UNIVERSITY OF GEORGIA
Warnell School of Forestry & Natural Resources

Publication WSFNR-23-50A

December 2023

TREES & SEAWATER (Part II): Soil & Tree Salt Stress Impacts

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> Note: This publication concerns seawater inundation and intrusion onto tree sites in coastal communities. The tree salt stress discussed here is not associated with dry-land or semi-arid saline or sodic soils, although some saline soil citations provide insight into seawater salt stress on trees. Some tree and site impacts, and associated treatments, might be similar, but this publication is targeted at only tree health care providers along coastal areas.

Increases in seawater inundation and intrusions of community tree sites are causing tree health issues, soil problems, and tree mortality. Salt stress treatments must be tuned for, and adjusted for, the variability and subtle nature of seawater impacts. As seawater infiltration of tree sites continue and become more common, tree health care providers must be more vigilant in recognizing coastal salt stress and be able to quickly treat seawater encroachment. Both soils and trees are impacted by seawater and the salt it carries.

Seawater Soil Impacts

Salinity, both acute and chronic, is one of the most devastating environmental stresses. Figure 1. (Hasanuzzaman & Fujita 2022; Kumari et.al. 2022b) One definition of tree damaging salinization is an increase of salts in tree soils above 2.5ppt (7% seawater concentration) levels. (Agarwal et.al. 2020) Salinity increases beyond 15ppt (43% seawater concentration) are tied to soil health damage, tree pest increases and improved effectiveness, amplified pollution impacts, and tree death. (Islam et.al. 2022) Two critical features of tree damage by salinity is its duration (how long salt water is present) and severity (how much salt is present), which is the salt stress dose. (Abobatta 2020) Damaging tree site salinity is maintained by lack of drainage, excess irrigation with high salt content water, and overuse of heavy organic material additions. (Kumari et.al. 2022b)

Salinity impacts on tree sites are dominated by osmotic stress (water movement) and ionic stress (toxicity). (Jaiswal et.al. 2022) Seawater inundation and intrusion cause several tree site changes associated with ionic stress issues, notably: 1. alkalinity, 2. sulfidation, and 3. nitrogen ion (NH+) loss. Figure 2.

1. Alkalinity is the accumulation of soluble salts which generate cations in solution, most notably sodium (Na+), calcium (Ca++), and magnesium (Mg++). Seawater introduces large amounts of both calcium and magnesium carbonates into a tree site which changes soil pH and decreases phosphorus availability. (Tully et.al. 2019) An alkaline soil solution is >pH7.3. Tree soils supporting strong growth are usually <pH7. Seawater flooding delivers >pH8.0 to tree sites significantly raising pH. Availability of phosphorus and many metals (especially iron (Fe) and zinc (Zn)) are greatly reduced. The shear volume of cations deposited by one salt water flooding event can completely change soil and site ecology.

2. Seawater contains high concentrations of sulfur compounds like different sulfates, which are reduced by microbes under low oxygen conditions to sulfite (SO3–) and sulfide (S–) over long-term chronic salt water intrusion. Tree damaging sulfidation is generated by an increase of sulfide within soil after seawater intrusion. Sulfide is a reduced material and is highly reactive. (Tully et.al. 2019) Sodium and potassium sulfites and hydrogen sulfide (H2S) are generated in seawater drowned sites, and are damaging to tree root systems and aerobic ecology of healthy soils. Hydrogen sulfide gas generated is very toxic, flammable, and odoriferous (stinks!).

3. Saltwater intrusion liberates ammonium ions (NH+) from soil particles due to competitive sodium, calcium, and magnesium ions. Salt water flooding can lead to anaerobic soil conditions if oxygen is limited, and nitrogen sources are chemically reduced and washed away, causing eutrophic water conditions in surroundings. (Tully et.al. 2019)

Across the scientific literature, salinity increases which impact tree sites and soils fall into several general areas of influence. Soil ecological health and sustainability supporting trees are highly damaged from water problems, ion toxicity, essential element availability issues, shifts from aerobic to anaerobic soil organisms, and wide-spread destruction of microbial functions. The detritus food web which powers the soil ecosystem is severely damaged. Figure 3 provides an itemized list of salinity-initiated and salinity-sustained soil problems listed in order by number of citations (since 2019). Tree site and soil damage by salt stress included 11 major impacts from 23 research citations. The top three most often cited issues with salt stress and soil are essential element availability problems and loss (especially ammonium (NH+) and phosphorus (PO4- -)), salt deposition around roots with its associated toxicity and water uptake disruption, anaerobic changes in sulfate processing, and pH increases.

The first primary component of salt impacts on tree sites is osmotic where soil salinity corrupts water availability and uptake. Figure 4. Normal tree site osmotic pressure differences between soil and root are less than -0.5 to -2 bars. Salinity adds large osmotic potentials between roots and soil, with reversed water flow sometimes possible from root to soil, or failure for roots to take-up water at all. Figure 5. Leaves must generate such large negative water potentials in order to pull water from high salinity soil as to damage photosynthetic machinery. The second primary component of salinity stress on tree sites is ionic toxicity and essential element availability problems. Note, each individual soil and site, and each tree species, may have quite variable tolerances to salinity changes. (Goyal et.al. 2022)

Alkalinity levels on tree sites jump quickly with seawater inundation and intrusion. As alkalinity increases (measured easiest by pH) with a deluge of seawater which is >pH8.0, many elements essential to tree growth become unavailable. Phosphorus (P) and calcium (Ca) can join to form an insoluble mineral making both elements unavailable for tree growth. With a sudden dousing of seawater over a tree site, many element become much more difficult to take-up, especially a majority of the metals. Figure 6.

Ionic Burning of Tree Sites

Large concentrations of ions in seawater like Na+, Cl-, Mg++, SO4–, inhibit tree growth. (Lambers & Oliveira 2019) Tree and site growth responses are measurable with rising sea levels even before visible stress signs become apparent. Figure 7 shows one common way to measure advancing salinity in soil solutions using electrical conductivity (salt bridge). (Hall et.al. 2022) Salinity impacted tree sites have significant: soluble salts, potassium, magnesium, sodium, iron, sulfur, boron, cation exchange capacity, organic matter and ammonium nitrogen in their soil and soil solution. Some of these materials can be at or above toxic levels. (Hall et.al. 2022) For example, soil boron (B) levels with saltwater flooding can build-up to be 2-4 times toxic levels for tree roots. (Hall et.al. 2022; Kozlowski et.al. 1991)

Fresh ground water elevation increases in soils associated with rising sea levels make aerated soil zones and adequate freshwater moisture more critical to tree survival. (Haaf et.al. 2021) If fresh water sources become limited by drought, salt stressed trees will die. Tidal inundation and salt water intrusion into ground water, coupled with lack of drainage and anaerobic soil conditions, push tree root systems to grow nearer the soil surface and force roots to use more stored food to process salt, both of which makes roots more susceptible to salt stress and drought. (Powell et.al. 2022) Along with sea level rise and inudation events causing salt stress, simple soil saturation levels and anaerobic soil conditions can greatly reduce annual tree growth and health. (Hall et.al. 2022)

Smothering

In aerated soils, CO2 is released to the atmosphere and humic materials are attached to clays and hydrous oxides of aluminum (Al) and iron (Fe). (Kozlowski et.al. 1991) In anaerobic soils, CO2, methane, volatile fatty acids, volatile sulfur compounds, alcohols, hydrogen, hydrocarbons, carbonyls, non-volatile acids and phenolic acids are all generated. Critical humic materials are generated at only roughly 1/3X the rate of an aerobic soil. (Kozlowski et.al. 1991) Nitrogen, phosphorus, and sulfur-using microbes are impacted by salinity and anaerobic conditions, changing soil health and element availability. (Jaiswal et.al. 2022)

One particularly reduced form of sulfur from chronic intrusion of saltwater and anaerobic conditions is hydrogen sulfide (H2S) which is highly toxic to tree roots and soil organisms. (Tully et.al. 2019) If iron is present in tree soils with elevated salinity, sulfides can react and form iron-sulfur precipitates which release phosphorus and temporarily reduces sulfide toxicity. As all available iron is consumed, phosphorus availability declines and free sulfides plague trees and site. (Tully et.al. 2019)

Salt Coatings

When first flooded with seawater, low levels of salinity will increases inorganic nitrogen and phosphorus availability in freshwater soils for a time, and might yield increased tree growth. With increasing salinity over time, tree growth plummets. (Noe et.al. 2021) Trees are forced to expell salts from roots. Active excess ion excretion from roots is energy expensive, starve roots, and causes an accumulation of salt around tree root exteriors, driving osmotic (water) stress. Rinsing with fresh water can help remove this salt cloak around roots. (Lambers & Oliveira 2019)

Figure 8 shows the decay rate for soil salinity levels after an acute flood of seawater. Natural processes do not significantly reduce salinity stress on sites and must be accelerated by fresh water rinsing. When salinity stress is combined with drought, overall stress on a tree site is compounded and requires even more fresh supplemental water to both alieve drought and rinse away salts in soils around roots. (Abobatta 2020) Fresh water rinsing sources need to be checked, especially after seawater flooding and storm surges for salt contents.

The historic legacy of salt water inundation keeps damaging tree sites after recovery. Tree sites will be more alkaline and more sulfidic after salinity pulses, with legacy concentrations of saltwater materials remaining in soil. These past problems make the next salt water pulse quicker to damage tree soils, and faster to accumulate materials, which will cause soil changes and damage. (Tully et.al. 2019)

Seawater Tree Impacts

Sea level rise is driving saltwater flooding, soil salinization, and salt accumulation within tree tissues, all causing essential element uptake problems, water uptake issues, and reduced tree growth. (Hall et.al. 2022) Primary salinity impacts on trees can be divided between osmotic (drought type water deficiency), ionic (ion toxicities within cells), and oxidative damage. Figure 9. (DeSedas et.al. 2020; Hasanuzzaman & Fujita 2022; Khan et.al. 2020; Khare et.al. 2022; Kozlowski et.al. 1991; Lupo et.al. 2022; Zhang et.al. 2019) Salinity responses by trees have both a quick and delayed response: the first quick response is managing osmotic changes in cells and cell walls; and, the second delayed response is management of ion accumulation to minimize toxic levels and controlling generation of oxidative molecules (Agarwal et.al. 2020)

Out of Proportion

Trees need 19 essential elements for their growth and reproduction, all carried in a freshwater bath. These elements must be available to a tree in the correct proportions to avoid deficiencies and toxicities. Figure 10. Seawater contains all tree essential elements, but not in life-sustaining proportions. (Coder 2021) Figure 11 shows tree essential elements and their concentrations in seawater.

Element issues can become important over both the short- and long-run, both in deficiency and toxicity. For example, essential elements chlorine (Cl), magnesium (Mg), sulfur (S), boron (B), silicon (Si), molybdenum (Mo), and nickel (Ni) can accumulate from seawater inundations and intrusions well beyond tree requirements, which generate toxicity. In addition, the combined amount of total essential metals (and non-essential metals) in seawater can generate toxicity issues even though any single metal element is not at toxic levels.

Going Wrong

The impacts of salinity on trees include water stress, electrolyte issues, ionic toxicity, essential element disorders, cell division reduction, cell differentiation and expansion decreases, activation of antioxidant enzymes, and formation of nitric oxides and polyamines. (Kumari et.al. 2022b) One almost immediate response to salinity is inhibition of root growth and a quiescence period before a tree reacts. (Sanchez-Romera & Aroca 2020) Salt stress then initiates a forced balancing of ion concentrations internally, activation of osmotic stress adjustment pathways, changes in tree growth regulators, and modification of cytoskeleton and cell wall composition. (Hasanuzzaman & Fujita 2022)

A tree is one organism making holistic adjustments for managing and surviving salinity changes in its environment. But, there has been debate among researchers regarding whether shoots or roots are the most sensitive and negatively impacted by salinity. One study cited shoot growth in trees is more sensitive to salinity than root growth. (Zhang et.al. 2019) Another researcher found roots were much more impacted by salinity than shoots. (Lupo et.al. 2022) In this case, the study showed a reduction in both root and shoot mass, but it was coupled with a reduction in root / shoot ratio, suggesting roots were most impacted. (Lupo et.al. 2022)

Growth Loss

The single most important macro-sign of salinity issues for a tree is decline in growth. Figure 12 shows declining tree biomass accumulation both above-ground and below-ground as salt stress levels increase. Both tree height and diameter growth are inhibited with increasing salinity. Figure 13 shows inhibition of diameter and height growth with increasing salinity levels. Because vegetative growth is a gross summation of many different life processes within a tree, a more detailed analysis is needed to identify major tree constraining points.

