.7	46.4	2.1
	1989	66.0	66.6	66.3	67.1	66.3	n.s.
Weight of 100 Berries (g)	1987	168	160	161	172	163	8
	1988	171	162	175	172	174	8
	1989	160	157	157	166	168	7
Bunches per vine	1987	348	351	345	336	338	n.s.
	1988	393	374	366	363	365	21
	1989	462	471	456	439	449	n.s.
Berries per bunch	1987	112	113	120	114	118	n.s.
	1988	72	73	72	74	74	n.s.
	1989	90	90	94	92	89	n.s.

weight. Salinity between bud-burst and full-bloom significantly increased the number of bunches per grapevine in treatment BB-FB. The increase in treatment BB-FB was insufficient to affect yield and its occurrence was limited to the 1987-88 season. In 1988-89, salinity reduced the berry weight in treatments BB-FB, FB-V and V-H confirming and extending the response established in 1987-88.

A comprehensive analysis of yield components obtained from four replicates is shown in Table 9. Salinity did not significantly affect these components, however two trends emerge. First, saline irrigation increased the number of bunches per shoot. Given all treatments had an equivalent number of nodes retained at pruning and a similar number of shoots per node, then the increase in bunches per shoot should lead to an increase in bunches per grapevine. Second, saline irrigation during berry ripening in the preceding season reduced flower initiation. Given berry set in treatment V-H was similar to that in the control the decrease in flower initiation should lead to less berries per bunch in treatment V-H.

Comparison between the comprehensive analysis of yield and that based on all 16 replicates showed the number of berries per bunch was higher in the comprehensive analysis. The reduction in number probably occurred because tendril-like bunches with fewer berries were included in the bunch counts from all 16 replicates.

5.3.6 Fruit Composition

Irrigation with saline water did not affect the juice TSS at harvest (Table 10). In 1986-87, saline irrigation before harvest increased the tartrate, sodium and chloride concentrations and pH in treatments FB-V and V-H. In 1987-88, saline irrigation before harvest increased malate and tartrate, potassium, sodium and chloride concentrations and the pH and titratable acidity. Saline irrigation after harvest in the first season increased sodium and pH in the second season. In 1988-89, saline irrigation, in any growth period, increased pH, Na and Cl. When applied before veraison it increased tartrate, malate and potassium, whereas when applied after veraison it decreased tartrate.

Table 9. Yield components per vine for 1987-88 season (differences between treatments were not significant).

Factor	Component	Treatment				
		BB-FB	FB-V	V-H	H-LF	CONT
Pruning	nodes/vine	227	213	204	200	211
Bud-burst	shoots/node	0.75	0.74	0.72	0.74	0.75
Bunch initiation	bunches/shoot	2.51	2.40	2.48	2.41	2.26
Flower formation	flowers/bunch	591	550	531	586	593
Berry set	berries/flower	0.18	0.21	0.16	0.16	0.14

Table 10. The effect of treatment on juice composition in the three seasons between 1986-89.

Component	Year of harvest	Treatment					l.s.d.
		BB-FB	FB-V	V-H	H-LF	CONT	(p = 0.05)
Total soluble solids (°Brix)	1987	17.8	17.3	17.6	17.5	17.7	n.s.
	1988	21.3	21.2	21.4	21.2	21.3	n.s.
	1989	18.9	19.0	19.0	19.0	18.7	n.s.
Titratable acidity (g/L)	1987	11.19	11.34	11.27	11.01	11.04	n.s.
	1988	9.31	9.04	9.03	8.56	8.64	0.25
	1989	8.73	8.71	8.51	8.24	8.44	0.33
Tartrate (g/L)	1987	8.13	8.19	8.21	8.00	7.95	0.20
	1988	7.46	7.88	7.21	6.93	6.81	0.36
	1989	8.02	7.81	7.24	7.13	7.58	0.22
Malate (g/L)	1987	5.01	4.99	4.79	4.66	4.87	0.25
	1988	4.3	3.5	3.32	2.96	2.87	0.23
	1989	3.18	3.04	2.94	2.81	2.92	0.20
K (mM)	1987	34.2	34.3	33.4	33.2	33.5	n.s.
	1988	42.2	46.6	45.4	40.0	38.3	2.0
	1989	34.9	35.8	34.1	33.7	32.9	1.6
pH	1987	3.091	3.100	3.067	3.066	3.067	0.014
	1988	3.160	3.230	3.217	3.188	3.156	0.023
	1989	3.293	3.299	3.291	3.268	3.243	0.021
Na (mM)	1987	1.1	3.1	1.7	0.5	0.7	0.6
	1988	1.8	5.2	4.1	1.2	0.6	0.5
	1989	2.0	3.8	3.4	1.4	0.4	0.6
Cl (mM)	1987†	0.46^{bc}	1.12^{a}	0.57^{b}	0.41^{c}	0.41^{c}	
	1988†	0.89^{b}	1.64^{a}	0.96^{b}	0.79^{c}	0.68^{c}	
	1989	0.9	1.3	0.9	0.7	0.3	0.2

† Cl data from the 1986-87 and 1987-88 seasons were log transformed for analysis.

5.4 DISCUSSION

5.4.1 Treatments and the annual salt load

Treatments differed not only in the timing of saline irrigation, but also in their annual salt loads. The annual salt loads of BB-FB and H-LF were similar and less than those of FB-V and V-H which were similar. Data can be normalised with regard to the salt load by expressing for a variable of interest the difference between the value in a salinised treatment and that in the control as a function of the difference between the value of the annual salt load in the salinised treatment and that in the control.

5.4.2 Soil

Changes in soil salinity followed, but lagged behind, those of the irrigation water salinity. In all treatments the changes in soil ECe could be osmotically related, on a one-to-one basis, to changes in Ψ_l which suggests that the RWECe characterised the soil water potential as integrated by the grapevine. The major rises in leaf Cl concentration also followed changes in RWECe, however changes in the leaf Na concentration did not follow those of the RWECe e.g. the rise in these ions in treatment V-H preceded a rise in RWECe. This suggests that RWECe did not necessarily characterise the grapevine's integration of the soil ionic environment.

In the present study, the one-to-one relationship between Ψ_l and the osmotic potential of the saturated soil paste suggests that the osmotic potential of the soil solution surrounding the roots was equivalent to that in the saturated paste i.e. the ratio ECe:ECsw is 1:1. This contrasts with the USDA (1954) estimate of the ratio of ECe:ECsw ratio at 1.5:1. Their relationship was determined before the advent of high frequency irrigation and the discrepancy between it and that determined in the present work may reflect a sensitivity of the relationship to variation in the frequency of irrigation.

L.D. Prior (pers. comm.) calculated that the ratio ECe:ECsw was 2.6:1 for her high frequency drip irrigated vineyard based on measurements of the water contents of the saturated soil paste and the soil at field capacity. As this ratio is higher than that of USDA (1954) it is unlikely that differences in the frequency of irrigation have caused the variation in ECe:ECsw ratios between the present experiment and USDA (1954). Both L.D. Prior (pers. comm.) and USDA (1954) developed their estimates of ECe:ECsw from data collected from sites where exposure to salinity had been long term. At these sites it was likely that concentration of salt in the soil was approaching equilibrium with that in the irrigation water. In contrast, exposure to salinity in the present trial was limited to short periods (of about two months) and the relationship between salt concentrations in the water and soil was dynamic e.g. see Figure 10. The difference between the effects of long and short term exposure to salinity on the ratio of ECe:ECsw may weaken between-experiment comparisons based on ECw and confound assumptions made in the interpretation of pot trials regarding the equivalence between ECw in glasshouse experiments and ECsw in the field e.g. Downton (1985).

After three years of continuous saline irrigation, ECw 3.5 dS/m, Prior *et al.* (1992c) found ECe had risen to 4 dS/m. In the present experiment irrigation with the same salinity water raised the ECe to 4 dS/m in two months i.e. in one-twelfth of the time (assuming the duration of a season was eight months). The discrepancy between the two studies in the time taken for the ECe to respond may have been due to differences in the soil sampling procedures.

Prior *et al.* (1992c) measured ECe on samples which were taken from their 'standard position' which was located 0.5 m out from the vine row and on a transect perpendicular to the vine row midway between the emitter and the vine (0.25 m from each) at 0.6 m depth. They found this sampling location gave a value which was nearest to the average for the entire rootzone. In the present study, samples were located in the area with the greatest root length (Stevens and Douglas, 1994) and soil salinity was sampled at a number of depths and a root weighted average was calculated. Ayers and Westcot (1985) suggested the root weighting technique

produces a measure representative of the soil water extracted by the plant. Prior *et al's.* (1992c) measure is probably a better indicator of the salt storage in the rootzone than the measure of RWECe used in the present study. However, the relationship between the grapevine Ψ_l and RWECe in the present study suggests that the root-weighted measure is a good indicator of the ECe to which the grapevine roots are exposed.

