

THE SCIENCE OF GRAPEVINES: ANATOMY AND PHYSIOLOGY

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by providing a physical barrier and/or by enhancing the production of phenolic compounds. Thus, although deemed a nonessential nutrient (i.e., one that is not required to complete the plant's life cycle), Si provides many benefits, such as improved resistance to pests and diseases, tolerance of drought, salinity, heavy metals, and high temperatures (Currie and Perry, 2007; Epstein, 1999; Ma and Yamaji, 2006), and even improved yield and fruit quality by enhancing the production of flavonoids. For this reason, Si is integrated in many fertilizers. Most of these stress-alleviating effects result from the strengthening of cell walls by Si and by its ability to enhance the binding of cations (e.g., Na^+ and Mn^{2+}) to the cell walls, which may prevent their buildup to toxic concentrations inside the cells (Saqib *et al.*, 2008). Plants high in Si may be able to reduce uptake of Na^+ from saline soils and to transport less of it to the leaves.

7.3.3. Salinity

The term salinity describes the occurrence of high concentrations of soluble salts (i.e., in ionic form) in water and soils. The development of salinity is termed salinization and occurs in regions where water evaporation from the soil exceeds precipitation so that salts dissolved in the soil solution tend to become concentrated at the soil surface. Whereas this process is characteristic of arid environments, the opposite process, called acidification, occurs in regions where rainfall consistently exceeds evaporation (i.e., especially in the tropics and subtropics and thereby leaches cations such as K^+ , Ca^{2+} and Mg^{2+} so that the soil pH decreases and the highly toxic Al^{3+} , along with Mn^{2+} and iron Fe^{2+} becomes soluble in the soil solution. Rainwater also contains some salt (≤ 50 mg NaCl L^{-1}), especially in coastal areas (Munns and Tester, 2008). However, irrigated vineyards are at much greater risk from salinization than nonirrigated vineyards because irrigation water

is relatively rich in dissolved salts and because irrigation tends to raise water tables. Therefore, irrigation in arid and semiarid regions over prolonged periods can lead to a buildup of salt near the soil surface. Most table and raisin grapes are grown in rather dry and warm climatic regions, such as southeastern Asia, California, Chile, or Australia, and are thus especially threatened by salinity.

The dominant soil salts are cations, such as Na^+ , K^+ , Ca^{2+} and Mg^{2+} , and their associated anions, such as chloride (Cl^-), sulfate (SO_4^{2-}), carbonate (CO_3^{2-}), and bicarbonate (HCO_3^-). Small amounts of other ions are also present in the soil solution. The relative amounts of different ions vary between water sources and soil types, but the ions most often associated with the effects of salinity on grapevines are Na and Cl^- . Dissolved ions increase the electrical conductivity of water, and thus salinity of irrigation water or water extracts of soils is expressed in electrical conductivity units (measured in decisiemens per meter or dS m^{-1}). The threshold above which salinity begins to affect *V. vinifera* growth and yield formation seems to be approximately 2 dS m^{-1} and above 16 dS m^{-1} vines cannot survive (Zhang *et al.*, 2002). Because dissolved ions decrease the osmotic potential (Ψ_π) of water, electrical conductivity is also a measure of Ψ_π . 2 dS m^{-1} corresponds to approximately 20 mM NaCl generating a $\Psi_\pi \approx -0.1 \text{ MPa}$.

Sodicity is related to salinity and refers to the presence of sodium relative to calcium and magnesium in the soil. Sodicity is expressed as the sodium adsorption ratio (SAR) because most cations in the soil are attracted to the negative charges of clays. The sodicity of irrigation water or soil water extracts is calculated as follows:

$$\text{SAR} = \frac{[\text{Na}^+]}{\sqrt{[\text{Ca}^{2+}] + [\text{Mg}^{2+}]}}$$

where [.] denotes the concentration of an ion in millimoles per liter (mM).