Osmotic (Water) Stress – A tree's physiological functions must be bathed in a potassium ($K+$) water solution. In addition, the environmentally driven transpiration stream of soil water uptake uses the strong negative water potential of the atmosphere to power water transport from soil to leaf. A tree is a water conduit positioned between slight (negative soil water potentials) and high (much more negative) air water potentials. Water is the most critical essential element within a tree system. The control of water within living cells (symplast), and externally in cell walls and dead tissue areas (apoplast), govern tree life and death.

In order to remain physiologically hydrated, tree structures carefully control their internal and immediate surrounding's water potential. Roots must have a more negative water potential than soil in order for water to move from soil to root. The stem must have a more negative water potential than roots in order for water to move from root to stem. The greatest water potential gradient is between the atmosphere and leaf cells. The atmosphere's large negative water potential (very dry) forces leaves to manage water flow by slowing water evaporation from internal leaf surfaces. Too fast of water movement out of a leaf generates a more negative water potential. Too much dryness and water loss can disrupt internal functions which require strong hydration.

The result of salinity increases is ions holding water more tightly, and drawing water into hydration spheres surrounding each salt ion. Salt water has a much lower (more negative) water potential than fresh water, slowing water uptake and movement in trees. The photosynthetic machinery of the leaf must have plenty of easily available, low water potential water in order to function. Under salt stress, movement of water into a tree is disrupted and slowed, defensive respiration costs increase, and photosynthesis processes decline. (Goyal et.al. 2022)

Salt can trigger osmotic stress by both reducing soil water availability and by increasing accumulation of excess sodium (Na+) in cells. (Rahman et.al. 2019) Salt stress water deficit conditions close stomates reducing photosynthesis activities, while accelerating accumulation of reactive oxygen and nitrogen molecules. Salinity stress mimics severe water deficits (drought) causing decreased stomate conductance and less CO2 uptake, leading to less food production, less tree growth, and more tree stunting and death. (Rahman et.al. 2019; Zhai et.al. 2018)

Trees must make osmotic adjustments by accumulating organic solutes and osmo-protectants within living cells. (Rahman et.al. 2019) Osmotic regulation in trees include rearranging and production of carbohydrates (sugars, sorbitols, mannitol, glycerol, and pinitol), nitrogen containing materials (proteins, betaine, glutamate, aspartate, glycine, proline, choline, aminobutyrate), and organic acids (malate, oxalate). (Hasanuzzaman & Fujita 2022) These materials are increased in cells as salinity levels climb in order to help off-set osmotic changes from salt stress. (Rahman et.al. 2019; Zhang et.al. 2019)

Ionic Stress – Ion management in trees involves uptake, transport, and distribution of both essential element ions, and exclusion or sequestration of toxic ions. (Rahman et.al. 2019) High levels of sodium-chloride (NaCl) is toxic to trees and causes internal ion imbalances. (Lambers & Oliveira 2019) For example, potassium (K+) is required for activating many enzymes and serves as an ionic water bath within trees cells, but Na+ ions disrupt enzyme systems by replacing potassium (K+) which causes enzymatic systems to be degraded and made non-functional. (Abobatta 2020)

Increasing ionic strength disrupts many tree life functions. (Tully et.al. 2019) Seawater salt is predominantly sodium chloride (NaCl) which easily disassociates into Na+ and Cl- ions in water. Figure 14 provides the dominant ions found in seawater. Note the presence of many sulfur compounds. Depending upon concentration, and duration of any salt dose, Na+ is the most toxic ion in seawater (Lambers & Oliveira 2019), and is actively excluded from roots and sequestered in woody stems and root rays cells. Unfortunately for a tree, compartmentalizing Na+, makes elevated Cl- concentrations relatively more toxic. (Lambers & Oliveira 2019; Lupo et.al. 2022)

Salt triggers ion toxicity through accumulation of excess Na+ and Cl- in cells, which impede common essential functions leading to tree death. (Rahman et.al. 2019) In the long-term, cell energy (ATPs) must be used to actively pump out excess ions for both ionic balance and membrane stability, which is very costly for a tree and limited by its local food reserves. (Khan et.al. 2020) Different tree parts can be starved to death through dealing with excess salt ions.

Growing tree roots avoid soil areas with high Na+ concentrations (i.e. halotropism). (Sanchez-Romera & Aroca 2020) Trees also try and avoid salinity stress by preventing Na+ uptake into the transpiration stream to the leaves. (DeSedas et.al. 2020) Short-term sequestering of Na+ and Cl- occur in root xylem. (Kozlowski et.al. 1991) Roots compartmentalize salt into cell vacuoles, and reduce salt levels in leaves by either root exclusion, or depositing overabundant ions into woody tissues. (Lupo et.al. 2022; Zhang et.al. 2019) Root xylem parenchyma take-up and hold Na+ and help excrete salt ions. Efflux of excessive salt ions is energy expensive for tree roots. (Lambers & Oliveira 2019) Roots use stored food reserves to move ions outward and away from living tissues, but these ions accumulate immediately around exterior root surfaces.

Sodium ions (Na+) are competitive with potassium ions (K+) for transporters across membranes and within metabolic systems. Sodium ions (Na+) also replace calcium ions (Ca++), which are removed from root cells and causes potassium ions (K+) to leak out of cells. (Lambers & Oliveira 2019) Maintaining calcium ion (Ca++) concentrations can obstruct Na+ influx and stimulates energy production in order to remove Na+. (Khare et.al. 2022)

In leaves, it is critical to exclude sodium (Na+) and salt particles in order to allow proper functions. (Kumari et.al. 2022b; Zhang et.al. 2019) Sequestering Na+ in roots is an effective way of preventing leaf damage. Low levels of chlorine (Cl- = a tree essential element) can improve water use efficiency in leaves by reducing stomate conductance without changing CO2 uptake. (Lupo et.al. 2022) But, higher Cl- levels need to be pushed into epidermal cells of a leaf to exclude them from damaging photosynthetic cells. Climbing Cl- levels in leaf tissues cause a long term reduction in leaf area and tissue growth. (DeSedas et.al. 2020; Lambers & Oliveira 2019)

For estimating salinity impacts in trees, ion ratios can be used. For example, decreasing leaf K+ / Na+ ratios are an indicator of salinity problems. (Lupo et.al. 2022) Trees attempt to maintain a steady K+ / Na+ ratio in their cells under high salinity, with too much Na+ leading to K+ loss, competition for uptake sites, and membrane damage. (Zhang et.al. 2019) Na+ and Cl- ion concentration increases in and around roots are associated with a reduced K+ / Na+ ratio in roots, and an associated increased Cl- level (but not Na+ level) in leaves. (Lupo et.al. 2022) High salinity causes low K+ / Na+, Ca++ / Na+, and Mg++ / Na+ ratios in trees. (Goyal et.al. 2022)

Oxidative Stress – Salinity impacts in trees are a combination of osmotic, ionic, and oxidative stress. (Khan et.al. 2020) Salt stress triggers turgor reductions, decreases cell expansion, initiates essential element deficiencies, accelerates senescence, reduces stomate control, impairs photosynthesis, damages protein synthesis, prevents K+ transporters from functioning, lowers K+ / Na+ ratios in living cells, disrupts enzyme activation, and disrupts carbon metabolism, all of which leads to production of reactive oxygen molecules causing oxidative damage to cells. (Kumari et.al. 2022b; Rahman et.al. 2019) The oxidative damage by reactive oxygen molecules can be partially controlled by antioxidant systems within tree cells, but can be quickly overwhelmed. (Zhang et.al. 2019)

Reactive oxygen molecules (oxidative stress) are generated in chloroplasts under salt stress damaging membranes, proteins, and nucleic acids. (Goyal et.al. 2022; Hasanuzzaman & Fujita 2022) Reactive oxygen molecules generated under salinity stress include hydrogen peroxide (H2O2), superoxide anions (O2-), hydroxyl radicals (OH+), and singlet oxygen (1O2). These molecules accumulate as salinity increases causing severe damage to living cells. (Goyal et.al. 2022; Kumari et.al. 2022b; Zhang et.al. 2019)

Reactive oxygen molecule accumulation causes membrane permeability problems, membrane damage, DNA damage, protein disruption, changes in enzyme activity, and cell death. (Hasanuzzaman & Fujita 2022; Kumari et.al. 2022b) The more K+ retained within cells, the greater activation of reactive oxygen scavengers, and the less reactive oxygen molecules are generated under salt stress. (Khan et.al. 2020; Zhang et.al. 2019) Note, reactive nitrogen molecules, including nitric oxide (NO), nitrous acid (HNO2), and dinitrogen tetroxide (N2O4) can also be generated in trees under salinity stress causing cell damage. (Zhang et.al. 2019)

Summing-Up

Figure 15 summarizes the primary categories of salt stress within trees presented as a salinity impact triangle. Reduced vegetative growth, and delayed or reduced reproductive growth are the results of increasing salinity. Eventually, growth functions can not be maintained and tree death occurs. Figure 16 shows example mortality curves for trees under two types of salt deposition, a short-term acute event and a long-term chronic level of salinity change.

A Litany of Impacts

Prioritizing tree impacts from salinity increases can be listed by general locations and by the processes where tree damage occurs. Figure 17. This figure lists, by number of citations of tree impacts described since 2018, the extent and scope of tree salt stress.

Figure 18 is a multi-page list of tree growth components cited as becoming problems inside a tree under salt stress from seawater. In this extended figure, individual tree changes are placed into anatomical, functional, and general impact focus areas. Remember, any one or all of these impacts can lead to severe tree stress and death. Figure 19 pulls out the top eight (8) cited tree impacts from salt stress research. Of all new research on salt stress, there are a number of consensus impacts cited by many authors since 2018. Salt stress impacts on the whole tree is concentrated around inhibition of, and damage to, tree growth, including continued development and survival, a decrease in tree biomass production, and inhibition of most measurable growth parameters. The leaf and photosynthesis impacts include an acceleration of leaf senescence and abscission, as well as stomate closure which degrades photosynthesis and chlorophyll maintenance. Resource gathering by the tree is impacted by reduced water uptake and a number of essential element deficiencies.

Metabolically, decreased carbohydrate (food) production facilitated by salinity issues generate internal oxidative molecules damaging tissues. In roots which are at the interface with salt accumulation, growth is hampered severely. Tree tissue respiration plummets due to electron transport damage and disruption of different respiration steps and pathways. Throughout a tree, salinity damages, destroys, and inhibits a host of processes required for life and survival.

Differing Tree Tolerances To Salt

One means to appreciate salt stress in trees is to examine more salt tolerant trees. Most trees, even along coastal areas, are intolerant of seawater inudation and salinity increases. By examining how salt tolerant trees survive and grow, a better understanding of salt stress impacts on all trees can be appreciated. Figure 20 provides salt water measures which will be used to describe tree health, growth, and mortality.

Salt tolerant trees rely on seven mechanisms: 1. Control of ion uptake; 2. Ion compartmentalization in cells and across the whole tree; 3. Synthesizing solutes for osmo-protection; 4. Active antioxidant defense; 5. Modify photosynthesis systems; 6. Change growth regulator signaling; and, 7. Adjust tree anatomy. (Rahman et.al. 2019)

The Line Between

Salt tolerant species, especially shrubs, began dominating areas as 1ppt (2.9% seawater concentration) salinity was exceeded. (Noe et.al. 2021) Salt tolerant trees may survive with a salinity of >1ppt, but will decline in growth. (Celik et.al. 2021) A salinity division between more salt tolerant tree species and salt intolerant species (of which most trees are salt intolerant) is around 2ppt (5.7% seawater concentration). (Celik et.al. 2021) Other authors place this threshold higher.