In the vineyard where the present experiment occurred, the soil salinity varied with depth (see Figure 10) and horizontal distance from the vine row (Stevens and Douglas, 1994). Shani *et al.* (1993) investigated grapevine water use in a split root experiment irrigating one side of the rootzone with saline water and the other with non-saline water. They found that the grapevine met most of its water requirements from the non-saline side. In the present experiment, the rootzone contained both saline and non-saline zones for a month or more following the change from non-saline to saline irrigation. After saline irrigation commenced, the length of time which elapsed before the root zone lost its heterogeneity with regard to salinity was dependent on the rate of irrigation. When the period of saline irrigation coincided with a period of low grapevine water use, e.g. bud-burst to full-bloom, then irrigation replaced about one quarter of the volume of water in the rootzone, whereas when it coincided with a period of high grapevine water use, e.g. full-bloom to veraison, then irrigation replaced nearly the whole volume of water in the rootzone.

The opportunity for avoidance was not equally available in all saline irrigation treatments. In treatments which annually received about 100 mm of saline irrigation, BB-FB and H-LF, less of the rootzone would have been salinised than in those which annually received about 400 mm of irrigation i.e. FB-V and V-H. Normalisation of results with regard to salt load does not remove the effect that a variation in the annual salt load has on the opportunity for avoidance. The significance of the opportunity for grapevine roots to redirect water uptake to zones of low salinity within the rootzone depends on the depth of the rootzone.

In the present experiment, the rootzone was about two metres deep and held about 480 mm of water at field capacity. With irrigation volumes of 50 mm or less per week, the volume of saline water added in any of the treatments was not sufficient to completely displace the water held within the rootzone. If, however, the rootzone had been shallow, e.g. 75 cm as is the case in some Sultana vineyards (Nagarajah, 1987), then the opportunity for avoidance would have been reduced.

Where the salinity of applied water (irrigation and effective precipitation) has the potential to significantly vary over the season then management of the rootzone to maximise its depth is an important aspect of a salinity management strategy. When soil is waterlogged for three days in every two weeks, grapevine roots do not grow (Stevens, Harvey and Johns, unpublished data). In the Riverland, transient waterlogging following irrigation is caused by perched watertables persisting for three or more days. The depth of the perched watertable is probably a major factor in setting the depth of a rootzone.

The interaction between timing of saline irrigation and the opportunity for the vine to avoid salinity can be reduced by practices which enhance salt uptake. Examples of such practices include: the common practice of over-irrigation just after bud-burst which raised the perched watertable - waterlogging soil of the lower rootzone which enhances salt uptake (Cock *et al.*, 1991; Stevens and Harvey, 1995); application of irrigation with over-canopy sprinklers which facilitates foliar uptake of salt - this uptake is insensitive to the proportion of the rootzone that is saline.

5.4.3 Water relations and tissue Na and Cl concentrations

Prior *et al.* (1992b) suggested that the primary cause of reduced yield in salinised grapevines was a reduction in photosynthesis. They found that photosynthesis declined in a curvilinear manner with increasing leaf chloride concentrations. At leaf lamina Cl concentrations below 600 mmol/kg d.w. decreases in photosynthesis were due to a decline in stomatal conductance (Walker *et al.*,1981; Downton *et al.*, 1990). In all treatments in the present experiment the

leaf chloride concentrations remained well below 600 mmol/kg d.w. and, with the exception of treatment BB-FB, saline irrigation did not reduce stomatal conductance and therefore it probably had no effect on the leaf photosynthetic rate.

In October, the depression of Ψ_l in treatment V-H suggests a carryover effect that cannot be attributed to soil salinity since the RWECe in V-H was similar to that in CONT. It is possible that the depression of Ψ_l was caused by a reduction in root hydraulic conductivity. Syversten and Graham (1985) noted such a response in salinised citrus.

During berry development and maturation in the present experiment, the leaf chloride concentration in the treatment which experienced a yield loss, FB-V, was equivalent to that in a treatment which suffered no yield loss, BB-FB, and the leaf sodium was equivalent to that in treatment V-H, which, again, suffered no yield loss. These results suggests that the yield decline was not due to a toxic effect on leaf metabolism by either ion individually.

Leaf Na and Cl had different time courses of change in concentration. The major increases in leaf chloride were coincident with increases in the salinity of irrigation water. This synchronism suggests that uptake during saline irrigation was the main source of elevated leaf chloride.

Most of the major increases in leaf sodium were asynchronous with increases in salinity of irrigation water. In treatment BB-FB, leaf Na concentration fell during saline irrigation and did not begin to rise until one month after it had ceased and one month after the maximum RWECe. In treatments V-H and H-LF it began to rise two months before saline irrigation commenced and eight months after saline irrigation had ceased in the preceding season. The asynchronism between the rise in leaf sodium and the salinity of irrigation water suggests that between the end of saline irrigation and the rise in leaf sodium, sodium was carried over within either the soil or elsewhere within the plant.

The increases in leaf Na in treatments BB-FB and V-H occurred whilst the RWECe of these treatments were equivalent to that in CONT. Therefore the rises in leaf Na cannot be attributed to a carryover of Na in the soil. In salinised peaches, Boland *et al.* (in press) found that perennating tissue preferentially accumulated sodium. This result provides support of West's (1986) proposition that toxic ions may accumulate in metabolically inactive storage and structural organs prior to movement into metabolically active organs. In the present experiment it is likely that sodium was stored in perennating tissue prior to its movement to metabolically more active tissue such as leaves. However the time course of sodium remobilisation suggests that control of the process is complex. For example, in treatment V-H the rise in leaf Na began eight months after the last saline irrigation and it proceeded at a rate equivalent to that in treatment FB-V whilst this treatment was receiving saline irrigation. The rise occurred whilst the sodium load in the substrate was low and this pattern of Na accumulation does not reconcile with a model of sodium movement based on overflow from a pool into which sodium was otherwise sequestered.

The concentrations of Na and Cl in the leaf did not fall during the season which suggests that neither ion was re-transported out of the leaf.

In order to separate the effect of the timing of saline irrigation from the effect of differences in the annual salt load, the data were normalised with regard to the annual salt load. Based on the leaf lamina sample taken in March, the uptake rates for chloride for treatments BB-FB, FB-V, V-H and H-LF were 180, 49, 55, 44 mmol/kg.(dS/m) and for sodium were 139, 104, 121, 77 mmol/kg.(dS/m), respectively. Similarly, based on the grape juice concentrations at harvest, the uptake rates for chloride were 0.8, 0.9, 0.2 and 0.3 mM.(dS/m), and for sodium were 4.8, 4.7, 3.0 and 1.8 mM.(dS/m) in treatments BB-FB, FB-V, V-H and H-LF, respectively.

The normalised chloride accumulation rates in the leaf and berry were dependent on the timing of saline irrigation. The leaves which were sampled for

ion analysis had finished growing before full-bloom (data not presented). Chloride accumulation was much greater when the annual salt load was applied during leaf growth (cell division and expansion), i.e. between bud-burst and full-bloom, than after growth had ceased. Pericarp cell division finishes during the first third of the period between full-bloom and veraison, whereas cell expansion continues till harvest. Chloride accumulation rates in the berry were much greater when saline irrigation was applied before veraison than after it. Chloride uptake in treatment H-LF probably occurred early in the season, whilst the RWECe was still elevated from saline irrigation in the preceding season. The absence of high chloride accumulation rates when only cell expansion was in progress suggests that chloride uptake was most active during cell division in the pericarp.

The xylem pathway to the berry is interrupted at veraison (Findlay *et al.*, 1987). The coincidence of a drop in berry chloride accumulation rate with interruption of the xylem suggests that chloride uptake is dependent on xylem transport. In contrast, during the fall in chloride accumulation rates in the leaf, the stomatal conductance remained high indicating that the xylem was intact. This suggests that this fall in Cl accumulation is unrelated to the functional integrity of the xylem.

In contrast with the variation amongst treatments in the normalised Cl uptake rates, the rates of sodium uptake in the leaf lamina and grape berry were relatively constant across the treatments (excepting treatment H-LF) suggesting that Na uptake was not dependent on organ age nor on the functional integrity of the transpiration process.

