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THE EFFECTS OF SALINITY ON CELLULAR AND BIOCHEMICAL PROCESSES ASSOCIATED WITH SALT TOLERANCE IN TROPICAL PLANTS

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Abstract. **Tropical plant species exhibit a high degree of variability in salt tolerance, probably as a result of evolution in diverse ecosystems, intensive year-round selection pressures, and high temperatures. Salinity may cause major problems for agricultural production in semiarid tropics and areas subjected to seawater intrusion, and is also a concern in any irrigated region subjected to high temperatures. Mechanisms for salt tolerance vary among different species and range from the selective filtration systems of mangrove species to the more subtle ion accumulation and selective distribution mechanisms of wild tomato species. In crop species, sugarcane and date palm seem to exhibit high salt tolerance due to the accumulation of organic solutes in the form of sugars; whereas, some tropical legume species depend solely upon the restriction of salt uptake as a mechanism for tolerance. Abilities of particular plant genotypes to grow and produce yield under high salinity, well-drained environments are dependent upon restriction of salt from cytoplasmic compartments and maintenance of positive water balance. Temperature, humidity and light intensity have profound interactive effects with salinity at the upper limits of ionic and osmotic stress. Research efforts are needed to develop comprehensive plant models that integrate and interpret many of the known physiological and morphological responses to salt stress, initiate long-range breeding programs to select high salt tolerance in conventional crops and exploit agronomic suitability in salt-tolerant wild species. Aggressive research in the area of molecular biology is required to identify and transfer genes and gene systems that confer salt tolerance in wild species to either related or unrelated crop species.**

Salt tolerance in tropical species has not been studied as extensively as in species of more temperate regions. Nonetheless, there are a number of-excellent reviews concerning salt tolerance physiology in plants that probably have general applicability to tropical crops (3, 14, 26, 27, 32, 55, 61, 87). This review will be limited to the effects of salt exposure through root zone salinity and will present examples of tropical species when applicable; the interested reader is directed to reviews by Maas (57, 58) for discussions concerning salt effects that occur through the leaf as the result of sea spray or irrigation.

General Response of Higher Plants to Salinity

Salinity concentrations that restrict plant growth vary widely among species and plants have adapted to a wide range of saline environments. Terrestrial halophytes survive root salt concentrations from 1.2 to 30 g L^{-1} salt and vary markedly in the amounts of the various salts that they accumulate or restrict. Knowledge concerning variability in salt tolerance responses of tropical species is extremely limited, but the issue of salt tolerance is expected to become more serious as human population growth in the tropics begins to compete for finite water resources. Santo (72) indicated that over 42,000 acres of sugarcane are irrigated with saline water (over 0.75 dS m-l). Banana, *Musa acuminata* Colla, is usually grown in the humid tropical lowlands where salinity problems are not incurred, but efforts to grow them under irrigated conditions in Jordan indicate that salinity could be a potential problem if competition for land or water force their production into other locations (43).

Table 1. Physiological responses of *salt* stress.

Sensory	=> osmotic effects on root	
		=> pressure-volume changes- -
		=> electrical potential changes
		=> cystolic calcium changes
		=> hormonal responses
		=> reduced leaf elongation
		=> reduced assimilate transport
Constitutive	=> ion discrimination	
		= > filtration
		=> ion regulation
		=> compartmentation
		=> salt glands
	=> morphology	
		= > succulence
		=> rosette growth
Inducible	=> transcriptional changes	
		=> RNA and protein regulation
	=> structural changes	
		=> membranes, cell walls
	=> metabolic changes	
		=> increased respiration and energy demand
		=> reduced transpiration (stomata1 closure)
		=> increased mesophyll resistance
		=> organic solute synthesis
		=> decreased CO, fixation
		=> CAM metabolism
		=> reduced growth rate
	=> morphological adaptations	
		= > increased root/shoot ratio
		= > succulence
		=> rosette growth
		=> changes in reproductive initiation
Pathological	=> salt loading	
		=> leaf burn, scorching
		=> reduced photosynthesis
	=> salt shock	
		=> membrane damage