Two authors cited a threshold salinity concentration between salt tolerant and non-tolerant tree species to be around 11.5ppt (33% seawater concentration). (DeSedas et.al. 2020; Tiwari et.al. 2022) Most salt tolerant species reduced growth by 10-50% at 17.5ppt (50% seawater concentration), with some salt tolerant tree species showing no reduction in growth. (DeSedas et.al. 2020) One salt tolerant tree was able to grow in soils with 20ppt (57% seawater salinity), survive at 26ppt (75% seawater salinity), and continued to survive for short periods in soils with up to ~50ppt (142% seawater salinity). (Zhang et.al. 2019)

Managing Ions

In the short term, salinity increases cause K^+ efflux and leakage from cells as they try to balance Na^+ influx. The effective retention of K^+ within cells is a sign of improved salt tolerance. (Khan et.al. 2020) Tolerance to salt also represents an ability to effectively manage Na^+ and Cl^- foliage toxicity. (DeSedas et.al. 2020) Salinity tolerance is associated with using K^+ to maintain a stable K^+ / Na^+ ratio, a high NO_3^- / Cl^- ratio, and manage Cl^- toxicity. (DeSedas et.al. 2020; Khare & Jain 2022; Rahman et.al. 2019) Salt tolerant trees restrict transport of Na^+ to leaves in order to facilitate uptake of other essential elements, while accumulating K^+ and Ca^{++} in leaves. (Rahman et.al. 2019; Zhang et.al. 2019) Tolerant trees sequester Na^+ ions into root cell vacuoles and xylem cells, functionally detoxifying cytoplasm and providing for osmotic support to take-in water. (Rahman et.al. 2019; Zhang et.al. 2019)

Still Standing

When a salt tolerant tree was exposed to 17.5ppt (50% seawater salinity), tree height was reduced by -31%, diameter was reduced by -46%, photosynthesis rates decreased -48%, and leaf numbers were reduced by -20%, all reducing average leaf area by -60% and causing permanent leaf wilting and chlorosis within 10 days. Salt tolerance does not signify "no damage," just an ability to tolerate salt stress. (Zhang et.al. 2019) For this same salt tolerant tree, 3ppt (8.6% seawater salinity) showed no growth impact. (Zhang et.al. 2019) Some salt tolerant trees are able to handle short-term spikes of salt water concentrations, as well as some prolonged submergence. (Celik et.al. 2021)

Alternatively, some salt intolerant trees showed a -31% leaf growth reduction at 4.5ppt (12.9% seawater concentration), with leaves becoming chlorotic and abscised. These same trees completely stopped growth at 7ppt (20% seawater salinity). (DeSedas et.al. 2020) In another study, a salt intolerant tree exposed to 6ppt (17% seawater salinity) saw major reductions in leaf elongation, shorter internode lengths, more short branches, and increased bud numbers, all coupled with leaf epinasty, browning, death, and abscission. (Zhang et.al. 2019) These salt intolerant trees had reduced heights, diameters, and leaf numbers. The same species exposed to 3ppt (8.6% seawater salinity) showed only minor salt stress symptoms. (Zhang et.al. 2019) Salt intolerant trees were shown to generate damaging high root respiration rates trying to exclude salts. (Lambers & Oliveira 2019) One author stated salt intolerant trees need <1.6ppt (4.6% seawater concentration) to properly survive and grow. (Tiwari et.al. 2022)

Living & Dying

Tree growth after salt stress was applied showed two distinct phases. Figure 21. The first phase was dominated by osmotic stress where most trees responded similarly in declining growth. The second phase is ionic stress and shows a sharp divergence between salt tolerant and salt intolerant tree growth. (Goyal et.al. 2022) Salt tolerant trees clearly handle ionic stress better than salt intolerant trees. General differences between salt tolerant and salt intolerant trees are summarized in Figure 22. In human terms, salt tolerant trees are able to continue plodding along under heavy environmental burdens, while salt intolerant trees (i.e. most trees) fight quickly and die quickly.

From many studies, combined salt stress limits can be estimated for most trees. Figure 23 provides a list of salt stress thresholds cited for causing major tree health decline, averaging 2.4ppt (6.9% seawater concentration). Figure 24 provides a list of salt stress thresholds cited for causing tree mortality, averaging 8.5ppt (24.3% seawater concentration).

Coastal Community Tree Issues

A number of studies have found various levels of salinity initiating decline symptoms or causing tree death across a diversity of tree species. In one study, tree mortality rates were 4% (2X normal) on slightly saline sites, and 26% mortality on the most saline sites. (Conner et.al. 2022) Many authors have provided detailed cause and effect reasoning for why coastal trees are dying from increased salinity. They can be summarized into five primary reasons for tree death, ordered by number of citations since 2018:

1. **Sea Level Rise.** (Haaf et.al. 2021; Hall et.al. 2022; Noe et.al. 2021; Powell et.al. 2022; Ury et.al. 2021; Zhai et.al. 2018)
2. **Acute Salinization Events / Storm Surge.** (Conner et.al. 2022; Haaf et.al. 2021; Hall et.al. 2022; Noe et.al. 2021; Ury et.al. 2021; Zhai et.al. 2018)
3. **Salt Water Inudation / Tide Height / Phosphorus Stress.** (Celik et.al. 202; Noe et.al. 2021; Powell et.al. 2022; Ury et.al. 2021; Zhai et.al. 2018)
4. **Hydrologic Alterations.** (Celik et.al. 2021; Conner et.al. 2022; Hall et.al. 2022; Ury et.al. 2021)
5. **Drought With Salinization.** (Haaf et.al. 2021; Noe et.al. 2021)

Ghost forests (standing dead trees) and salt marsh expansion represent visual signs of salinity changes killing trees. (Chen & Kirwan 2022) In one study area over 34 years, tree mortality was 50% (23% in pines / 27% in hardwoods), with ghost forest areas increasing by +6%, and non-tree areas increasing by +47%. (Ury et.al. 2021)

Making It Worse

In coastal community forests, strong winds (causing defoliation, uprooting) and storm surges (causing soil anaerobic conditions, sulfide production, and toxic soil conditions) are leading to tree stress and mortality. (Powell et.al. 2022) Soil salinity constraints coupled with drought conditions interact to cause tree damage. (Haaf et.al. 2021) Severe drought, especially during hot growing seasons, can cause seawater intrusion into groundwater, salt pulses from tides not being flushed out, and strong soil surface evaporation, all of which lead to tree mortality. (Powell et.al. 2022) Salinity increases mimic drought by increasing osmotic stress. When saltwater floods occur in the latter part of a growing season, tree growth is greatly constrained. (Haaf et.al. 2021) Young trees are usually first to show signs of salt stress and mortality. (Hall et.al. 2022)

Flooding is stressing trees through greater quantities of soluble elements present, especially boron (B), sodium (Na), sulfur (S), potassium (K), and magnesium (Mg), some of which exceed toxic levels. (Hall et.al. 2022) Tree mortality is occurring both gradually through chronic inundation and salinization, and acutely through episodic events. (Hall et.al. 2022) Salinity is leading to coastal tree losses, with one single storm event killing many trees, and incremental pulses of salinity changing site quality for any surviving trees. (Tully et.al. 2019) Most trees can tolerate infrequent periodic salinity exposures, but chronic salinity conditions lead to major tree mortality. (Ury et.al. 2021) Increased interconnections with saline water areas and poor drainage drive soil salinization and tree mortality. (Powell et.al. 2022)

Community Tree Issues

Moderate salinity tends to kill native trees and accelerates salt tolerant invasive tree species success, while high salinity levels tend to kill all trees. (Tully et.al. 2019) Invasive species tend to be less sensitive to salt and drought stress, and continue to grow better than native trees under mild to moderate stress, but are more sensitive under extreme salinity. (Paudel et.al. 2018) In addition, communities containing many of the same tree species, native or exotic, are more at risk of salt water damage to many trees at once than a landscape with many diverse species of trees. (Tully et.al. 2019)

Saltwater intrusion from sea level rise, freshwater withdraws, and storms all damage trees and their sites. (Tully et.al. 2019) Trees in low-lying areas are susceptible to upland runoff and saturation, tidal flooding, and saltwater intrusion. Under these conditions, only slight increases in soil salinity cause serious problems (Conner et.al. 2022) Salt water impacts trees through intrusion into groundwater before noticeable effects of increased tidal flooding. (Powell et.al. 2022) Rising water tables driven by sea level rise, constrained ecological viable volumes, and salinity increases, all impact trees well inland of the ocean edge. (Ury et.al. 2021) As rising sea levels elevate the water table, tree responses include more shallow and asymmetrical root development, reduced tree root stability, and increased windthrow potential during storms. (Hall et.al. 2022)

Treatments For Trees & Tree Sites

Seawater inundation and intrusion events continue to stress and strain community trees and tree sites. Along with acute events, a long-term progression of increasing salt contents will push inland due to sea level rise and changes in salt content of local irrigation wells and ground water. Tree salt issues are accelerating in importance in coastal community forests. Treatments and stress mitigation processes require both prompt actions and slow subtle changes to tree and soil health care. Slow incremental changes made to counteract salt stress is much more effective, and without major unintended results, than single massive and intense treatments.

Seawater salt stress is devastating to site ecology and tree health. Seawater drowns, smothers, poisons, and desiccates tree sites. Soil desalination is required quickly after salinity increases. (Kumari et.al. 2022b) Reducing soil salinity requires many treatments and applications, including tuned irrigation, reduced levels of fertilizers, and carefully planned organic matter additions. (Kumari et.al. 2022b) The two most important treatments for trees after seawater innundation is to both assure drainage of the site (surface and sub-surface), and freshwater rinsing (wells and water sources must be salt-free). (Coder 2022a; Coder 2022b; Hodson & Bryant 2012; Willey 2016)

0. Pre-Treatments

Multiple studies have shown pre-treatments with small amounts of organic amendments improved soil resistance to salinity changes by both increasing soil drainage and aeration, and improving the detritus food web processes. Soil enrichment with inorganic pore space enhancement materials can be effective if site drainage is assured. Most importantly, everything which can provide fast and adequate drainage on the site must be completed. (Zhai et.al. 2018) Pre-treatments also include planting more salt tolerant trees. Figure 25 lists the categories of salt stress treatments for community trees, their sites, and soils.

1. Drainage & Aeration

To prevent seawater access to tree sites, barriers have been built intentionally through soil and hardscape placement. These above and below ground structures can channel small salt water events away and prevent direct impacts on trees, but these same structures can be overwhelmed by large seawater inundation events. Any structure preventing salt water infiltration or flooding will serve as a barrier to salt water drainage after any large flooding event. Whatever the structure, or landscape sculpting installed, it is critical to allow water to flow away from tree sites. Drainage is a primary treatment.

Drainage and associated aeration are the most important of treatments for salt stress. Drainage across tree site surfaces and drainage downward through soil are key. Complete prevention of salt water inundation either as acute events or long term changes will not be possible over the life-span of many coastal community trees. Assuring drainage and aeration of tree soils is made more difficult when sea level rise blocks or backs-up drainage systems, and rising fresh water tables are buoyed-up by rising seawater levels. An important result of poor drainage and aeration is propelling tree soil into anaerobic conditions, accelerated by warm water and warm air temperatures. Drainage must both remove salt water and increase oxygenation of soil. Because soils can become anaerobic quickly (within days), fast action to drain tree sites is paramount to begin any tree treatments.

At times due to a legacy of building and development, tree sites may be placed in low landscape positions, making drainage and aeration extremely difficult. Storm water removal systems usually work in both directions, bringing flood waters in and then taking them away. More flooding from these systems can be expected as sea levels rise. Flooding for any length of time and depth are always damaging. In addition, seawater inundation is damaging because of its salt content. Seawater constrains oxygen movement into soil especially when warm, shifting soils toward anaerobic conditions. (Coder 2022a; Coder 2022b) Anaerobic conditions mean much less oxygen is available in soil, and limited oxygen is moving into and through soil. Little to no oxygen in tree soils lead to a chemically reducing soil environment. (Coder 2020)

Under these conditions, toxic levels of materials can be generated or can become available, and organic matter is not mineralized or decomposed effectively, consuming any remaining oxygen. (Coder 2020) As oxygen is consumed, an anaerobic respiration sequence begins among soil microorganisms, starting with the use of (i.e. respiring of) soil nitrogen (N) and moving through manganese (Mn), iron (Fe), sulfur (S), and ending with carbon (C) (i.e. fermentation of organic matter including roots). (Coder 2020) The last two elements in anaerobic soil respiration (sulfur and carbon) are the most damaging to trees. If only partial drainage can be accomplished, or saturation levels of freshwater or saltwater are close to the soil surface, aeration will be compromised. Anaerobic soil conditions can lead to root rots, new pests, and tree mortality.