In own-rooted grapevines, petiole concentrations of sodium and chloride at full-bloom greater then 217 and 423 mmol/kg, respectively, had been considered to be toxic (Robinson and McCarthy, 1985; Prior *et al.*, 1992b) In the second season of the present experiment, the concentrations of Na and Cl in the petiole of treatment FB-V at full-bloom were 195 and 212 mmol/kg, respectively. Although both values were below the suggested toxic levels, yield declined. This suggests

that guidelines for acceptable concentrations of Na and Cl developed in own-rooted grapevines under conditions of constant salinity may not apply to rootstock grapevines where the salinity of the irrigation is highly variable. Such situations occur where the major exposure is caused by foliar deposition from oceanic winds which are often limited to a particular period in the growing season or in a climatic region where half the grapevine water requirements are met by precipitation and the major exposure is caused by saline irrigation applied after the end of late spring rains.

In mature own-rooted Sultana vines (Prior *et al.*, 1992b) and in potted own-rooted Cabernet Sauvignon (Downton and Hawker, 1980) the chloride concentrations of the leaf lamina and petiole expressed on a fresh weight basis were similar. In the present experiment, in treatment BB-FB the petiole Cl concentration expressed on a dry weight basis was double that in the leaf lamina. The relative difference was maintained when the Cl concentrations were expressed on a fresh weight basis, assuming the petiole had water contents similar to that found by Prior *et al.* (1992b). Under non-saline conditions, Downton (1977c) also observed that the chloride concentration, expressed on a dry weight basis, was higher in the petiole than in the lamina, and based on this observation he suggested that petioles control lamina Cl concentration by preferentially accumulating Cl. The leaf chloride concentrations in the studies of Prior *et al.* (1992b) and Downton and Hawker (1980) were much greater than in the present study. The absence of a gradient between lamina and petiole at higher salinities suggests that any protective role of the petiole is readily saturated at higher salinities.

5.4.4 Vegetative Growth

Primary leaf growth, which had ceased by veraison, was reduced in treatment BB-FB. This agrees with Thomas (1934) who found salinity reduced leaf size, however, unlike the present study, he found the decrease in size was associated with premature leaf-fall.

In the present study, saline irrigation between full-bloom and veraison, which coincided with major periods of berry and shoot growth only reduced the growth of the berry. This suggests that fruit growth is more sensitive to salinity than shoot growth. In contrast, Prior *et al.* (1992b) found with a different irrigation strategy that salinity reduced shoot growth more than fruit growth. The reversal suggests that the relative sensitivity of organs to salinity stress is dependent on the irrigation strategy. Differences between irrigation strategies in the opportunity each provides for the grapevine to avoid stress may be the cause of this reversal.

The opportunity for grapevines in treatments BB-FB to avoid extracting water from saline regions of the rootzone was greater than that for grapevines in treatment FB-V and therefore it is likely that this irrigation strategy would favour avoidance of stress during vegetative growth over avoidance during fruit growth. The opportunity to generate rootzones containing both saline and non-saline zones did not occur in the experiment of Prior *et al.* (1992a) with its regime of continuous saline irrigation.

5.4.5 Yield

If the yield response to salinity is not affected by the distribution of the annual salt load then the yield decline with the salt load spread evenly across the season should be the equivalent to that with the same salt load delivered in a two month period within the season. The experiment of Prior *et al.* (1992a) on own-rooted Sultana grapevines spread the salt load evenly across the season. This study cannot be directly compared with the present study because the experiments used different cultivars and rootstocks and were conducted at sites with different soils.

Comparison between the present glasshouse experiment and Downton (1985) suggest that Sultana on Ramsey and Colombard on Ramsey have a similar sensitivity to salinity. Downton (1985) has shown the loss of growth by Sultana on Ramsey rootstocks irrigated with 12.5 mM NaCl was only half that of own-rooted Sultana.

Based on these studies the yield decline found by Prior *et al.* (1992a) should be double that found in Colombard grapevines on Ramsey rootstock (see also section 2.1.4).

Prior *et al.* (1992a) found that yield fell as the silt plus clay content in the soil between 60 and 90 cm depth increased from 19% to 28%. Prior *et al.* (1992c) were uncertain of the nature of the causal link between yield and the soil's silt plus clay content. They suggested that the link may be an association between % silt plus clay and soil oxygen concentration. At their site the watertable resided within 1.3 to 1.5 m depth from the surface, whereas at the site of the present experiment it was below 2.5 m. A high watertable retards drainage and predisposes the lower rootzone to extended periods of waterlogging i.e. a soil water content greater than field capacity (Rowe and Beardsell, 1978). If the causative link was dependent on proximity of the watertable to the surface, then substitution of the percentage silt plus clay at the present site (41% in soils between 60 and 90 cm depth) into the equation of Prior *et al.* (1992a) for the purpose of prediction would produce spurious predictions. To avoid this risk it has been assumed that for the purpose of predicting losses the percentage silt plus clay was in the middle of the range at the site of Prior *et al.* (1992a) i.e. 24%.

For the first three seasons of saline irrigation, Table 11 shows the yield, expressed as a percentage of that in the non-saline control, for the present study and that predicted from the work of Prior *et al.* (1992a) for the three annual salt loads equivalent to those applied to treatments BB-FB (equivalent to values in H-LF), FB-V and V-H. Predictions from Prior *et al.* (1992a) have been adjusted for the use of Ramsey rootstock i.e. the losses predicted by Prior *et al.* (1992a) have been halved. Over the first three seasons of saline irrigation, the average yield in the control treatments of Prior *et al.* (1992a) and the present study were 29 and 68 t/ha., respectively.

Comparison at similar annual salt loads between the present study and one with an irrigation strategy which spread the salt load evenly across the season

showed the former strategy avoided a 10% yield loss associated with the latter strategy *cf.*, losses of V-H and the continuous treatment for an annual salt load of 1.6 dS/m. These results show replacement of up to 40% of the annual water requirements with saline water does not necessarily reduce yield.

In Table 11, the losses to be expected if the irrigation regime of Prior *et al.* (1992a) had been applied may have been under-estimated. The use of a value of 24% silt plus clay in calculating the loss predicted by Prior *et al.* (1992a) was conservative. Calculation of the predicted losses using the actual value of percentage silt plus clay at the site of the present experiment (41%) gives a mean estimated yield loss for the three seasons of 52% for treatments FB-V and V-H. When adjusted for the use of a rootstock this loss equates to 26% ie 2.5 times the loss estimated assuming 24% silt plus clay.

Prior *et al.* (1992a) developed equations describing yield loss as a function of the EC of irrigation water (ECi) without regard to the dilution due to effective rainfall during the irrigation season. Over the six year experiment, the average seasonal application of saline water was 341 mm and the average depth of effective rainfall was 101 mm. If the ECi was 1.6 dS/m then taking into account rainfall for calculation of ECw gives an ECw of 1.2 dS/m or stated another way for an ECw of 1.6 dS/m the corresponding ECi would have been 2.1 dS/m.

Even when saline water was applied at the most sensitive growth stage (treatment FB-V) the reduction in yield was one third of that to be expected had the same salt load been spread evenly over the season. In FB-V, all of the salt load was applied in the most sensitive period and this would be expected to produce a greater loss than spreading an equivalent salt load evenly across the season i.e. one-quarter applied in the most sensitive period (full-bloom to veraison) and three-quarters applied in less sensitive periods. The avoidance of two-thirds of the predicted loss suggests that factors other than the annual salt load confer an advantage to an irrigation strategy which confines the salt load to one part of the

Table 11. A comparison of yields† with the same annual salt load applied either as a constant salinity throughout the season or as a saline irrigation during one of the four growth phases (pre-anthesis BB-FB, berry development FB-V, berry maturation V-H, post-harvest H-LF).

Annual salt load (dS/m)‡		0.79		1.46		1.60	
Application method		Constant	BB-FB or H-LF	Constant	FB-V	Constant	V-H
Season	1	100	101	100	97	100	102
	2	95	101	88	94	87	99
	3	97	101	88	100	86	100
Mean		97	101	92	97	91	100

†Yield expressed as a per cent of that in the non saline control (EC 0.44 dS/m)
‡Annual salt load refers to the volume weighted EC for the whole season (Table 2)

season. Minhas and Gupta (1993) made a similar finding in wheat. They compared a number of strategies for managing saline irrigation with a fixed annual salt load. Their treatments included mixing saline and non-saline water to produce irrigation water with a constant salt concentration throughout the season and limiting saline irrigation to particular growth stages. They concluded that a strategy of mixing to provide water of a constant salinity produced the greatest yield decline. This aspect of the results is also addressed in the next section on yield components where the interaction between the irrigation regime in the present study and the opportunity for the vine to avoid salinity is given further consideration.

5.4.6 Yield Components

Yield is a product of berry weight, berries per bunch and the number of bunches per grapevine. The identity of the yield component which was most responsive to salinity also depended on the irrigation strategy. With discontinuous salt stress the component which underwent the greatest decline was berry weight (Table 8), whereas with continuous salt stress it was bunch number (Prior *et al.*, 1992a).