Salt effects on plants are quantitative, qualitative, and dependent on variables such as salt concentration, duration of exposure, and specific salt composition. Plant-dependent variables of response include species and variety differences, growth stage and exposure site on the plant. Responses to salt stress differ among plant species, but common responses do occur even in species that are distantly related. At low concentrations, salt may have no effect on plant growth or may even stimulate growth to a small degree. At moderate salt concentrations, plant growth rate decreases and stunted plants may develop darker green leaves and / or succulence. At relatively high salt concentrations, more obvious visual symptoms such as leaf burn and wilting develop. Salts exert these effects upon plants through both osmotic and ionic influences. The osmotic effects of salinity are a result of increased ion concentrations at the root-soil water interface which decreases the water potential. Growth is reduced as a function of total electrolyte concentration, soil water content and soil matrix effect and is evidenced by reduced cell enlargement and changes in metabolism. Thus, isosmotic concentrations of different combinations of salts cause nearly equal growth reduction at moderate salinities, but single salts and extreme ion ratios can cause specific ion toxicities. A general scheme for plant responses to the various effects of salt stress includes the primary *sensory* responses, and subsequent responses designated herein as *constitutive, inducible,* and *pathologic* (Table 1). Salts may also interfere with plant nutrition in rather complex ways which will not be discussed in detail herein (see reviews by Grattan and Grieve (31), Page and Chang (65)).

Sensory Response of Plants

Sensory responses are those that occur as a result of initial exposure of the plant to salt stress; they probably originate as biochemical or biophysical feedback mechanisms that are responsive to perturbations of the environment by salt. The primary mechanism(s) that triggers the physiological adaptive responses of the plant to salinity has not been agreed upon. Likely candidates include osmotic or turgor pressure changes or ion concentration gradients. Cell *walls* allow plants to produce internal osmotic and turgor pressures which are necessary for cell expansion and cell division. Turgor pressure exceeding 2 MPa may develop and. facilitate the breaking of chemical bonds in the wall matrix and stretch the walls (91). Obvious components of turgor and volume changes in the cell include water and solute concentrations and the elastic properties of the cell wall coupled to the cell membrane. Solute synthesis in alga is activated within 3 min of the onset of hypertonic conditions and is independent of protein synthesis. This suggests that membranes are sensitive to either a direct compression or relaxation of the membrane or to stretching as a result of pressure gradients. These stimuli may be links to the activation of preexisting enzymes which regulate osmotic adjustment (91). One hypothesis is that pressure signals in the root are generated by external osmotic stress **and** transformed into electrical transients that are carried as action potentials to the distal shoot tissues of higher plants (92). Forces acting upon the highly structured plasma membrane and its constituent charged molecules of protein and lipid may develop into mechanical or electrical forces which, in turn, alter the dynamics of the active or passive ion transport systems (16, 18, 19, 38, 91, 93).

In rice, Oryza sativa L., the occurrence of NaCl KCl, or mannitol in the root medium caused leaf elongation to cease within one minute (88). Growth restarted after a lag period that depended upon salt concentration, up to 50 mM NaCl, and esposure duration. Earlier, Munns and Termaat (63) had shown that the earliest response of a nonhalophytic higher plant to salinity is that leaves grow more slowly. Based on their technique of growing plants under high root pressures, they concluded that although the plants may experience water stress for a short period until they adjust osmotically, shoot water deficit was not the factor that limited growth even at relatively high salinities. However, root water deficits may occur and may stimulate a signal which leads to decreased leaf expansion.

Kramer (52) has argued that direct hydraulic effects upon roots are responsible for salt stress in shoots. Measurements of osmotically-induced backflow in maize root apices indicate that salinity increases hydraulic conductivity (23). It was also found that added $Ca2+$ mitigated both the effects of salinity and the observed increase in hydraulic conductivity. Salinity stress also lowers root hydraulic conductivity in citrus but not as much in salt tolerant genotypes as in sensitive ones (89). Conversely, salinity does not alter root permeability in tomato or sunflower (75). Over long time periods, developmental patterns of stomata1 conductance in leaves of sugarcane, *Saccharum officinarum* L., has been linked to hydraulic properties based upon the composition and flux of the xylem sap (62).

Recently, Rengel (70) has tied together evidence that $Na+$-induced Ca^{2+} deficiencies are the primary metabolic signal in salt stress. The hypothesis that cytosolic Ca^{2+} is a transducer between environmental stress and phosphorylation reactions that control a large number of biochemical processes is an attractive one that is supported by a large body of evidence. Other investigators have implicated hormones such as ABA (49) and cytokinin (53) as signal transducers. The roles of hormones as elicitors of salinity-induced responses is a lucrative area for future investigations.