Returning to a healthy soil ecology as quickly as possible is the best treatment for tree salt stress. Test holes can be installed with perforated pipe liners to help understand soil water levels. Drainage away from tree sites is both an above ground and below ground process. Designing and installing an effectively draining topographic and hydrologic gradient ahead of salt water events would be ideal. Drainage features in the area around a tree site must be installed, while not damaging tree root systems. Water must flow away from soil areas containing tree roots.

2. Fresh Water Rinse

The second critical treatment for seawater salt stress, after assuring drainage and aeration, is fresh water rinsing. Fresh water rinsing of tree exteriors and surrounding surfaces, and fresh water rinsing in discrete pulses across the soil surface, will help dilute and wash away salt accumulations. Fresh water rinsing must be done in multiple bursts and then allowed to drain away. The periodicity of each rinse cycle depends upon soil and site drainage. Well-spaced fresh water bursts act like a heartbeat, helping move oxygen into soil in-between water applications. When a fresh water application is applied, more applications are delayed until site water levels have fallen through the soil.

The term "fresh water" after a flooding event and sea level rise must be measured. A salt bridge test (electrical conductivity) can be used to determine if salt water has polluted a well or water source used to rinse the site. Using brackish water to rinse a tree site will continue to damage trees. Be sure not to add additional salts to the site and do not saturate the site up to the soil surface – no puddles or run-off. Fresh water is applied for rinsing, not drowning or generating swampy conditions.

Active ion excretion from tree roots is energy expensive and causes an accumulation of salts around tree root exteriors, driving water potential down (more negative). Rinsing with fresh water helps remove this salt jacket. (Lambers & Oliveira 2019) When salinity stress is combined with drought, overall stress on a tree is greatly compounded and fresh water needs to be applied to both alieve drought, and rinse away salts in soils and around roots. (Abobatta 2020)

3. Soil / Site Enrichment

Given the preceding information concerning salt and tree soils, there are several more active treatments or applications which can be made. Remember small iterations of treatments will allow tree and soil ecology adjustments after salt stress events, rather than one large application for mitigating salt stress. Always think "trickle not gusher."

For many trees, essential element stress may be more important to survival than water stress issues, suggesting supplemental enrichment of a site with essentail elements may help mitigate effects of salinity. (Zhai et.al. 2018) Salinity especially reduces availability of tree essential elements calcium (Ca), iron (Fe), potassium (K), nitrogen (N), phosphorus (P), silicon (Si), and zinc (Zn), so limited elemental enrichment of tree sites might be warranted. (Gupta et.al. 2022) Every individual tree and species have a slightly different response to salinity changes and chronic salinity levels. Every enrichment treatment must be tailored to the specific soil and site, and to the tree.

Essential element enrichment with low concentrations of slow release nitrogen in nitrate form (N), phosphorus (P), potassium (K), and calcium (Ca) have been found to improve salt tolerance, help in root development, pushes Na^+ exclusion, and can help reduce accumulation of damaging reactive oxygen molecules thus enhancing membrane stability. (Khare & Jain 2022; Sanchez-Romera & Aroca 2020; Zhang et.al. 2019) Any nitrogen (N) source dependent upon moving through an ammonium (NH^+) stage should be avoided.

Small additions of potassium (K^+) and nitrate (NO_3^-) must be applied only if soil aeration has been reestablished and elevated seawater pH levels are declining. (Coder 2022a; Coder 2022b; Hodson & Bryant 2012; Willey 2016) Enriching tree sites with supplemental additions of small, low concentrations of slow release phosphorus (P) and potassium (K) components, while assuring zinc (Zn) and iron (Fe) are available, has been shown to alleviate some portion of increased salinity impacts on trees. (Gupta et.al. 2022) Do not add anything to the site with sulfur components.

Cation problems need careful solutions. Alkalinity levels added from seawater can be massive. A tree requires strong levels of Ca++ and K+ ions. These ions are especially impacted by salinity increases, making it more difficult for trees to take-up these ions. (Kumari et.al. 2022b) Calcium ions (Ca++) enhance Na+ exclusion, restrict K+ loss, and sustain membrane integrity. (Lambers & Oliveira 2019; Zhang et.al. 2019) Small amounts of calcium (Ca++) can be of value, but do not add a calcium source which increases the salt or sulfur content level. (Coder 2022a; Coder 2022b; Hodson & Bryant 2012; Willey 2016) Potassium (K+) availability is required for health and salt resistance. (Khare et.al. 2022) Management for strong K+ / Na+ and Ca++ / Na+ ratios will help minimize tree salt damage. (Gupta et.al. 2022) Do not attempt to lower site pH (alkalinity) through amendments until drainage and aeration are assured and healthy soil ecology has been restored.

There are several issues with site enrichment with essential elements. First is to minimize metals as a whole. Do not add micro-elements (primarily metals). (Coder 2022a; Coder 2022b; Hodson & Bryant 2012; Willey 2016) Many essential metals may become unavailable due to pH issues of seawater, but their shear amount delivered by seawater can be damaging. Individual metal elements, and the combined total of all metal elements together, can build-up to be toxic in the aftermath of seawater flooding or intrusion. Tree essential elements which are metals include: Co cobalt; Cu copper; Fe iron; Mn manganese; Mo molybdenum; Ni nickel; and, Zn zinc. (Coder 2020; Coder 2021; Coder 2022b) Minimize any "micro-element" additions to sites until aeration is reestablished, pH levels have declined, and a tissue and soil testing tree health care program can resume.

Secondly, both silicon (Si) and boron (B) are essential elements for trees. (Coder 2021) Silicon applications in moderation can be made to help trees both structurally and physiologically mitigate salt stress. (Khan et.al. 2020) Boron (B) is needed for salinity management in trees, but can easily reach toxic levels at low concentration levels, and is found in significant amounts in seawater. (Sanchez-Romera & Aroca 2020) Careful small applications for recovering soils and trees can be prescribed, but must be limited to what a healthy soil and tree can process.

4. Organic Matter Management

Organic matter in an oxygenated soil helps power the detritus food web which supports strong tree growth. Too much organic matter can consume too much oxygen in soil, and coupled with saturated conditions, can push soils more quickly to anaerobic conditions. Careful small additions of well composted, tree-based organic matter can help mitigate modest levels of salinity changes. Large, single organic matter additions can be detrimental to soil and tree health after seawater inundation.

Healthy soil ecology built with organic matter fuel and plenty of aerobic rhizosphere organisms, can increase phosphorus (P), magnesium (Mg), and nitrogen (N) availability and uptake, while reducing sodium (Na+) uptake. (Kumari et.al. 2022b) Tree-derived compost and humic enrichment of soil increases tree tolerance to salinity, enhances essential element availability, and improves cation and anion exchange capacity. (Gupta et.al. 2022; Kumari et.al. 2022b)

Tree-growth-promoting-rhizobacteria, mycorrhizal fungi, phytohormones, and organic acid additions can be used to generate some level of salt tolerance in trees and salt stress recovery. (Hasanuzzaman & Fujita 2022) Mycorrhizal fungi infection and tree-growth-promoting-rhizobacteria (TGPR) can act as salt ion barriers and support better functioning of tree tissues. (Kumari et.al. 2022b) Addition of biological enhancements to tree sites to combat salinity could include: cyanobacteria / blue green algae, rhizobacterium, mycorrhizal fungi, and phosphate solublizing bacteria. (Gupta et.al. 2022) But, all of these additions require a well aerated and drained soil to be effective.

5. Debris & Deposited Soil Removal

After some seawater flood events, debris and erosion materials may have accumulated on a tree site. Remove debris and pull back soil and sand which may have been deposited. Attempt to have the soil surface at the same height as before. Do not disrupt, sculp, or dig into the soil surface where tree roots will be damaged.

6. Pruning

Tree site management first needs to counteract seawater salt stress. Dead-wooding or pruning should be delayed at least one full growing season, if not more. Young trees overtopped by seawater flooding events and mature trees under salt stress will make many allocation decisions internally, which can lead to defoliated branches, dead branches, stag-heading, and branch / crown decline. Delaying crown treatments will allow trees to determine which branches are to be kept and which may be compartmentalized off. While trees are recovering from seawater stress, do not root prune, damage the tree or surrounding soil, or complete any greenwood pruning. (Coder 2022a; Coder 2022b; Hodson & Bryant 2012; Willey 2016)

Conclusions

Seawater management will become even more important to trees and tree sites in coastal community forests and across landscapes. The salt content of seawater flooding events will accelerate impacts on community trees with sea level rise, storm surges, tidal flooding, and ground water intrusion. Tree health care providers need to understand seawater salt stress, tree responses to salinity, measurement of salt water, and prescribing treatments for salt stressed trees and soils. Increasing seawater impacts on trees can not be avoided for long, and coastal arborists and tree owners need to be prepared to maintain tree health and soil ecological functions.

Citation:

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TREE DAMAGE

Acute Salt Stress

-EXTREME EVENTS

-TIDAL FLOODING

Chronic Salt Stress

-SEA LEVEL RISE

-LAND SUBSIDENCE

-COASTAL EROSION

-GROUND WATER INTRUSION

Figure 1: Duration of water source salt stress in trees over short durations (acute impact) and long time frames (chronic impact).

Site / Soil: Effects of Salinization

INCREASED IONIC STRENGTH

osmotic stress / dehydration
ion exchange / imbalance
mobilization of ammonium

ALKALINIZATION

pH change / phosphorus issues
drainage problems
organic matter / detritus tied-up

SULFIDATION

high sulfates / sulfide toxicity
iron-sulfur compounds formed
phosphorus released then loss

Figure 2: Major impacts of acute and chronic salinization on tree sites. (Tully et.al. 2019)

TREE SITE / SOIL IMPACTS

major impact of salt stress	(research source citation)
-decreased essential elements Ca, Fe, K, Mg, N (NO3-), P (PO4–), Si & Zn availability and assimilation, with site loss of ammonium (NH+) and phosphate (PO4--).	(Abobatta 2020; Goyal et.al. 2022; Gupta et.al. 2022; Islam et.al. 2022; Khare & Jain 2022; Lambers & Oliveira 2019; Tully et.al. 2019)
+increased soluble salt deposition and accumulation around root exteriors forming barrier to water movement and toxic crusts.	(Abobatta 2020; Goyal et.al. 2022; Hall et.al. 2022; Islam et.al. 2022; Kumari et.al. 2022b).
+increased microbial sulfate reduction.	(Celik et.al. 2021; Tully et.al. 2019; Ury et.al. 2021)
+increased soil alkalinity.	(Celik et.al. 2021; Tully et.al. 2019; Ury et.al. 2021)
-decreased aerobic microbial growth & soil aeration.	(Goyal et.al. 2022; Kumari et.al. 2022b)
-decreased detritus food web energy flow.	(Jaiswal et.al. 2022)
-decreased decomposition rate of organic matter.	(Jaiswal et.al. 2022)
-decreased soil respiration.	(Ury et.al. 2021)
+increased root rots (i.e. *Phytophthora* spp.).	(Tiwari et.al. 2022)
+increased methane emissions.	(Ury et.al. 2021)

Figure 3: Research identified impacts on tree sites and soils due to salinity increases and salt stress, listed by number of citations since 2019.