Berry pericarp growth involves processes of cell division and cell enlargement. Cell division begins one month before full-bloom, i.e. during the last month of saline irrigation of treatment BB-FB, and finishes about one month after full-bloom i.e. continues throughout the first month of the saline irrigation of FB-V. Cell enlargement begins after fruit set and ceases close to harvest i.e. throughout nearly the entire periods of saline irrigation in treatments FB-V and V-H (Harris *et al.*, 1968). In the second season, berry size was reduced by saline irrigation between full-bloom and veraison i.e. saline irrigation in the second month of cell expansion and in the first two months of cell division. In the third season, it was reduced in the two treatments where saline irrigation was applied during cell division (BB-FB and FB-V) and in the two treatments where saline irrigation was applied during cell expansion (FB-V and V-H). Based on these results both growth processes appear to have similar sensitivities to salt stress, however this comparison

between treatments is confounded by differences between treatments in annual salt loads.

In the third season, normalisation of the changes in the weight of 100 berries with regard to the annual salt load gives rates of -21, -14, and -10 g/dS.m for treatments BB-FB, FB-V and V-H, respectively. The coincidence of the greater decline with the application of saline irrigation during the period of cell division (BB-FB and FB-V) suggests cell division is more sensitive to saline irrigation than cell expansion. Normalised Cl and Na uptake rates for the berry juice were also higher during cell division; for treatments BB-FB, FB-V and V-H they were 1.5, 1.3 and 0.5 mM/dS.m for Cl and 4.1, 4.4 and 2.6 mM/dS.m for Na, respectively.

When normalised for differences in the annual salt load, the results of the present study are in agreement with those of Hawker and Walker (1978). They investigated the effect of timing of saline irrigation on berry growth with fruiting rootlings. They concluded that berry growth was more sensitive to saline irrigation during the period coincident with cell division than during that coincident with cell expansion.

Expression of results normalised for salt load ignores the interaction between the size of the annual salt load and the opportunity for the grapevine roots to avoid saline regions of the rootzone. The opportunity for such avoidance is greater in treatments BB-FB with a moderate annual salt load than in treatments FB-V and V-H with high annual salt loads. This suggests that if the opportunity for avoidance was reduced, i.e. at sites with a shallow rootzone, then the decline of berry weight in treatment BB-FB when normalised for the annual salt load would have been greater. Yield decline was solely due to a reduction in berry weight. Berry growth was most sensitive to salinity between bud-burst and full-bloom i.e. the normalised rate of decline in berry weight in treatment BB-FB was much greater than those in treatments FB-V and V-H. The absence of a yield decline in BB-FB demonstrates how important the opportunity for avoidance is in determining the effect of salinity.

The major effects of saline irrigation have been attributed to two modes of action, osmotic and toxic effects. Where the response of a grapevine to salt stress has diverged from the response to water stress then it is likely that this response may be due to toxic effects of salinity.

The temporal characteristic of berry growth sensitivity to salt stress is similar to that in response to water stress. Over a three year period, both Matthews and Anderson (1989), and Van Zyl (1984) recorded the response of grapevines to water stress during berry development and maturation. Both studies found berry weight was more sensitive to water stress during berry development.

Neither the present study nor that of Prior *et al.* (1992a) found saline irrigation to have an effect on fruit set. This suggests that the reduction found by Hawker and Walker (1978) with fruiting grapevine rootlings which were salinised for three weeks beginning 10 days before flowering may not apply to mature field grown grapevines.

The insensitivity of fruit set to saline irrigation contrasts with its sensitivity to water stress. Water stress after full-bloom was found to reduce fruit set in field grown Colombard grapevines (Van Zyl, 1984) and potted Cabernet Franc grapevines (Hardie and Considine, 1976). The absence of a response under saline irrigation suggests a reduced role for the osmotic effect of salinity in the response of yield to salinity.

In the 1987-88 season, saline irrigation between bud-burst and full-bloom decreased the primary leaf area which probably increased the amount of radiation falling on buds in the axils of primary leaves. It is likely that a similar response was present in 1986-87. Buttrose (1974) found bunch initiation is stimulated by an increase in the incident radiation falling on the bud. The increased number of bunches in BB-FB in 1987-88 may have been due to an increase in the light reaching the buds in the preceding season, however the absence of an increase in the

number of bunches in treatment BB-FB in 1988-89 suggests that the increase in 1987-88 must be attributed to a factor other than the increase in bud illumination.

5.4.7 Composition

The sensitivity of yield to saline irrigation was limited to the period between full-bloom and veraison in one of three seasons. In contrast, the responses of juice composition to saline irrigation were present in all three seasons and occurred in all treatments. Further, unlike yield where the effect was associated with a high annual salt load, the greatest effects on some juice components occurred with a low annual salt load.

In agreement with the present study, Makhija *et al.* (1986), Prior *et al.* (1992a) and McCarthy (1981) working on the varieties Perlette and Delight, Sultana, and Shiraz, respectively, found the concentration of TSS (as °Brix) did not respond to salinity.

The values of all measured compositional variables change during maturation. The absence of an effect on TSS suggests that the maturation processes in all treatments were synchronous. Thus, comparison of other compositional variables between treatments is not confounded by differences in ripening (Freeman and Kliewer, 1983). The presence of significant effects of saline irrigation on composition variables in treatments where salinity did not affect berry weight suggests that effects on composition were not a secondary effect of a salinity induced reduction in berry volume.

Salinity increased the juice pH, and concentrations of K and acids. Titratable acidity and malate concentration were highest in treatment BB-FB which had a low seasonal salt load, whereas treatment FB-V with a high annual salt load had the highest concentrations of potassium and tartrate and the highest pH. Salinity did not affect pH in treatments V-H and H-LF until the second season and in treatment BB-FB pH was not affected until the third season.

The effect of salinity on the juice acid concentration and titratable acidity was greatest in treatment BB-FB. The biggest response occurred in the 1987-88 season. This was coincident with a smaller crop and higher TSS. In BB-FB, the RWECe and the berry Na and Cl in 1987-88 were the same as in 1988-89. The behaviour in the second season indicates that the effects of salinity were mediated by other unidentified factors.

In agreement with this study, Makhija *et al.* (1986) also found salinity increased juice titratable acidity, but Prior *et al.* (1992a) and McCarthy (1981) found juice titratable acidity was not affected by salinity. These differences remain unexplained.

Boulton (1980) proposed that juice pH was dependent on the balance between proton sources, malic and tartaric acid, and the extent of proton exchange for the metal cations, sodium and potassium. Since both acids and metal cations were increased by salt stress the rise in pH indicates that the increase in metal cations had a greater effect on pH than the increase in the concentration of acids.

Entry of Australian wine into the European Economic Community (EEC) may be refused when the concentration of free sodium (sodium equivalents greater than chloride equivalents) is above 60 mg/L (Lee, 1990) and where the chloride expressed as sodium chloride is above 1 g/L (Lee, 1993). Salinisation increased the value of the ratio of juice sodium to chloride concentration e.g. in 1987-88 it ranged from 1.5 to 4.3 in salinised treatments *cf.* a value of 0.9 in CONT. The free sodium in the second season was above the critical concentration in treatments FB-V and V-H and in the third season in treatment V-H. As sodium is not lost during vinification of grapes (A.J.W. Ewart, pers. comm.) these concentrations may preclude from entry into the EEC wine made from grapes grown under conditions similar to these treatments. Lower free sodium could be obtained by combining saline irrigations during either full-bloom to veraison or veraison to harvest with saline irrigation before full-bloom, which would favour Cl uptake and thereby reduce free sodium levels.

In the three seasons in all treatments the juice chloride concentration expressed as sodium chloride was much less than 1 g/L and as such indicates that wine produced from grapes grown under salinity regimes similar to those in the present experiment is unlikely to be refused entry to the EEC based on its Cl concentration. Lower chloride concentrations in the juice were obtained by avoiding irrigation with saline water between full-bloom and veraison.

Table 12 shows the compositional data from the 1987-88 season after it has been normalised with regard to the annual salt load. For every composition variable except pH the most sensitive period to increased salinity was before full-bloom.

The high sensitivity of pH to saline irrigation after harvest in the 1987-88 season may have been due to the elevated soil salinity in the H-LF treatment just after bud-burst. This suggests that events which occur before flower fertilisation have a strong affect on the hydrogen ion concentration in the juice.

Water stress has the opposite effect to salt stress on the juice pH and titratable acidity. During berry development, Van Zyl (1984) and Matthews and Anderson (1989) found that water stress reduced titratable acidity and malate but did not affect pH. During ripening, it reduced titratable acid without affecting either malate or pH. Van Zyl (1984) found tartrate was increased by water stress during berry development.