In addition to their elevated Na^+ content, sodic soils are afflicted with a deterioration of structure due to clay dispersion and a rise in hydraulic resistance. Saline and sodic soils are usually classed together as "salt-affected soils." Such soils contain a sufficient concentration of soluble salts or exchangeable Na^+ to interfere with plant growth. The most common cause of salt stress is a high concentration of Na^+ and Cl^- in the soil solution. Both of these are essential plant nutrients but become toxic at much lower concentrations than other nutrients. Plant damage due to salt-affected soils is the outcome of a combination of hyperosmotic stress and hyperionic stress due to a disruption of homeostasis (Greek *homois* = similar, *stasis* = stand still, steady) in water status and ion distribution (Hasegawa *et al.*, 2000; Zhu, 2001). Initially, buildup of salt ions in the soil decreases Ψ_π of the soil solution, the Ψ_π in "normal" soils is generally approximately -0.01 MPa but can drop to less than -0.2 MPa in saline soils. The resulting decrease in Ψ_{soil} impedes water uptake by the roots (Shani *et al.*, 1993; see also Chapter 3), increases root hydraulic resistance due to closure of aquaporins (Luu and Maurel, 2005), and results in water deficit for the vine and a decline in Ψ_{leaf} (Cramer *et al.*, 2007; Downton and Loveys, 1981; Walker *et al.*, 1981). Thus, the initial effects of a rise in soil salinity are identical to the effects of drought stress (see Chapter 7.2). The ensuing collapse of the water potential gradient necessary for growth curtails shoot growth and leaf expansion and inhibits lateral shoot development, whereas root growth is usually less sensitive (Munns and Tester, 2008). Nonetheless, in some instances, root growth of grapevines was found to be more sensitive to salinity than shoot growth (Hawker and Walker, 1978). Growth may also slow through deactivation of gibberellins under salt stress (Yamaguchi, 2008). The decrease in Ψ_{leaf} and increase in root-derived and locally produced ABA also induce closure of the stomata,

which in turn decreases transpiration and photosynthesis and consequently the production of sugar for export to other plant parts (Downton *et al.*, 1990; Shani and Ben-Gal, 2005). Rising Cl^- concentration in the leaves also reduces stomatal conductance (Walker *et al.*, 1981), although Na^+ tends to counter this by replacing K^+ in the guard cells and thereby keeping the stomata partially open. However, the rate of photosynthesis declines as leaf Cl^- concentration increases well before any visible symptoms of salt damage become apparent (Downton, 1977).

The challenge for grapevines growing in saline environments is that their roots must take up nutrient ions while keeping out the toxic Na and Cl. "Toxic," as usual, is a relative term; it is important to remember that plants require some Cl^- for the water-splitting reaction that produces electrons, protons, and oxygen during photosynthesis (see Chapter 4.1). Roots effectively "pick" the nutrient ions from the toxic ions in the soil solution or pump the toxic ions taken up back out again so that more than 95% of Na^+ and Cl^- is prevented from entering the xylem (Munns, 2002; Munns and Tester, 2008). Nonetheless, although Na^+ is not an essential nutrient, the ion is taken up into cells down the electrochemical gradient, competing with K^+ for uptake (Hasegawa *et al.*, 2000). The hypodermal and endodermal cells of salt-stressed grapevine roots appear to selectively accumulate K^+ over Na^+ and Cl^- compared with cortical and pericycle cells (Storey *et al.*, 2003). In contrast, the cortex and pericycle cells sequester large amounts of Na^+ and Cl^- in their vacuoles (Storey *et al.*, 2003). However, grapevines take up more Cl^- than Na^+ from saline soils that have equivalent concentrations of both ions (Walker *et al.*, 1981), and a small portion of each ion ends up in the xylem and is transported to the shoot with the transpiration stream. Consequently, Cl^- and, to a lesser extent, Na^+ accumulate in the older leaves, building up with increasing concentration in the soil solution, and they continue to

do so as the growing season progresses (Downton, 1985; Munns, 2002; Shani and Ben-Gal, 2005; Stevens and Walker, 2002). Over time, the ions may accumulate to toxic concentrations; this ion-specific phase of salinity stress is associated with premature death of older leaves (Munns and Tester, 2008).

Excessive Cl⁻ uptake interferes with NO₃⁻ nutrition because NO₃⁻ uptake seems to respond to the concentration of NO₃⁻ + Cl⁻ rather than to NO₃⁻ alone (Clarkson, 1985). This requires application of abundant nitrogen fertilizer to improve plant N status. High Na⁺ concentration, on the other hand, is toxic to plants because it interferes with K⁺ nutrition, which reduces K⁺-stimulated enzyme activities, metabolism, and photosynthesis. At concentrations exceeding approximately 100 mM, Na⁺ and Cl⁻ also directly inhibit many enzymes (Munns, 2002; Munns and Tester, 2008; Zhu, 2001). High salinity eventually overwhelms the leaf vacuoles' capacity to sequester Cl⁻ and Na⁺, leading to toxic concentrations in the cytoplasm and disturbing the cells' ionic balance; Na⁺ accumulates at the expense of K⁺ and can even result in a loss of K⁺ and Ca²⁺ from the cells. Sodium can compete with Ca²⁺ and displace it from the cell wall and thus affect cell wall properties. Because Ca²⁺ in turn can reduce Na⁺ uptake and increase K⁺ and Ca²⁺ uptake, addition of Ca²⁺ can somewhat alleviate the toxic effects of salinity (Hasegawa *et al.*, 2000; Plieth, 2005). However, prolonged exposure to high soil Ca²⁺ may itself be stressful for the plant.