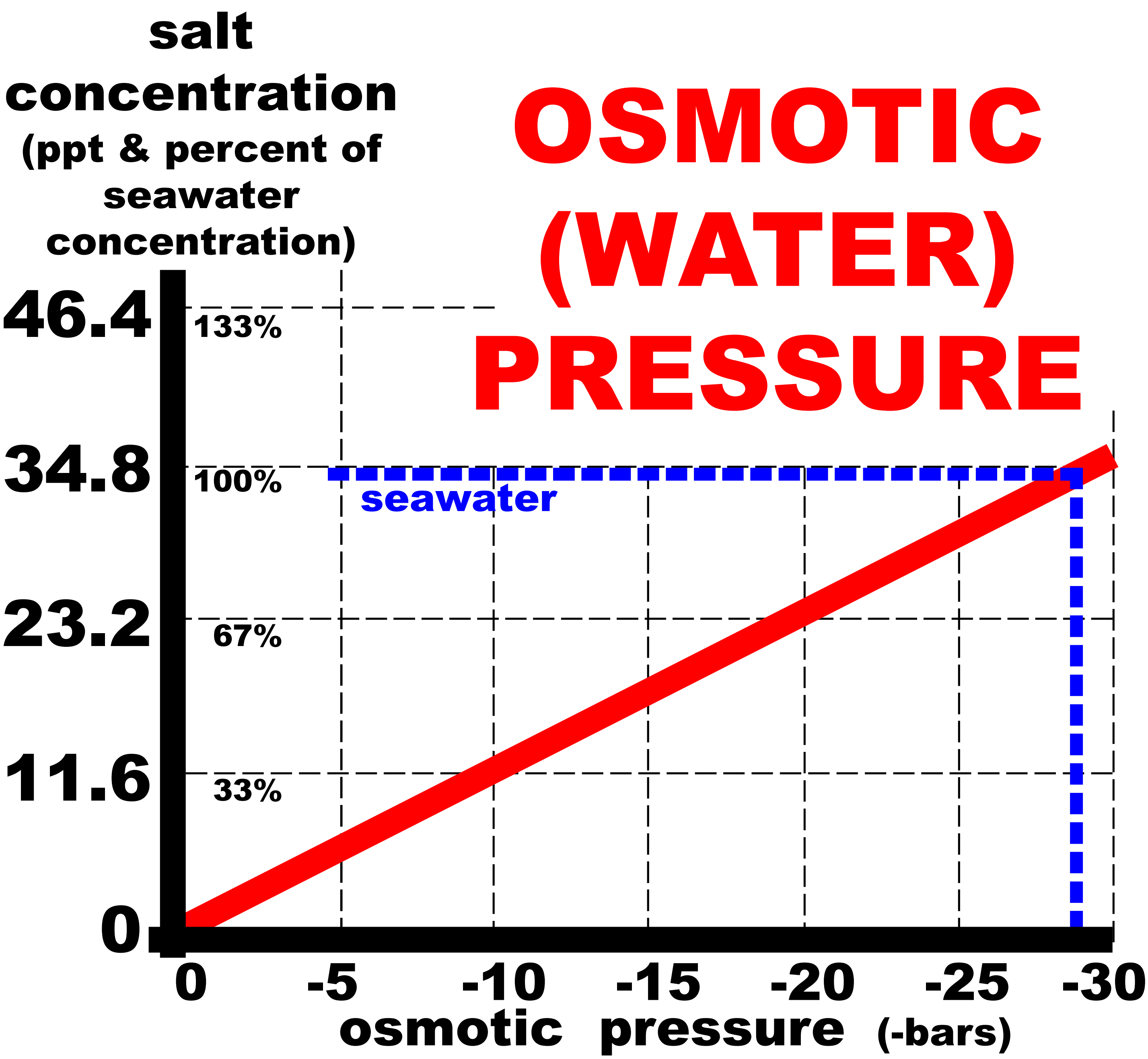

Figure 4: Water osmotic pressure (in negative bars) due to seawater salts in ppt and percent of seawater concentration.
Blue dotted lines represent average surface seawater values.

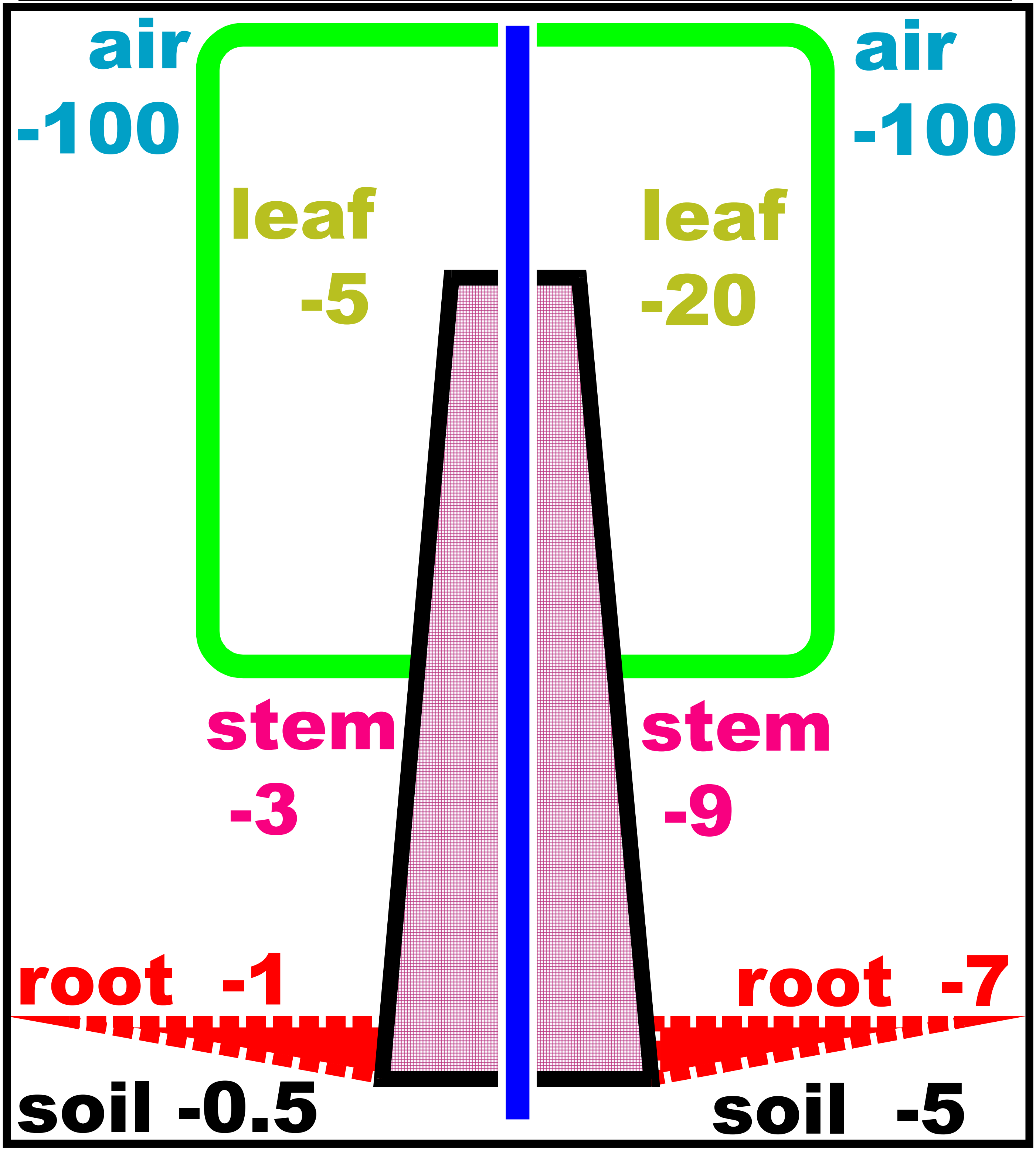

Figure 5: Relative water potentials between soil and atmosphere running through a tree.
Normal values on left side and salt stress values on right side with damaging water potentials generated. (after Goyal et.al. 2022)

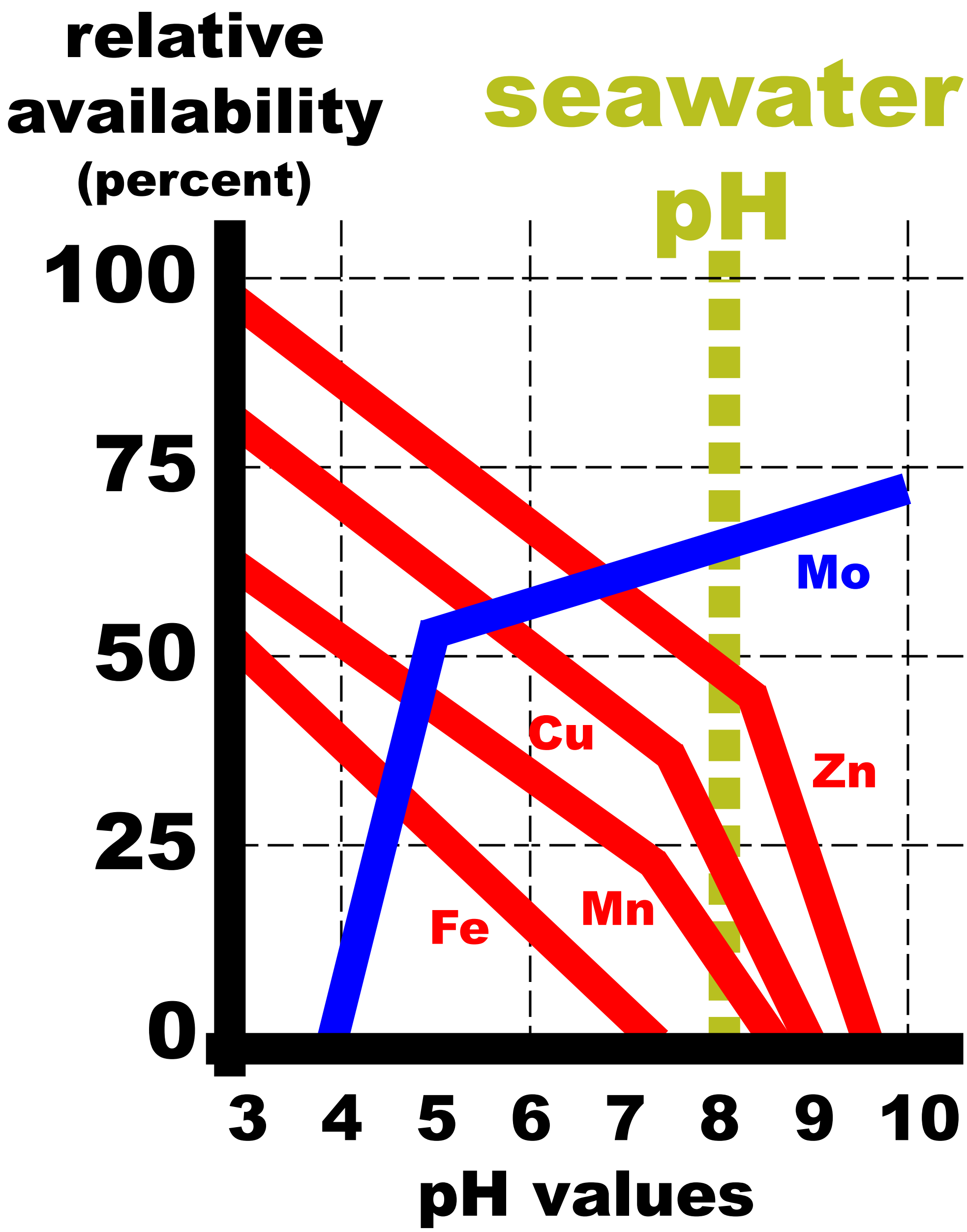

Figure 6: Relative availability of select tree essential element metals in soil across changing pH values.
(Coder 2021)

Salt Water Electrical Conductivity (EC)

salinity class	(ppt)	EC (mS/cm)	tree effect
Non-saline	(<1.2ppt)	0 - 2	-no tree impact
Low saline	(1.3-2.5ppt)	2.1 - 4.0	-sensitive trees impacted
Moderate saline	(2.5-5ppt)	4.1 - 8.0	-most trees impacted
High saline	(5-11ppt)	8.1 - 16.0	-salt tolerant survive
Severe saline	(11-23ppt)	16.1 - 32.0	-all damaged or dead
Extreme saline	(>23ppt)	>32.1	-all trees dead

Figure 7: Electrical Conductivity (EC) of salt water (in mS/cm units) divided into salinity classes with listed tree impacts.
(Hardie & Dolye 2012; Kumar et.al. 2022)