Matthews and Anderson (1988) found that water stress during berry development reduced malate. Water stress during berry development also reduced shoot growth which increased bunch exposure (Van Zyl, 1984: Smart *et al.*, 1985). Increased exposure of the berry raises its temperature and thereby favours respiratory processes such as those involved in the loss of malate after veraison. Excepting treatment BB-FB, salt stress did not affect shoot growth and therefore it is unlikely that the increase in malate can be attributed to changes in bunch exposure.

Table 12. The difference between juice composition values in salinised treatments and those in the control expressed as a rate per unit increase in annual salt load above that of the control for the 1987-88 season.

	Treatment			
	BB-FB	FB-V	V-H	H-LF
Titratable acidity [g/L.(dS/m)]	2.60	0.39	0.34	- *
Tartrate [g/L.(dS/m)]	2.60	1.04	0.35	-
Malate [g/L.(dS/m)]	5.72	0.61	0.39	-
pH [pH.(dS/m)]	-	0.072	0.047	0.094
K [mM.(dS/m)]	15.6	8.1	6.2	-

* treatments which were not significantly different from the control have not been included

5.5 CONCLUSIONS

Irrigation in the experimental vineyard was scheduled to replace water as it was used by the grapevines. This schedule produced a variation in both the volume of water applied in each growth stage and in the annual salt load applied to treatments which received saline irrigation in any one of the four growth stages.

Saline irrigation increased the ECe and this rise followed, but lagged behind, that in ECw. Leaf water potential fell and Cl concentration rose with increases in ECe. However, increases in leaf Na concentration did not necessarily follow those in ECe. It is likely that the changes in leaf Na reflected a process involving storage and then remobilisation of Na within the grapevine.

The grapevine rootzone was 2 m deep and its salinity was variable. The extent of the variation was such that even in the treatments with the higher annual salt loads substantial areas of the rootzone were low in salinity for both the first month of the two month period of saline irrigation and the month immediately following the end of saline irrigation. With such a variation it is likely that the vine partially avoided salinity by 'redirecting' its water withdrawal to less saline areas. This opportunity for redirection was greater in treatments which had lower annual salt loads. These opportunities are reduced where the rootzone is shallow, where transient waterlogging increases salt uptake from areas of low salinity and where substantial salt uptake occurs via pathways other than the root i.e.the foliage. Where the risk of occasional saline conditions prevails, maximising these opportunities is an important part of good on-farm management. The relationships that ECe and ECsw have with ECw when saline irrigation is limited to a two month periods in an irrigation season of eight months duration are different from those established when the salinity of irrigation water is held constant. These relationships are important for the translation of pot experiments to the field and in predicting the likely response of plant to changes in ECw.

The salt concentrations in the leaf and fruit at harvest were normalised to remove the effect of different annual salt loads. The highest rate of Cl uptake in the leaf occurred when saline irrigation was applied between bud-burst and full-bloom, and the highest rate in the berry occurred when saline irrigation was applied between either bud-burst and full-bloom or full-bloom and veraison. These results suggest that Cl uptake during cell division is greater than that either during cell expansion or after cessation of growth. The rates of Na uptake by both the leaf and berry were similar during the periods of cell division and expansion and after cessation of growth.

Saline irrigation had only a small effect on the primary leaf area of the treatment which received saline irrigation before full-bloom.

Saline irrigation reduced yield, but only in the second season of the three year trial and then only in the treatment which received saline irrigation between full-bloom and veraison. Yield reduction was due to a reduction in berry weight.

Comparison between reports where the salt load was distributed evenly across the season and the result of the present experiment showed that an irrigation strategy which delivers the annual salt load in a two month period can avoid a yield loss of at least ten percent. Even when the annual salt load was delivered at the most sensitive growth stage, between full-bloom and veraison, the yield loss was probably less than if the same salt load had been spread evenly across the season. It is postulated that part of the advantage gained with an irrigation strategy which confines the saline irrigation to a two month period is that it creates opportunities for the vine to avoid stress. These opportunities are probably not present when the salt load is spread evenly across the season.

By the third season, saline irrigation in any growth stage before harvest reduced berry weight. When this reduction was normalised to remove the effect of a variation amongst treatments in their annual salt load, the greatest rate of decline was shown to occur when saline irrigations were applied between bud-burst and

full-bloom. Normalisation of Cl and Na uptake rates by the berry showed that the higher rates occurred when saline irrigations were applied between either bud-burst and full-bloom or full-bloom and veraison.

Grape juice composition responded to saline irrigation in all three seasons and by the third it responded to salinity applied in any two month period within the season. The greatest increase in titratable acidity and malate concentration occurred with saline irrigation between bud-burst and full-bloom i.e. with a low annual salt load. In contrast, the greatest increase in tartrate, Na and K concentrations and pH occurred with saline irrigation between full-bloom and veraison i.e. with a high annual salt load.

When the changes in juice composition were normalised to remove the effect of different annual salt loads and isolate the effect of the timing of saline irrigation, the greatest increases in juice titratable acidity, and malate, tartrate, Na, K, and Cl concentrations occurred with saline irrigation between bud-burst and full-bloom. The rootzone during this period held water stored from winter rains and in combination with the low annual salt load, conditions in this treatment were very favourable for a strategy where the vine roots avoid salt stress by 'redirecting' part of their uptake to non-saline areas in the rootzone. Had these conditions been absent then it is likely that the differences between BB-FB and the other treatments would have been greater.

Based on the presence of a response in all three seasons and in one or more growth periods, juice composition was more sensitive to salinity than berry growth which was more sensitive than yield or vegetative growth.

6. General Conclusions

Modelling the effect of salinity on the growth of grapevines and other perennial crops has relied heavily on results from experiments on immature potted plants. These models form the foundation of long term strategies which direct investment in the public infrastructure associated with the management of irrigation water supplies e.g. Maunsell and Partners (1979).

In the application of the result from experiments on immature potted vines to the prediction of the response expected in mature field grapevines Ayers and Westcot (1985) have assumed that the concentration of salt in the irrigation water and soil solution would have reached an equilibrium, and that under this condition the ratio in the pot between ECw and ECsw was 1:1 and in the field between 3:1 and 5:1. Therefore irrigation of a potted immature vine with water of ECw 3.5 dS/m should create conditions which equate to an ECsw in the field of between 0.7 and 1.2 dS/m. Such concentrations were probably well below those achieved in the present field experiment where the relationship between changes in Ψ_l and ECe suggest ECsw reached 3.5 dS/m, and this difference suggests that the growth response to saline irrigation found with immature vines should have under- rather than over-estimated the losses in field vines.

In the present experiments, the immature and mature grapevines received the same irrigation treatments. Growth in the immature grapevine declined on average by 12%, whereas in mature grapevines it only declined in one of three years and then by only 6% in one of the four saline treatments.

Many of the differences in the growth conditions between immature and mature grapevines should have favoured salinity tolerance by the immature grapevines. Immature grapevines were grown in conditions where pressure from soil pathogens was absent, insect and fungal pressure was minimal, nutrients were in constant supply, temperature and humidity did not rise or fall to extremes.

Although both immature and mature grapevines had a similar maximum levels of depression of Ψ_l, 0.15 MPa, the time course of their development was very different. In the glasshouse grown grapevines the changes in Ψ_l were proportional to those in ECw which rose to a maximum soon after saline irrigation commenced. During the entire two-month period of salinisation, ECsw in the glasshouse grapevines was 3.5 dS/m. In the field the changes in Ψ_l were proportional to changes in ECe which did not reach its maximum of about 3.5 dS/m until the end of the two-month period. During this period the ECsw of field vines rose steadily above that in CONT but did not necessarily reach 3.5 dS/m. The depression of Ψ_l in immature vines was fully established within one month of the commencement of saline irrigation and, in every treatment, saline irrigation produced a decline of about 0.15 MPa. In contrast the maximum level of depression of Ψ_l in mature grapevines was not equivalent in all treatments e.g. in treatment BB-FB it was much less than that in treatments FB-V and V-H, and took more than one month to develop fully.

Immature grapevines had the highest leaf concentrations of Na and Cl. In the March leaf samples from treatment FB-V, the maximum concentrations of Na and Cl in the immature grapevines, 228 and 280 mmol/kg respectively, were double those in the leaves of mature vines, 128 and 115 mmol/kg.

However, the differences between the growth responses of glasshouse and field grapevines cannot necessarily be explained as a consequence of differences in concentration of Na and Cl in grapevine tissue and in the values of Ψ_l. The March leaf samples from treatments V-H show the concentrations of sodium and chloride in the mature vine, at 144 and 117 mmol/kg, were much greater than the 31 and 65 mmol/kg found in the immature grapevines. In the glasshouse and the field, the duration and degree of the depression of Ψ_l was similar. Therefore the case for associating a growth decline with higher tissue Na and Cl concentrations and greater depression of Ψ_l is equivocal.