Oxidative stress is another characteristic of salinity-induced injuries to plant tissues (Munns and Tester 2008; Zhu, 2001). It is a secondary stress that results from the effects of ion imbalance and hyperosmotic stress and from the decline in photosynthesis (see Chapter 7.1). Excess free oxygen radicals especially ¹O₂) and hydrogen peroxide (H₂O₂) oxidize membrane lipids and other cellular components, which eventually leads to membrane leakage and tissue deterioration (Møller *et al.*, 2007). However,

even before such irreversible damage ensues, oxidative stress may increase the vine's light sensitivity because more photons are being absorbed than can be used by the declining photosynthesis. One way grapevines cope with such an energy overload appears to be an increase in photorespiration (Cramer *et al.*, 2007; Downton, 1977; Downton *et al.*, 1990; Walker *et al.*, 1981), which dissipates some of the excess energy but comes at the cost of lower photosynthetic efficiency. Another defense strategy is to boost the antioxidant systems (i.e., glutathione and xanthophyll cycles) that capture and inactivate some of the reactive oxygen species (Cramer *et al.*, 2007). Because Mn²⁺ acts as an antioxidant in plant tissues, (foliar) application of Mn-chelates (and possibly Zn-chelates) might alleviate effects of oxidative stress in plants grown on saline sites or irrigated with saline irrigation water (Aktas *et al.*, 2005).

The first visible sign of salt stress is an inhibition of shoot growth and leaf expansion (Walker *et al.*, 1981), whereas the roots are more robust so that their growth is less curtailed (similar to the response to water deficit). However roots are the first and most important organs to experience salinity, which decreases their ability to explore the soil for water and nutrients. Salinity impacts growth directly through the effect of ions on the physiology of the plant, whereas the influence of sodicity is indirect due to its deleterious effects on soil physical properties. Salinity and sodicity both impair root growth, respiration, and water uptake, reducing vine growth, yield, and fruit quality (Shani and Ben-Gal, 2005; Shani *et al.*, 1993). In some cases, salinity may be associated with changes that are typical of mild water deficit, such as earlier veraison; higher fruit sugar, proline, potassium, and Cl⁻ and greater decline in acidity during ripening (Downton and Loveys, 1978; Walker *et al.*, 2000). As the salinity becomes more severe, however, fruit set, berry size, as well as sugar and anthocyanin accumulation are increasingly restricted (Hawker and Walker, 1978).



FIGURE 7.9 Leaf symptoms of salt injury on Merlot. Photo by M. Keller

The reduction in growth is in part due to the decrease in photosynthesis and in part due to inhibition of cell division and cell expansion (Zhu, 2001). More severe salinity arrests lateral shoot growth and induces necrotic leaf margins ("marginal burn" or "salt burn"; Figure 7.9) in older leaves, followed by progression of the necrotic symptoms toward the petiole, whereas the main veins remain green (Williams and Matthews, 1990; Williams *et al.*, 1994). Such salt injury is the result of the accumulation of Na^+ and/or Cl^- in the transpiring leaves (i.e., ion concentrations gradually increase as the transpiration stream "deposits" salt ions in the leaves) to the point where the vacuoles can no longer contain these ions. Accumulation in the cytoplasm then leads to enzyme inhibition (salt poisoning), whereas accumulation in the cell walls leads to dehydration of the cells; both outcomes result in cell death (Munns, 2002). The threshold Cl^- content for marginal necrosis seems to be approximately 2.5% of the leaf dry weight (Walker *et al.*, 1981).

Although they vary somewhat in the extent of Na^+ and Cl^- uptake and accumulation in the leaves (Groot Obbink and Alexander, 1973), most cultivars of *V. vinifera* are moderately sensitive to salt. American *Vitis* species, especially *V. riparia*, *V. berlandieri*, and, to a

lesser extent, *V. candicans* and *V. champinii*, are more tolerant (Williams *et al.*, 1994). Some rootstocks derived from these species (e.g., Ramsey, 1103 Paulsen, 110 Richter, Ruggeri 140, and 101–14 Mgt) are able to exclude much of the salt from root uptake and root-to-shoot transport (Antcliff *et al.*, 1983; Sauer, 1968; Walker *et al.*, 2000). Therefore, these rootstocks and scions grafted to them are only marginally affected by high salt concentrations in the soil (Downton, 1985; Stevens and Walker, 2002; Zhang *et al.*, 2002). However, it appears that at least some of them (Ramsey, 1103 Paulsen, and 101–14 Mgt) progressively lose this salt-exclusion ability (Tregeagle *et al.*, 2006). Under long-term exposure to saline conditions, which tends to lead to salt buildup in the soil over time, these rootstocks may become less salt tolerant.