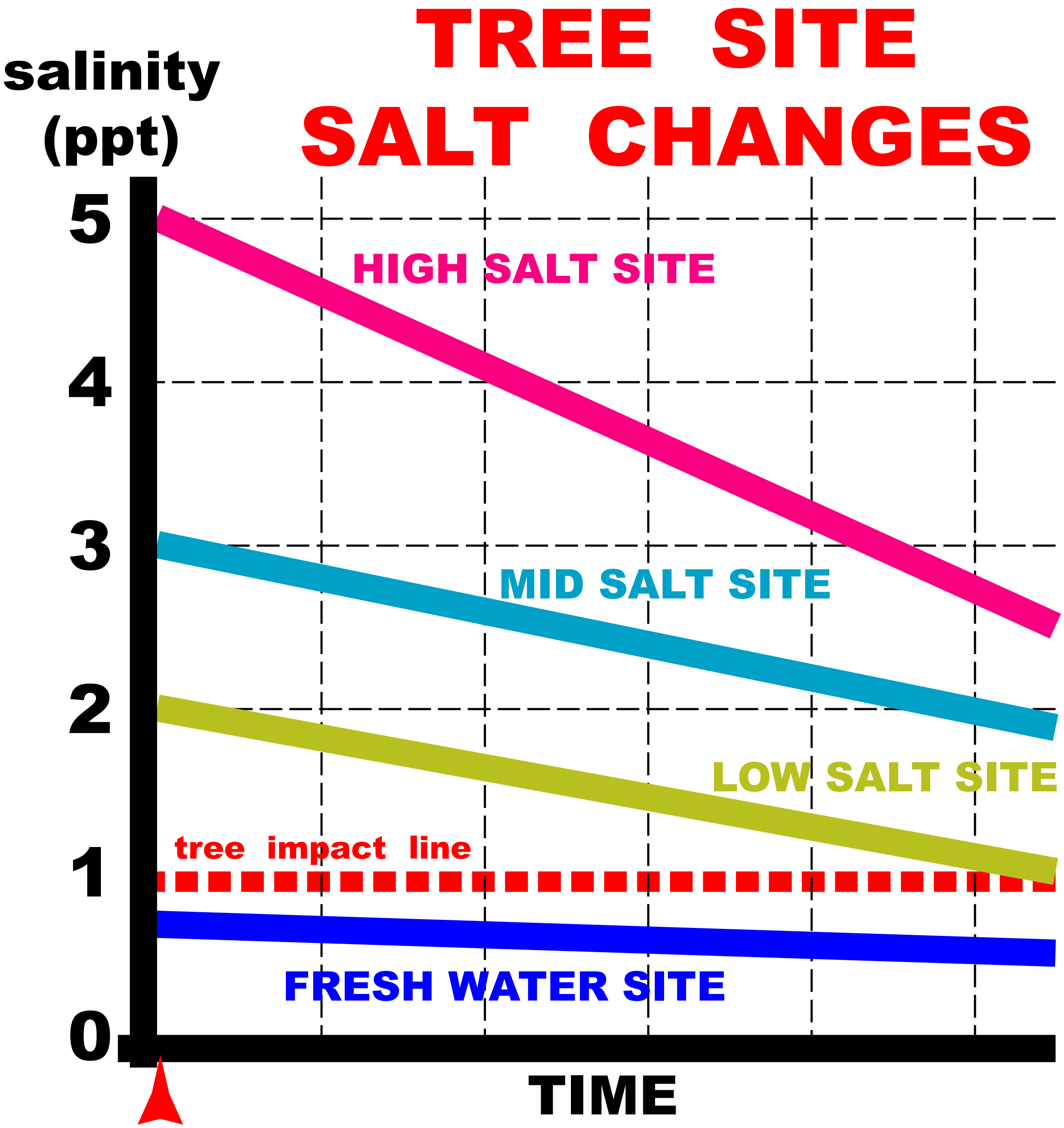

Figure 8: Soil water salinity dilution and decline over time after a seawater flooding event (red arrow) on four sites with different levels of salinity.
At 1ppt (~2.9% seawater concentration) most trees begin to decline.
(derived from Conner et.al. 2022)

TREE SALT IMPACTS

OSMOTIC STRESS

dehydration
reduced water uptake
stomates closed
reduced cell division & expansion

ION TOXICITY

photosynthesis inhibited
element deficiencies
protein synthesis disrupted
enzyme activities damaged

OXIDATIVE DAMAGE

membranes disrupted
life process disfunctions
increased tissue senescence

Figure 9: Primary impacts of salinity increases on tree growth.
(derived from Kumari et.al. 2022b)

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ELEMENTS IN TREES

element	symbol	average in tree (parts-per-million)	relative proportion in trees
group 1: (mega-elements)			
carbon	C	450,000 ppm	1,000,000
oxygen	O	450,000 ppm	1,000,000
hydrogen	H	60,000 ppm	133,000
group 2: (myri-elements)			
nitrogen	N	17,000 ppm	38,000
potassium	K	12,500 ppm	28,000
calcium	Ca	10,000 ppm	22,000
group 3: (kilo-elements)			
magnesium	Mg	2,500 ppm	5,500
phosphorus	P	2,250 ppm	5,000
sulfur	S	1,500 ppm	3,300
group 4: (hecto-element)			
chlorine	Cl	250 ppm	550
group 5: (deka-elements)			
iron	Fe	75 ppm	170
manganese	Mn	45 ppm	100
zinc	Zn	38 ppm	85
boron	B	30 ppm	65
copper	Cu	20 ppm	45
group 6: (deci-elements)			
silicon	Si	0.7 ppm	1.5
molybdenum	Mo	0.5 ppm	1.1
nickel	Ni	0.4 ppm	0.9
cobalt	Co	0.2 ppm	0.4

Figure 10: List of tree essential elements by concentration class, average concentration in trees (ppm), and relative proportion in trees with carbon and oxygen set at 1 million. (Coder 2021)

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TREE ELEMENTS IN SEAWATER

symbol	name	abundance
O	oxygen	857,000 ppm
H	hydrogen	108,000 ppm
Cl	chlorine	19,500 ppm
Mg	magnesium	1,290 ppm
S	sulphur	905 ppm
Ca	calcium	412 ppm
K	potassium	380 ppm
C	carbon	28 ppm
B	boron	4.4 ppm
Si	silicon	2.2 ppm
N	nitrogen	0.5 ppm
P	phosphorus	0.06 ppm
Mo	molybdenum	0.01 ppm
Zn	zinc	0.005 ppm
Fe	iron	0.002 ppm
Ni	nickel	0.0006 ppm
Cu	copper	0.0003 ppm
Mn	manganese	0.0002 ppm
Co	cobalt	0.00002 ppm

Figure 11: Tree essential element abundance in seawater (parts per million). (Rumble 2017)

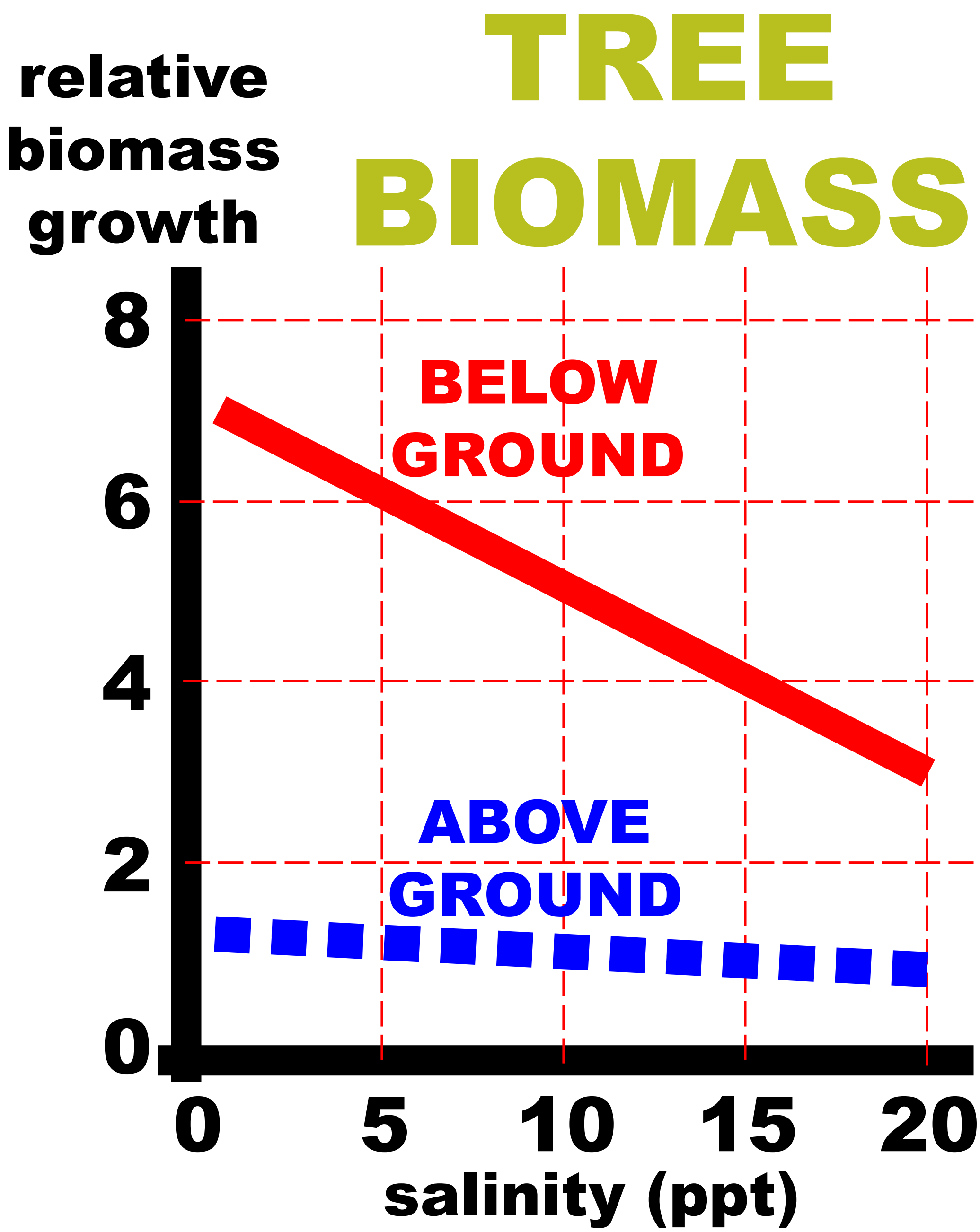

Figure 12: Relative tree biomass growth above ground and below ground per year with increasing salinity.
(20 ppt = ~57% seawater concentration)
(derived from Islam et.al. 2022)

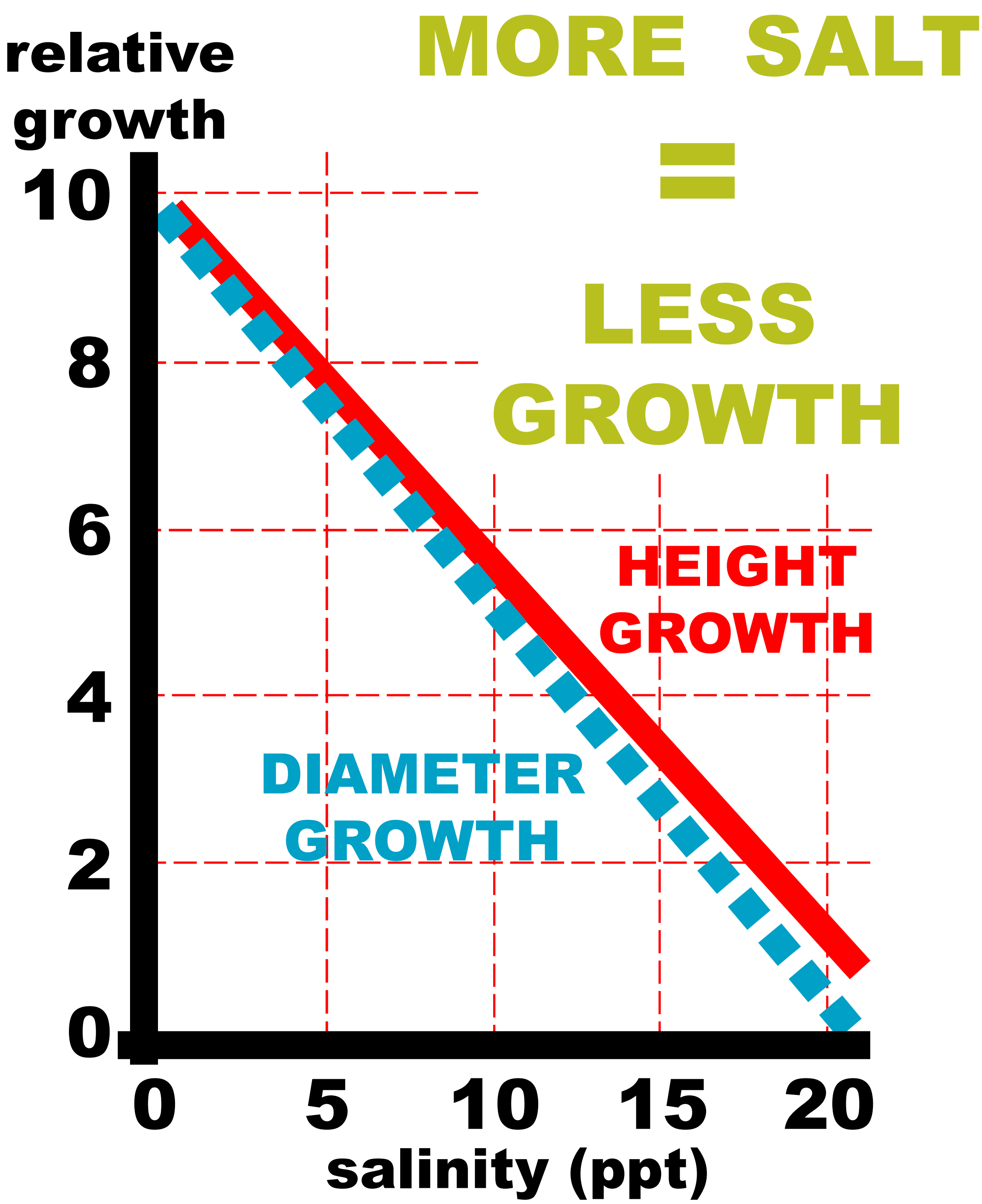

Figure 13: Relative tree height and diameter growth with increasing salinity. (20 ppt = ~57% seawater concentration)
(derived from Islam et.al. 2022)