Use of the results from immature vines to estimate the losses expected in the field produced an over-estimate of the losses. This was associated with a ratio of ECw:ECsw in the field that was dynamic rather than constant and that had a value which was a third or less that assumed to occur under equilibrium conditions in the field. It is questionable whether such equilibrium conditions are ever likely to occur in the field. In another study within the Murray-Darling Basin, after application of water with a constant salinity for six consecutive seasons, Prior (1992c) found that the ECw:ECe was still rising (and therefore so too was ECw:ECsw). Records of the ECw in the Murray River over the last 50 years (Close, 1990) show that such an extended period of constant ECw has not occurred. Within the Murray-Darling Basin, it is unlikely that equilibrium conditions will occur in the field, and therefore, under these conditions, predictions based on an assumption of equilibrium are probably invalid. These comments also apply to other perennial crops.

Another potential reason for the failure of the immature vine model to predict the behaviour of field vines was the difference between the two systems in the opportunities they create for the vine to avoid salt stress. In the experiment with immature grapevines, the maximum daily water use by the grapevines extracted 50% of the water held in the rootzone of the small pots, whereas in the field, with a 2 metre deep rootzone, maximum monthly water use rates by grapevines extracted less than 50% of the water held in the rootzone. In pots, the rootzone may be completely salinised within two days of commencement of saline irrigation because of the high turnover of rootzone water. It may take more than two months to reach the same degree of salinisation in the rootzone of field grapevines. Whilst the salinity of soil within the rootzone is heterogeneous, the grapevine may minimise stress by preferentially extracting water from the least saline zones as has been shown in grapes by Shani *et al.* (1993) and in apples by West (1978).

Results of the present study and those in the only published report on the response of mature vines to salinity (Prior *et al.*, 1992a) demonstrate that attempts to predict the response of mature vines from the results of experiments on immature vines have failed. Based on the results of the present experiment with mature vines,

up to 40% of the vine's annual irrigation requirement can be met with water of EC 3.5 dS/m without loss of yield. Saline irrigation between full-bloom and veraison reduces yield, however the loss is much less than that predicted had the same annual salt load been spread evenly across the season. During periods of high water salinity in the River Murray, vignerons would gain the most benefit from non-saline dilution flows released between mid-November and mid-January. Further the results suggest that in seasons with a high annual salt load, damage can be reduced by selecting a strategy which concentrates the annual salt load into a two-month period over a strategy which evenly spreads the annual salt load over the entire season. Timing of saline irrigations affects the levels of free sodium in the juice and this level rose above that acceptable in wine destined for export to the EEC. The sensitivity of juice composition to salinity was greater than that of yield or berry weight. Changes in composition were not secondary effects of salinity induced changes in maturity or berry volume. The response of mature vines could not be predicted from the results of the experiment with immature vines.

REFERENCES

ABARE (1989). Supply projections for wine grapes. Australian Bureau of Agricultural and Resource Economics, Canberra.

Alexander, D. McE., and Woodham, R. C. (1968). Relative tolerance of rooted cuttings of four vinifera varieties to sodium chloride. Aust. J. Exp. Agric. Anim. Husb. 8:461-65.

Alexander, D. McE., and Groot Obbink, J. (1971). Effect of chloride in solution culture on growth and chloride uptake of Sultana and Salt Creek grape vines. Aust. J. Exp. Agric. Anim. Husb. 11:357-61.

Ayers, R. S., and Westcot, D. W. (1985). 'Water Quality for Agriculture'. FAO Irrigation and Drainage Paper No. 29, Rev. 1. (FAO: Rome.)

Atkinson, D. (1983). The growth, activity and distribution of the fruit tree root system. Plant and Soil 71:23-35.

Baver, L.D. Gardner, W.H., and Gardner, W.R. (1972). 'Soil Physics'. 4th edition (John Wiley: New York, USA) 498 pp.

Begg, J. E., and Turner, N. C. (1976). Crop water deficits. Adv. Agron. 28:161-217.

Bernstein, L. (1961). Tolerance of plants to salinity. J. Irrigation and Drainage Division, Proceedings of the American Society of Civil Engineers 87(IR4):3005-3017.

Bernstein, L. (1964). Salt tolerance of plants. Agriculture Information Bulletin No 283. U. S. Department of Agriculture, Washington.

Bernstein, L. (1975). Effects of salinity and sodicity on plant growth. Ann. Rev. Phytopathol. 13:295-312.

Bernstein, L., and Hayward, H. E. (1958). Physiology of salt tolerance. Ann. Rev. Plant Physiol. 9:25-46.

Blackburn, G., and Wright, D. A. (1972). Soil survey of the Loxton Irrigation Area, South Australia. CSIRO Div. of Soils, Soils Land Use Series No 53. Adelaide, S.Aust.

Blackburn, G., and McLeod, S. (1983). Salinity of atmospheric precipitation in the Murray-Darling drainage division. Aust. J. Soil Res. 24:411-34.

Blesing, N.V., and Tuffley, J.R. (1977). Study of potential economic benefits from reduction in salinity of River Murray water. Amdel Report Nos. 1179. Engineering and Water Supply, Adelaide. 57 pp.

Boland A-M., Jerie, P.H., Mitchell, P.D., Irvine, J. L., and Nardella, N. (in press). The effect of a saline and a non-saline water table on peach tree water use, growth, productivity and ion uptake. Aust. J. Agric. Res.

Bollard, E. G. (1970). The physiology and nutrition of developing fruits. In 'The Biochemistry of Fruits and their Products'. (Ed. A. C. Hulme.) Vol. 1, pp 387-425. (Academic Press: London.)

Boulton, R. (1980). The relationship between total acidity, titratable acidity and Ph in wine. Am. J. Enol. Vitic. 31:76-80.

Bradford, K.J., and Hsiao, T.C. (1982). Physiological responses to moderate water stress. In 'Encyclopedia of Plant Physiology' (Eds. P. S. Nobel, C. B. Osmond and H. Ziegler). New Series, Vol. 12, pp 263-324 (Springer-Verlag: Berlin).

Buttrose, M. S. (1974). Climatic factors and fruitfulness in grapevines. Hort. Abstr. 44:319-26.

Chew, V. (1976). Comparing treatment means: a compendium. HortSci. 11:348-57.

Christensen, P. (1969). Seasonal changes and distribution of nutritional elements in Thompson Seedless grapevines. Am. J. Enol. Vitic. 20:179-90.

Close, A. (1990). River Salinity. In 'The Murray' (eds Mackay, N. and Eastburn, D.). Murray Darling Basin Commission, Canberra, pp.127-144.

Cock, G. J., Cole, P.J., Zimmermann, A., and Harvey, G. C. (1991). Water balances of irrigated Sultana vineyards in the Riverland of South Australia. Technical Report No. 179. 114 pp. South Australian Department of Agriculture, Adelaide.

Conradie, W. J. (1980). Seasonal uptake of nutrients by Chenin blanc in sand culture: 1. Nitrogen. S. Afr. J. Enol. Vitic. 1:59-65.

Coombe, B. G. (1973). The regulation of set and development in the grape berry. ACTA Hortic. 34:261-69.

Coombe, B. G. (1976). The development of fleshy fruits. Ann. Rev. Plant Physiol. 27:507-28.

Coombe, B.G. (1992). Research on development and ripening of the grape berry. Am. J. Enol. Vitic. 43:101-110.

Coombe, B. G., and Bishop, G. R. (1980). Development of the grape berry. II. Changes in diameter and deformability during veraison. Aust. J. Agric. Res. 31:499-509.

de La Harpe, A. C., and Visser, J. H. (1985). Growth characteristics of Vitis vinifera L. cv. Cape Riesling. S. Afr. J. Enol. Vitic. 6:1-6.

Doorenbos, J., and Pruitt, W. O. (1977) Crop water requirements. FAO Irrigation and drainage paper No 24. FAO, Rome.

Downton, W. J. S. (1977a). Photosynthesis in salt-stressed grapevines. Aust. J. Plant Physiol. 4:183-92.

Downton, W. J. S. (1977b). Salinity effects on the ion composition of fruiting Cabernet Sauvignon vines. Am. J. Enol. Vitic. 28:210-14.

Downton, W. J. S. (1977c). Influence of rootstocks on the accumulation of chloride, sodium and potassium in grapevines. Aust. J. Agric. Res. 28:879-89.

Downton, W. J. S. (1985). Growth and mineral composition of the Sultana grapevine as influenced by salinity and rootstock. Aust. J. Agric. Res. 36:425-34.