Pathologic Responses to Salt Stress

Pathologic responses to salinity are those that lead to the eventual death of the plant. Instantaneous exposure of plants to high salt concentrations, or ‘salt shock,' causes severe and irreversible membrane damage and leads to rapid loss of water and ion control; death follows. Bernstein (1) suggested that plants could osmotically adjust to about 0.5 MP a day^{-}’ change in salt concentration. Rapid changes in salt concentration are atypical in nature; but gradual increases to high concentrations of salt in the root zone do occur in irrigated, poorly-drained areas and in coastal regions. Exposure of plants to slow increase to high salt concentrations can be lethal too. Munns and Termaat (63) have shown that the eventual demise of the plant is related most to salt loading into shoots. Salt loading into green tissues will eventually decrease the photosynthetic capacity of the plant and exacerbate reduced growth rate to the point the plant is overwhelmed.

Some species survive accumulations of salt that would be lethal to most others. Mangroves, for example, possess efficient filtration systems that restrict salt uptake from seawater. The grey mangrove. *Avicennia marina,* can exclude 90% of the salt in the medium surrounding its roots (IO). Other mangrove species can survive salt concentrations 2 to 3 times that of seawater (15). The degree of salt tolerance shown by mangroves is not found in crops, but palms (date palm, coconut palm) also seem to be able to withstand unusually high concentrations of salts (12, 28). Coconut, Cocos *nucifera* L., yield along seacoasts is generally higher than in inland areas and high $Cl-$ is thought to be responsible for improved development and number of female flower clusters (69). On a molar basis, $Cl-$ concentrations of coconut leaves were about twice that of Na^+, indicating the presence of a mechanisms for restricted uptake or retranslocation of Na^+. However, even at extremely high salinities, leaf $Cl-$ concentrations in coconut were generally less than 1.5 percent on a dry weight basis. In the cultivated tomato, *Lycopersicon esculentum* Mill., leaf $Na+$ remains less than 1.5 percent on a dry weight basis (%dwt) up to a concentration of 0.5 seawater in the root zone (7 1). At this point, salt rapidly enters the tissues and kills the plant. One-month-old stem cuttings of cassava, *Manihot esculenta* Crantz, rapidly succumbed to salinity treatments over 2500 mg/L and 2000 mg/L was toxic over a period of a week (42). Severe leaf burn (browning) and wilting occurred and symptoms in damaged roots included disorganization of the cortical parenchyma and the presence of tyloses in the vessels.

If salt shock and salt over-loading can be avoided, a condition of salt tolerance exists during which plant growth and development continue toward the reproductive stage, or in the case of perennials, toward many reproductive phases. The remainder of this paper will deal with plant responses during salt tolerance.

Constitutive Responses

Constitutive salinity responses are defined here as those that are within the normal ability of plant response and do not require gross morphological and developmental changes. A plant’s ability to respond to some salt stress exists under nonsaline conditions as a preadaptation. In as much as the filtration of salts through the roots is imperfect and the leaf tissues serve as dead-ended sinks to the xylem, plant survival is dependent upon mechanisms by which salts can be kept from interfering with metabolic processes related to growth. But how much salt can actually be tolerated in the cytosol? In hatobacteria, enzyme isoforms have been found with the ability to maintain form and function at salinities exceeding 4 molar (54). However, the range of ionic concentrations at which normal cellular physiological processes occur in higher plants is very limited and little variation for salt tolerance may exist based upon the extent that basic metabolism of certain processes, e.g. photosynthesis and respiration, are common among species. Salt accumulation in leaves has been correlated with reduced photosynthetic activity and with ultrastructural and metabolic damage (87). Oxidative phosphorylation in mitchondrin of both pea (Pisum sativum L.) and Suaeda *maritima,* for example, is sensitive to similar $Na+$ concentrations (24). Alt hough certain isozymes may hypothetically differ in stability or activity under saline conditions, direct evidence for *in vitro* differences in enzyme activity as a mechanism for salt stress in higher plants is scant.

Therefore, the ability of a plant to sequester salt away from its sensitive metabolic processes is especially important in salt tolerance.