The impact of salinity on vines seems to be more severe on heavier clay loam soils than on lighter loamy sands. Moreover, irrigation and soil management also affect the extent of physical degradation of salt-affected soils. Irrigation is a common cause of agricultural land degradation because salt dissolved in the irrigation water is left in the soil following evaporation. Excessive irrigation, particularly with saline water, as well as frequent cultivation (tillage) and intense trafficking are a good recipe for rapid loss of soil fertility. However, salts can also build up under highly efficient drip irrigation (Stevens and Walker, 2002), when ions move down the soil profile and below the emitters and then move laterally and rise again to the soil surface with the evaporating water. The resulting high-salt zone around the edges of the wetting zone can restrict root growth similar to the restriction imposed by a pot. The "pot" size is smaller in sandy soils than in loam soils. Waterlogging due to the formation of impermeable soil layers or as a result of excessive irrigation also increases the risk of salt damage because waterlogged grapevine roots lose the ability to exclude Na^+ and Cl^-

from uptake. Waterlogging also appears to increase the amount of Na^+ in the soil solution relative to other ions so that Na^+ uptake is often favored over Cl^- uptake (Stevens and Walker, 2002). Even if only a portion of the root system is exposed to saline conditions while other portions continue to have access to freshwater, the latter ostensibly do not compensate for the decline in water uptake by the former (Shani *et al.*, 1993). Prolonged exposure to saline soil water ultimately results in vine death (Shani and Ben-Gal, 2005). On the other hand, where soil salts can be leached out of the rootzone by using a fresh source of irrigation water, the harmful physiological effects can often be quickly reversed. Thus, as long as no irreversible damage has been caused, grapevines restore root functionality, growth, and water uptake to drain the excess ions from the leaves, and growth and gas exchange recover rapidly (Shani *et al.*, 1993; Walker *et al.*, 1981).

7.4. TEMPERATURE: TOO COLD OR TOO WARM

Higher temperatures tend to accelerate plant growth and development so that phenological stages occur in more rapid succession than under cooler conditions (Alleweldt *et al.*, 1984b; Chuine *et al.*, 2004; Jones and Davis, 2000; Wolfe *et al.*, 2005). In other words, an increase in temperature accelerates and compresses the temporal program of plant development—up to an optimum—and provided no other factors (e.g., water deficit, which is often coupled with high temperatures) are limiting growth. Grapevines growing in cool climates are exposed to a large daily temperature range and often experience widely fluctuating temperatures during spring and autumn. Low temperature may limit growth by decreasing the rate of protein production or cell wall extensibility. Restricting cell wall extensibility

also inhibits cell division by preventing cell expansion (see Chapter 3.1). Furthermore, cold temperatures increase the rigidity of the normally fluid cell membranes (Chinnusamy *et al.*, 2007). Because low temperatures restrict cell division more than photosynthesis (the duration of cell division increases exponentially with decreasing temperature), sugar and starch tend to accumulate in the leaves during a cool episode (Wardlaw, 1990). When the temperature drops too low, it can result in damage to plant tissues. The type and extent of damage depend on whether or not the temperature drops below the freezing point and on the developmental status of the plant.

7.4.1 Chilling Stress

Damage to plant tissues caused by low but above-freezing temperature (typically in the range of 0–15°C) is referred to as chilling stress. The photosynthetic cell organelles, the chloroplasts, are particularly sensitive to chilling stress (Kratsch and Wise, 2000). Swelling of chloroplasts, distortion of thylakoid membranes, and starch depletion (decrease in number and size of starch granules) inside the chloroplasts are usually the first microscopically visible signs of chilling injury. At the same time, chilling also decreases phloem loading and phloem transport. Accumulation of sugar in the chloroplasts (lowering Ψ_{π}) due to reduced export and continued starch degradation may be responsible for chloroplast swelling by osmotic water influx. Of course, damage to the photosynthetic “hardware” usually has severe consequences for photosynthesis, although the reduction in photosynthesis could also be caused by feedback inhibition due to sugar accumulation. Sugar may accumulate in the leaves because cell division, and hence growth, ceases at low temperature, which decreases sink demand for assimilates and may result in an oversupply of fixed carbon (Körner, 2003). With prolonged chilling,