Downton W. J. S., and Loveys B. R. (1978). Compositional changes during grape berry development in relation to abscisic acid and salinity. Aust. J. Plant Physiol. 5:415-23.

Downton, W. J. S., and Hawker, J. S. (1980). Interaction of boron and chloride on growth and mineral composition of Cabernet Sauvignon vines. Am. J. Enol. Vitic. 31:277-82.

Downton, W. J. S., and Loveys, B. R. (1981). Abscisic acid content and osmotic relations of salt-stressed grapevine leaves. Aust. J. Plant Physiol. 8:443-52.

Downton, W. J. S., and Millhouse, J. (1983). Turgor maintenance during salt stress prevents loss of variable fluorescence in grapevine leaves. Plant Sci. Lett. 31:1-7.

Downton, W. J. S., Loveys, B. R., and Grant, W. J. R. (1990). Salinity effects on the stomatal conductance of grapevine. New Phytol. 116:499-503.

Due, G., Morris, M., Pattison, S., and Coombe, B.G. (1993). Modelling grapevine phenology against weather: considerations based on a large data set. Agric. and Forest Meteorol. 65:91-106.

Düring, H., and Oggionni, F. (1986). Transpiration and accumulation of mineral nutrients in grape berries. Vitis 25:59-66.

Ehlig, C. F. (1960). Effects of salinity on four varieties of table grape grown in sand culture. Proc. Amer. Soc. Hort. Sci. 76:323-331.

Findlay, N., Oliver, K. J., and Coombe, B. G. (1987). Solute accumulation by grape pericarp cells IV. Perfusion of pericarp apoplast via the pedicel and evidence for xylem malfunction in ripening berries. J. Exper. Bot. 38:668-679.

Freeman, B. M., and Smart, R. E. (1976). Research note: a root observation laboratory for studies with grapevines. Am. J. Enol. Vitic. 27:36-39.

Freeman, B.M., and Kliewer, W.M. (1983). Effect of irrigation, crop level and potassium fertilization on Carignane vines. II. Grape and wine quality. Am. J. Enol. Vitic. 34:197-206.

Gardner, W.R. (1964). Relation of root distribution to water uptake and availability. Agron. J. 56:41-45.

Gay, A. P. (1983). Transit time diffusion porometer calibration: an analysis taking into account temperature differences and calibration non-linearity. J. Exper. Bot. 34:461-469.

Gorham, J., Wyn Jones, R. G., and McDonnell, E. (1985). Some mechanisms of salt tolerance in crop plants. Plant and Soil 89:15-40.

Greenway, H., and Munns, R. (1980). Mechanism of salt tolerance in nonhalophytes. Ann. Rev. Plant Physiol. 31:149-90.

Grismer, M. E., and Gates, T.K. (1988). Estimating saline water table contributions to crop water use. Californian Agriculture 42(2):23-24.

Groot Obbink, J., and Alexander, McE. D. (1973). Response of six grapevine cultivars to a range of chloride concentrations. Amer. J. Enol. Vitic. 24:65-68.

Groot Obbink, J., and Alexander, McE. D. (1977). Observations of soil water and salt movement under drip and flood irrigation in an apple orchard. Agric. Water Manage. 1:179-190.

Gutierrez, A. P., Williams, D. W., and Kido, H. (1985). A model of grape growth and development: the mathematical structure and biological considerations. Crop Sci. 25:721-28.

Gutteridge, Haskins and Davey in association with Hunting Technical Services (1970). 'Murray Valley Salinity Investigation'. Vol. 1. (River Murray Commission: Canberra.)

Hardie, W.J., and Considine, J. A. (1976). Response of grapes to water deficit stress in particular stages of development. Am. J. Enol. Vitic. 27:55-61.

Harris, J. M., Kriedemann, P. E., and Possingham, J. V. (1968). Anatomical aspects of grape berry development. Vitis 7:106-19.

Hawker, J. S., and Walker, R. R. (1978). The effect of sodium chloride on the growth and fruiting of Cabernet Sauvignon vines. Am. J. Enol. Vitic. 29:172-76.

Hoffmann, G.J., Catlin, P.B., Mead, R.M., Johnson, R.S., Francois, L.E., and Goldhamer, D. (1989). Yield and foliar injury responses of mature plum trees to salinity. Irrig. Sci. 10:215-29.

Iland, P. G. (1984). Studies on the composition of pulp and skin of ripening grape berries. M. S. Thesis, University of Adelaide, Adelaide.

Jones, H. G., (1990). Physiological aspects of the control of water status in horticultural crops. Hortsci. 25:19-26.

Joolka, N. K., Singh, J. P., and Khers, A. P. (1977). Mineral composition of grape as affected by chloride and sulphate salts of sodium in soils. Indian J. Agric. Sci. 47:201-3.

Lai, R. K. (1985). Effect of salinity applied at different stages on seed yield and its constituents in field peas (Pisum sativum Linn. var. arvensis). Ind. J. Agron. 30:296-99.

Lee, T.H. (1990). Chloride and sodium ions in Australian wines. Aust. Wine Research Inst., Technical Review 68:2-7.

Lee, T.H. (1993). Australian/EC wine agreement. Aust. Wine Research Inst., Technical Review 82:10-12, 33-36.

Leece, D.R., and Short, C.C.. (1967) A routine procedure for the nutrient-element analysis of peach leaves utilising atomic absorption spectroscopy. New South Wales Department of Agriculture, Division of Science Services, Chemistry Branch Bulletin No. F78.

Maas, E. V., and Hoffman, G. J. (1977). Crop salt tolerance - current assessment. A.S.C.E. J. Irrig. Drain. Div. 103:115-134.

Maas, E. V., Poss, J. A., and Hoffman, G. J. (1986). Salinity sensitivity of Sorghum at three growth stages. Irrig. Sci. 7:1-11.

Maas, E. V., and Poss, J. A. (1989). Salt sensitivity of cowpea at various growth stages. Irrig. Sci. 10:313-20.

Makhija, M., Kainsa, R. L., Dhawan, S. S., and Yamdagni, R. (1986). A note on the effect of soil salinity levels on wine quality. Haryana J. Hort. Sciences 15:218-20.

Marschner, H. (1986). 'Mineral Nutrition of Higher Plants'. (Academic Press: London.)

Matthews, M. A., and Anderson, M. A. (1989). Fruit ripening in Vitis vinifera L.: responses to seasonal water deficits. Am. J. Enol. Vitic. 39:313-20.

Maunsell and Partners (1979). 'Murray Valley Salinity and Drainage: Development of a Co-ordinated Plan of Action, vol. 4, Economics'. (Murray Valley Salinity Study Steering Committee, Canberra.)

May, P. (1987). The grape vine as a perennial, plastic and productive plant. In Proceedings of the Sixth Australian Wine Industry Technical Conference (Lee, T. ed). Australian Industrial Publishers, Adelaide, pp 40-49.

McCarthy, M. G. (1981). Irrigation of grapevines with sewage effluent. 1. Effects on yield and petiole composition. Am. J. Enol. Vitic. 32:189-96.

McKay, N., Hillman, T., and Rolls, J. (1988). 'Water Quality of the River Murray'. (Murray-Darling Basin Commission: Canberra.)

McKenry, M. V. (1984). Grape root phenology relative to control of parasitic nematodes. Am. J. Enol. Vitic. 35:206-11.

Minhas, P.S., and Gupta, R.K. (1993). Conjunctive use of saline and non-saline waters. I. Response of wheat to initial salinity profiles and salinisation patterns. Agric. Water Manag. 23:125-37.

Nagarajah, S. (1987). Effects of soil texture on the rooting patterns of Thompson Seedless vines on own roots and Ramsey rootstock in irrigated vineyards. Am. J. Enol. Vitic. 38:54-60.

Nauriyal, J. P., and Gupta, O. P. (1967). Studies on salt tolerance of grape. I. Effect of total salt concentration. J. Res., Ludhiana, 4:197-205.

Nitsch, J. P., Pratt, C., Nitsch, C., and Shaulis, N. J. (1960). Natural growth substances in Concord and Concord Seedless grapes in relation to berry development. Amer. J. Bot. 47:566-76.

Nobel, P. S. (1983). 'Biophysical Plant Physiology and Ecology'. (Freeman: San Francisco.)

Olsson, K.A., and Rose, C.W. (1988). Patterns of water withdrawal beneath an irrigated peach orchard on a red-brown earth. Irrig. Sci. 9:89-104.

Passioura, J. B. (1980). The meaning of matric potential. J. Expt. Bot. 31:1161-69.

Peynaud, E., and Ribereau-Gayon, P. (1971). The grape. In 'The Biochemistry of Fruits and their Products'. (Ed. A. C. Hulme.) Vol. 2, pp 171-205. (Academic Press: London.)