SEAWATER IONS

ion	percent
Cl^-	55.0%
Na^+	30.6%
SO_4^{--}	7.7%
Mg^{++}	3.7%
Ca^{++}	1.2%
K^+	1.1%
minor / trace	0.7%
total =	100%

Figure 14: Major ion components of surface seawater in percent. Note both the amount of sulfur and cations present.

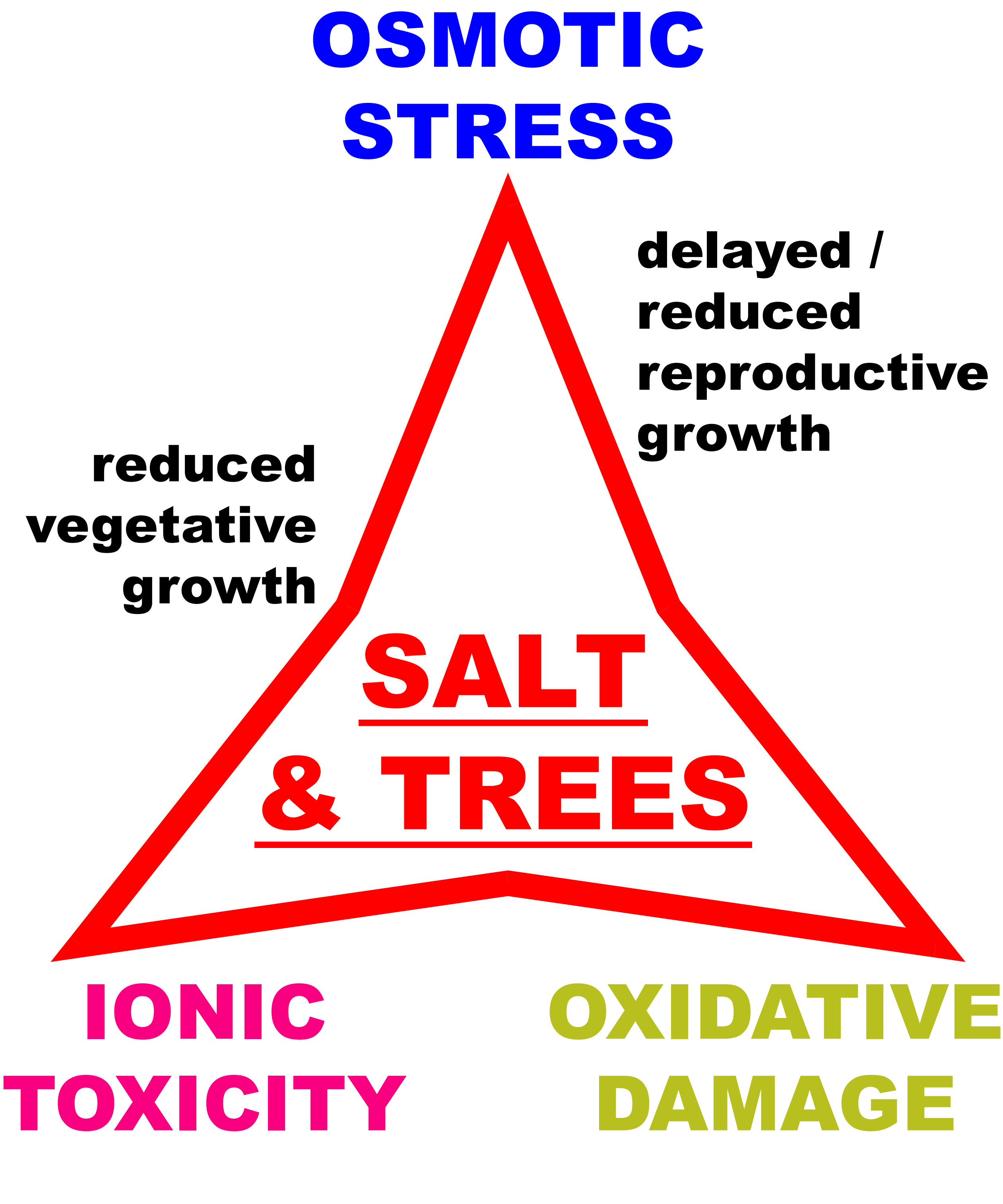

Figure 15: Primary impacts of salinity increases on tree growth, presented as a salt stress triangle.

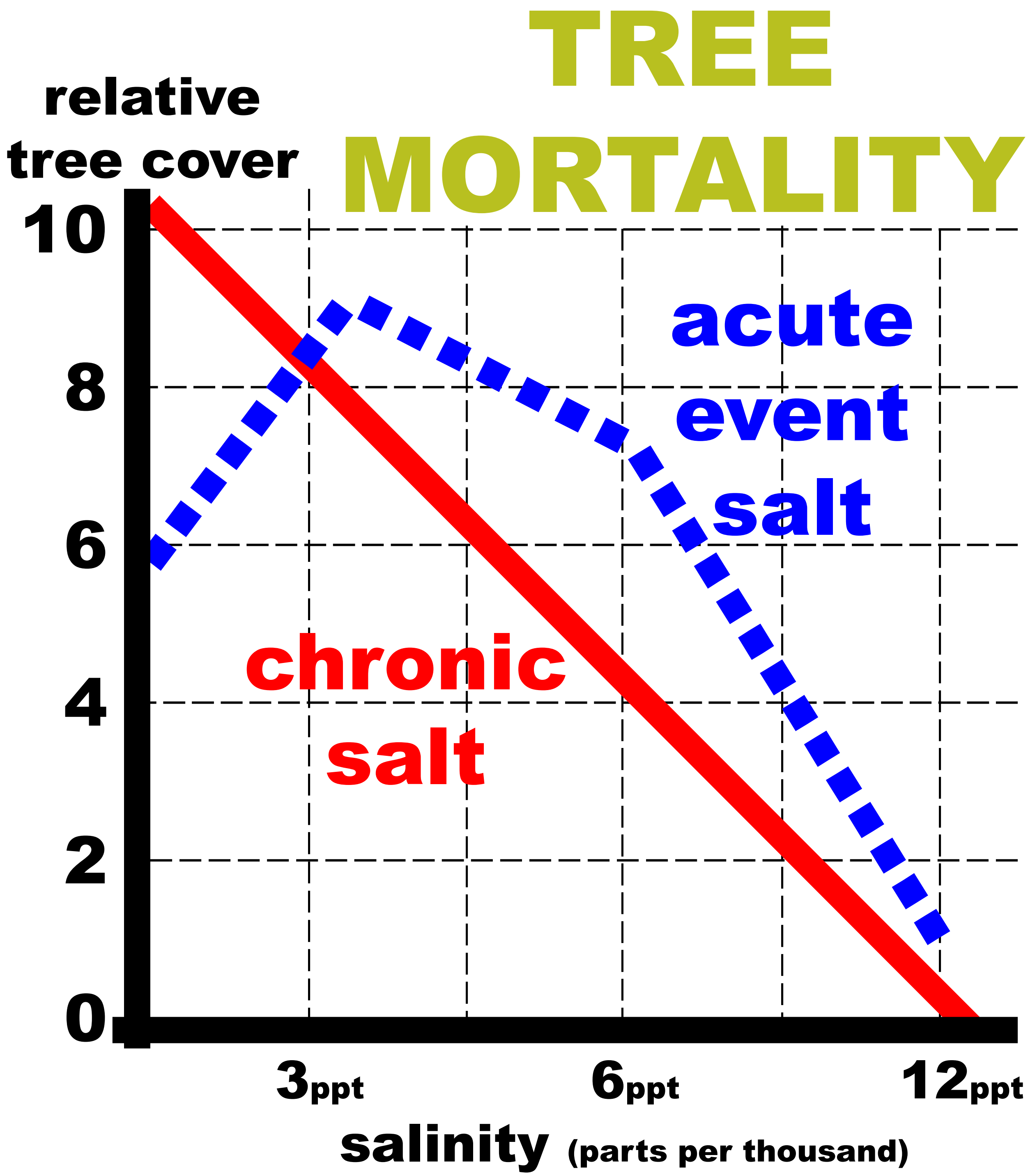

Figure 16: Changes in potential tree cover under chronic salinity (i.e. sea level rise), and an acute event (i.e. storm surge). (12 ppt = ~34% seawater concentration).
(derived from Paudel et.al. 2018)

tree area impacted	number of citations	tree impacts
Whole Tree	30	9
Leaf	24	8
Photosynthesis	17	6
Resource Gathering	17	7
Metabolism	14	9
Roots	10	9
Respiration	6	3
Stems & Periderm	1	1
total	119	52

Figure 17: Priority order of major tree impacts from salt stress by tree physiological or anatomical area, based upon number of citations (since 2018) and number of unique described tree impacts.

TREE IMPACTS

WHOLE TREE

damages tree growth, development, and survival. (Abobatta 2020; Conner et.al. 2022; DeSedas et.al. 2020; Hall et.al. 2022; Hasanuzzaman & Fujita 2022; Kumari et.al. 2022b; Lupo et.al. 2022; Zhang et.al. 2019)

decreases stem and root biomass. (DeSedas et.al. 2020; Islam et.al. 2022; Kumari et.al. 2022b; Lupo et.al. 2022; Rahman et.al. 2019)

decreases tree height, tree diameter (DBH), and basal area. (DeSedas et.al. 2020; Islam et.al. 2022; Powell et.al. 2022; Rahman et.al. 2019; Tully et.al. 2019)

accelerates tree decline and death. (Abobatta 2020; Kumari et.al. 2022b; Rahman et.al. 2019)

generates smaller tree canopy size, fewer branches and more dead limbs. (Conner et.al. 2022; Hall et.al. 2022; Powell et.al. 2022)

decreases shoot growth. (Hasanuzzaman & Fujita 2022; Kumari et.al. 2022b)

inhibits lateral bud formation and growth. (DeSedas et.al. 2020; Hasanuzzaman & Fujita 2022)

initiates tree and leaf senescence. (Hasanuzzaman & Fujita 2022)

generates canopy browning and defoliation. (Powell et.al. 2022)

LEAF

accelerates early leaf senescence and abscission. (Abobatta 2020; DeSedas et.al. 2020; Hasanuzzaman & Fujita 2022; Islam et.al. 2022; Kumari et.al. 2022b; Lupo et.al. 2022; Rahman et.al. 2019)

increases stomate closure. (Abobatta 2020; DeSedas et.al. 2020; Hasanuzzaman & Fujita 2022; Islam et.al. 2022; Kumari et.al. 2022b; Rahman et.al. 2019; Zhang et.al. 2019)

(continued)

Figure 18: List of major impacts on trees from salinity increases and salt stress, listed by number of citations.