Pongrácz, D. P. (1978). 'Practical Viticulture'. (David Philip: Capetown.)

Possner, D. R. E., and Kliewer, W. M. (1985). The localisation of acids, sugars, potassium and calcium in developing grape berries. Vitis 24:229-40.

Pratt, C. (1971). Reproductive anatomy in cultivated grapes - a review. Am. J. Enol. Vitic. 22:92-109.

Prior, L. D., Grieve, A. M., and Cullis, B. R. (1992a). Sodium chloride and soil texture interactions in irrigated field grown Sultana grapevines. 1. Yield and fruit quality. Aust. J. Agric. Res. 43:1051-66.

Prior, L. D., Grieve, A. M., and Cullis, B. R. (1992b). Sodium chloride and soil texture interactions in irrigated field grown Sultana grapevines. 2. Plant mineral content, growth and physiology. Aust. J. Agric. Res. 43:1067-83.

Prior, L. D., Grieve, A. M., Slavich, P. G., and Cullis, B. R. (1992c). Sodium chloride and soil texture interactions in irrigated field grown Sultana grapevines. 3. Soil and root system effects. Aust. J. Agric. Res. 43:1085-1100.

Ravikovitch, S., and Bidner, N. (1937). The deterioration of grape-vines in saline soils. Empire J. Exp. Agric. 5:197-208.

Robinson, J. B., McCarthy, M. G., and Nicholas, P. R. (1982). Petiole analysis as a tool in assessing the nutritional status of vineyards of Vitis vinifera in South Australia. Proc. Int. Plant Nutrition Colloquim. pp. 545-50. Warwick, Gt. Britain.

Robinson, J. B., and McCarthy, M. G. (1985). Use of petiole analysis for assessment of vineyard nutrient status in the Barossa district of South Australia. Aust. J. Exp. Agric. 25:231-40.

Rowe, R. M., and P. V. Beardsell (1978). Waterlogging of fruit trees. Horticultural Abstracts 43:533-48.

Ruffner, H. P. (1982a). Metabolism of tartaric and malic acids in Vitis: A review - part A. Vitis 21:247-59.

Ruffner, H. P. (1982b). Metabolism of tartaric and malic acids in Vitis: A review - part B. Vitis 21:346-58.

Salisbury, F.B., and Ross, C. R. (1969). 'Plant Physiology'. (Wadsworth: Belmont, California.)

Shani, U., Waisel, Y., Eshel, A., Xue, S., and Ziv, G. (1993). Responses to salinity of grapevine plants with split root systems. New Phytologist 124:695-701.

Shapiro, S. S., and R. S. Francia (1972). An approximate analysis of variance test for normality. J. American Statistical Association 67:215-16.

Scholander, P. F., Hammel, H. T., Bradstreet, E. D., and Hemmingsen, A. E. (1965). Sap pressure in vascular plants. Science 148:339-346.

Slatyer, R. O. (1967). 'Plant-water Relations'. (Academic Press: London.)

Smart, R. E., Robinson, J. B., Due, G. R., and Brien, C. J. (1985). Canopy microclimate modifications for the cultivar Shiraz. 2. Effects on must and wine composition. Vitis 24:119-128.

Smith, R. J., and Kliewer, W. M. (1984). Estimation of Thompson seedless grapevine leaf area. Am. J. Enol. Vitic. 35:16-22.

Snedecor, G. W., and W. G. Cochran. Statistical Methods. 507 pp. Iowa State University Press, Iowa (1980).

Sourail, G. F., Miligi, M. A., Tawfik, A. A., and El-Demerdash, A. M, (1985). Effect of saline irrigation on chemical constituents of one-year-old rooted vines: sugars and N.P.K. content. ACTA Horticulturae 158:169-85.

Srinivasan, C., and Mullins, M. G. (1981). Physiology of flowering in the grapevine - a review. Am. J. Enol. Vitic. 32:47-62.

Staudt, G., Schneider, W., and Leidel, J. (1986). Phases of berry growth in Vitis vinifera. Ann. Bot. (London) 58:789-800.

Stevens, R. M., and Douglas, T. (1994). Distribution of grapevine roots and soil salt under drip and full-cover microjet irrigation systems. Irrig. Sci. 15:147-52.

Stevens, R.M., and Harvey, G. (1995). Effects of waterlogging, rootstock and salinity on Na, Cl and K concentrations of the leaf and root, and shoot growth of Sultana grapevines. Aust. J. Agric. Res. 46:541-51.

Stevens, R.M., Harvey, G. and Davies, G. (in press). Separating the Effects of Foliar and Root Salt Uptake on Growth and Mineral Composition of Four Grapevine Cultivars on their Own-roots and on Ramsey Rootstock. J. Amer. Soc. Hort. Sci.

Swanepoel, J. J., and Archer, E. (1988). The ontogeny and development of Vitis vinifera L. cv. Chenin blanc inflorescence in relation to phenological stages. Vitis 27:133-41.

Syversten, J.P., and Graham, J.H. (1985). Hydraulic conductivity of roots, mineral nutrition, and leaf gas exchange of citrus rootstock. J. Amer. Soc. Hort. Sci. 110:865-869.

Taha, M. W., El-Azab, E., and Fasiah, Z, (1972). Ionic leaf accumulation in grapes, guava and olive plants as affected by the salinity of irrigation water. Alex. J. Agr. Res. 20:299-309.

Thomas, J. E. (1934). The diagnostic value of the chlorine content of the vine leaf. J. Coun. Sci. Ind. Res. (Aust.) 7:29-38.

Turner, N.C. (1981). Techniques and experimental approaches for the measurement of plant water relations. Plant and Soil 58:339-66.

Turner, N.C., and Long, M.J. (1980). Errors arising from rapid water loss in the measurement of leaf water potential by the pressure chamber technique. Aust. J. Pl. Physiol. 7:527-37.

USDA (1954). 'Diagnosis and improvement of saline and alkali soils'. (Ed. L. A. Richards) USDA Agricultural Handbook No. 60. (USDA: Washington, D.C..)

Van Rooyen, F.C., Weber, H.W., and Levin, I. (1980). The response of grapes to a manipulation of the soil-plant-atmosphere continuum. I. Growth, yield and quality responses. Agrochemophysica 12:59-68.

Van Zyl, J. L. (1984). Response of Colombar grapevines to irrigation as regards quality aspects and growth. S. Afr. J. Enol. Vitic. 5:19-28.

Van Zyl, J. L., and Weber, H. W. (1977). Irrigation of Chenin Blanc in the Stellenbosch area within the framework of the climate-soil-water-plant

continuum. Proc. O.I.V. Symposium on the 'Quality of Vintage'. pp. 331-50. Capetown, S. Africa.

Walker, R. R., Törökfalvy, E., Steele Scott, N., and Kriedemann, P. E. (1981). An analysis of photosynthetic response to salt treatment in Vitis vinifera. Aust. J. Plant Physiol. 8:359-74.

Wermelinger, B., and Koblet, W. (1990). Seasonal growth and nitrogen distribution in grapevine leaves, shoots and grapes. Vitis 29:15-26.

West, D.W. (1978). Water use and sodium chloride uptake by apple trees. 1. The effect of non-uniform distribution of sodium chloride in the root zone. Plant and Soil 50:37-49.

West, D. W. (1986). Stress physiology in trees - salinity. ACTA Horticulturae 175:321-32.

West, D. W., and Taylor, J. A. (1984). Response of six grape cultivars to the combined effects of high salinity and rootzone waterlogging. J. Amer. Soc. Hort. Sci. 109:844-51.

Wetherby, K.G. (1973). Soils of the Northern Mallee of S.A. (Counties Alfred, Albert) and the relationship to quaternary geology -- with notes of agricultural potential. M. S. Thesis, University of Adelaide, Adelaide.

Wetherby, K. G., and Oades, J. M. (1975). Classification of carbonate layers in highland soils of the Northern Murray Mallee, SA, and their use in stratigraphic and land use studies. Aust. J. Soils Res. 13:119-132.

Whiting, G. C. (1970). Sugars. In 'The Biochemistry of Fruits and their Products'. (Ed. A. C. Hulme.) Vol. 1, pp 1-31. (Academic Press: London.)

Williams, L. E. (1987). Growth of 'Thompson Seedless' grapevines: 1. Leaf area development and dry weight distribution. J. Amer. Soc. Hort. Sci. 112:325-30.

Winkler, A. J. (1962). 'General Viticulture'. (Univ. California Press: Berkley, California.)

Woodham, R. C. (1956). The chloride status of the irrigated Sultana vine and its relation to vine health. Aust. J. Agric. Res. 7:414-28.