decreases leaf area. (Conner et.al. 2022; DeSedas et.al. 2020; Kumari et.al. 2022b; Rahman et.al. 2019; Zhang et.al. 2019)
generates smaller, wilted leaves. (Hall et.al. 2022)
generates discolored foliage. (Hall et.al. 2022)
increases Na+ accumulation in leaves. (Kumari et.al. 2022b)
increases stomate density. (Zhang et.al. 2019)
reduces leaf expansion. (Hasanuzzaman & Fujita 2022)

PHOTOSYNTHESIS

inhibits photosynthesis. (Abobatta 2020; DeSedas et.al. 2020; Kumari et.al. 2022b; Lupo et.al. 2022; Rahman et.al. 2019; Tiwari et.al. 2022; Zhang et.al. 2019)
decreases chlorophyll content, maintenance and production. (Kumari et.al. 2022b; Rahman et.al. 2019; Tiwari et.al. 2022; Zhang et.al. 2019)
damages chloroplast membranes and functions. (Kumari et.al. 2022b; Rahman et.al. 2019; Tiwari et.al. 2022)
decreases carbon fixation. (Rahman et.al. 2019)
disrupts photosynthate allocation among root, stems, and leaves. (Rahman et.al. 2019)
reduces photosynthesis electron transfer systems. (Kumari et.al. 2022b)

RESOURCE GATHERING (ELEMENTS & WATER)

reduces transpiration and internal water content. (DeSedas et.al. 2020; Kumari et.al. 2022b; Powell et.al. 2022; Rahman et.al. 2019; Zhai et.al. 2018; Zhang et.al. 2019)
initiates essential element deficiencies. (Kumari et.al. 2022b; Powell et.al. 2022; Rahman et.al. 2019; Zhai et.al. 2018)

(continued)

Figure 18: List of major impacts on trees from salinity increases and salt stress, listed by number of citations. (continued)

reduces essential element uptake, especially nitrogen, potassium, phosphorus & calcium. (Kumari et.al. 2022b; Zhai et.al. 2018)
decreases soil water potential (more negative). (Hasanuzzaman & Fujita 2022; Kumari et.al. 2022b)
increases absorbed sodium (Na+) ions. (Zhai et.al. 2018)
increases cell lignification and suberin production. (Khan et.al. 2020)
inhibits function of K+ transporters and lowers K+ / Na+ ratio. (Kumari et.al. 2022b)

METABOLISM

decreases carbohydrate production and metabolism. (Kumari et.al. 2022b; Rahman et.al. 2019; Zhang et.al. 2019)
generates oxidative damage to proteins, lipids, DNA, and RNA. (Hasanuzzaman & Fujita 2022; Kumari et.al. 2022b; Rahman et.al. 2019)
decreases meristem activity (cell division and expansion). (Kumari et.al. 2022b; Rahman et.al. 2019)
disrupts cell membranes. (Hasanuzzaman & Fujita 2022)
disrupts defensive mechanisms. (Kumari et.al. 2022b)
disrupts enzyme activation. (Kumari et.al. 2022b)
disrupts auxin management systems causing ethylene production. (Kumari et.al. 2022b)
increases more osmolytes (soluble sugars, mannitol, proline, glycine and betaine). (Kumari et.al. 2022b)
increases cell swelling and death. (Kumari et.al. 2022b)

ROOTS

decreases root growth. (Rahman et.al. 2019; Zhai et.al. 2018)
generates thinner diameter and greater surface area roots. (Lupo et.al. 2022)
generates shorter root cells. (Lupo et.al. 2022)

(continued)

Figure 18: List of major impacts on trees from salinity increases and salt stress, listed by number of citations. (continued)

generates lower root tissue density. (Lupo et.al. 2022)
increases abscission of thicker roots (>1mm). (Lupo et.al. 2022)
increases thickness of root endodermis cell walls. (Sanchez-Romera & Aroca 2020)
increases lignification of newly formed xylem in root tip. (Sanchez-Romera & Aroca 2020)
decreases nitrogen fixation. (Kumari et.al. 2022b)
inhibits root enzymatic functions. (Zhai et.al. 2018)

RESPIRATION

decreases respiration system and electron transport. (Kumari et.al. 2022b; Lambers & Oliveira 2019; Zhang et.al. 2019)
increases short-term respiration due to ion transport requirements. (DeSedas et.al. 2020; Lambers & Oliveira 2019)
decreases by >1/3 energy production (ATPs). (Lambers & Oliveira 2019)

STEM & PERIDERM

generates flaky and discolored periderm. (Hall et.al. 2022)

Figure 18: List of major impacts on trees from salinity increases and salt stress, listed by number of citations.

TOP TREE IMPACTS FROM SALT STRESS

1. damages tree growth.

2. accelerates leaf senescence & loss.
2. increases stomate closure.
2. inhibits photosynthesis.

3. reduces transpiration.

4. decreases biomass.
4. decreases height, diameter & BA.
4. decreases leaf area.

Figure 19: Top eight (8) tree impacts from salinity increases based upon number of citations.

SEAWATER SALT

salt content in ppt	percent of seawater concentration	salt content in ppt	percent of seawater concentration
35 ppt	100%	15	43%
30	86%	11.5	33%
26.3	75%	10	29%
		8.7	25%
25	71%		
23	66%	7	20%
20	57%	5	14%
17.5	50%	3.5	10%
		2	6%
		1	3%

Figure 20: Approximations of salt concentrations in parts-per-thousand (ppt) and percent of seawater concentration as used in cited papers.

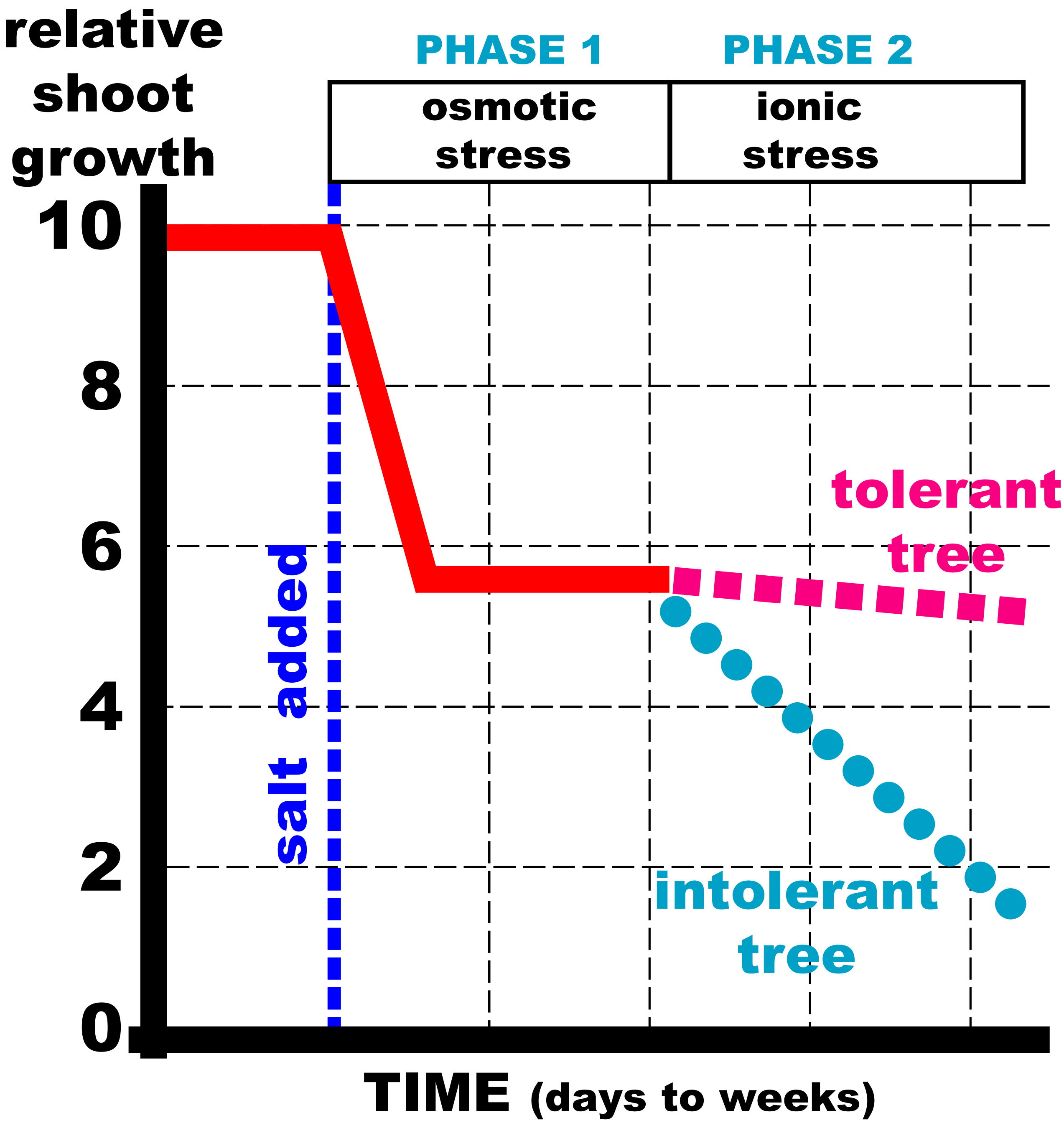

Figure 21: Two phases of change in tree shoot growth rates for salt tolerant trees and salt intolerant trees after salt stress was applied. Most trees are salt intolerant.
(based upon Goyal et.al. 2022)

SALT STRESS TOLERANCE

salt intolerant	salt tolerant
less photosynthesis chlorophyll loss	maintain photosynthesis maintain chlorophylls
less leaf area less biomass	leaf area maintained stable biomass
cell dehydration / shrinkage osmotic stress low stomatal conductance	cell turgidity stable osmolyte accumulation good stomate control
toxic ion accumulation reactive oxygen molecules generated	ion balancing / excretion antioxidants generated
premature senescence	maintain seasonal functions
growth inhibition	continues growth

Figure 22: Selective salinity impact differences between salt tolerant and salt intolerant trees. A majority of trees are salt intolerant. (derived from Kumari et.al. 2022b)

Tree Health Decline

0.6-3.7ppt	(1.7-10.6%)	(Zhai et.al. 2018)
>0.5ppt	(1.4%)	(Celik et.al. 2021)
>1ppt	(2.9%)	(Conner et.al. 2022; Noe et.al. 2021; Celik et.al. 2021)
<1.6ppt	(4.6%)	(Tiwari et.al. 2022)
>2ppt	(5.7%)	(Celik et.al. 2021)
>2.5ppt	(7.1%)	(Agarwal et.al. 2020)
<3ppt	(8.6%)	(Zhang et.al. 2019)
<4.5ppt	(12.9%)	(DeSedas et.al. 2020)
<5ppt	(14.3%)	(Tiwari et.al. 2022)

value range = 0.5ppt (1.4%) to 5ppt (14.3%).

average = 2.4ppt (6.9%)

Figure 23: List of salt stress thresholds cited to cause major tree health decline in parts-per-thousand (ppt) of salt concentration and percent of seawater concentration.

Tree Death

>1ppt	(2.9%)	(Noe et.al. 2021)
1.3 - 5.5ppt	(3.7% - 15.7%)	(Zhai et.al. 2018)
>2ppt	(5.7%)	(Celik et.al. 2021; Conner et.al. 2022; Tully et.al. 2019)
5.6ppt - 11.5ppt	(16% - 32.9%)	(Kumari et.al. 2022a)
>6ppt	(17.1%)	(Zhang et.al. 2019)
>7ppt	(20%)	(DeSedas et.al. 2020)
>11.5ppt	(32.9%)	(DeSedas et.al. 2020; Tiwari et.al. 2022)
>15ppt	(42.9%)	(Islam et.al. 2022)
>17.5ppt	(50%)	(DeSedas et.al. 2020)
>18ppt	(51%)	(Zhang et.al. 2019)

value range = 1ppt (2.9%) to 18ppt (51%).

average = 8.5ppt (24.3%)

Figure 24: List of salt stress thresholds cited to cause tree death in parts-per-thousand (ppt) of salt concentration and percent of seawater concentration.

Salt Stress Treatments

0. Pre-treatments

1. Drainage & Aeration
2. Fresh Water Rinse

3. Soil / Site Enrichment
4. Organic Matter Management

5. Debris & Deposited Soil Removal

6. Pruning

Figure 25: List of tree and tree site / soil treatments for salt stress based upon cited seawater inundation and intrusion impacts..