Compartmentation Ions at the soil-plant-water interface can be accumulated as useful nutrients, restricted by membrane barriers, or sequestered within the plant as wastes. Ions not excluded by the root may be sequestered by a variety of mechanisms within the plant in vacuoles, intracellular spaces, specialized cells, and within stems and older leaves with *lower* metabolic activity, or even in salt glands. Rice has the ability to keep ion concentrations in the xylem low and thus prevent the toxic accumulation of salts in the growing tissues of the shoot. Sodium transport in the xylem can be reduced by mechanisms chat accumulate Na+ within vacuoles of individual cells and in stellar parenchyma cells in roots (47). Ions can also be removed from both xylem and phloem by stem and petiole tissues in both monocots and dicots (45, 85). In some species retranslocation of Na' from xylem to phloem and back through the root is possible (46), but in most species, retranslocation does not appear to be a major adaptation to salinity. There is also evidence that some salt may accumulate in the apoplast, and although cell walls consist of less than 3% of leaf volume, salt loading in these tissues may have an inordinate effect on plant water balance (25, 83). Recently, Boursier and Lauchli (8) have found that *Sorghum bicolor* (L.) Moench has the capacity to sequester Cl- preferentially in sheaths, particularly in adaxial epidermal cells; whereas, Cl- concentrations in photosynthetically active mesophyll and bundle sheath cells remained lower. Other species have increased tolerance which is achieved by selectively directing ions into older leaves or specialized salt organelles (glands and bladders) and away from the growing and photosynthetically active tissues (82). Sugarbeet *(Beta vulgaris* L.) and Bermuda grass *(Cynodon dactylon* (L.) Pers.), for example, have salt glands that harvest NaCl from the symplast or apoplastic water stream through the plant and extrude it in crystallized form onto leaf surfaces. In semiarid environments in which rain does not usually wash these esuded salts back into the root zone, this can be a useful adaptation that allows the plants to reach maturity and set seed in extremely saline environments. The energy costs of such a mechanism are probably quite high but in natural environments the expense may contribute towards species survival. The importance of this strategy in agriculture has not been formally determined.

Ion *regulation.* In saline soils plants must maintain favorable ion balances despite high external concentrations of Na+. High sodium concentrations relative to other salts can disrupt root permeability to ions by displacing calcium in the plasma membrane. Additional effects may be caused by upsetting calcium metabolism and nutrition within the cell (70). At higher sodium to calcium ratios, soil structure, tilth, and soil permeability to water may be reduced (74).

Regulation of ion transport is essential to mineral nutrition, osmotic adjustment and pH control (30). In tropical regions high solar intensities and high temperatures will contribute to the accumulation of ions in the shoots of plants, but high humidities will have a beneficial effect in that transpiration is decreased. If ion uptake cannot be balanced with growth there is a simple overloading of niches where salts can be sequestered; a slow poisoning of the tissues occurs that leads to a pathological condition. Banana has the ability to sequester Na+ in the root and to preferentially restrict both Na+ and Cl- movement into the photosynthetically active laminar tissues compared to the petioles (39). Competition exists at the level of the root between Na+ and K'. Other studies indicate that root Na+ levels are highly correlated with salinity stress.

In trees and vines the ability of rootstocks to restrict transport of specific ions to the shoots significantly influences salt tolerance. Differences in Cl- transport properties and tolerance of different rootstocks clearly account for much of the difference in tolerance of citrus species (59). Taha et al. (80), have suggested that olive (Olea *europaea* L.) is more salt tolerant than guava *(Psidium guajava* L.), and that guava is more salt tolerant than grape (Vitis) based on relative decreases in growth with increasing salinity. Additionally, they have shown that olive and guava exhibit leaf-burn due to the accumulation of ions at higher levels than do grape vines. However, toxicity symptoms in olive leaves occurred at lower absolute concentrations of Cl- than in grape or guava (8 1); this may indicate that the mechanisms for ion restriction into shoots are more developed in olive, but that the mechanisms for resistance to leaf-burn within the shoot itself are not as developed as in the other two species.

Another hypothesis for the low accumulation of ions in olive, may be that total water and ion uptake into the shoots were lower. Grape seedlings had higher growth rates under nonsaline conditions and olive had the lowest. Thus, relative salt tolerance was highest in olive, but productivity in terms of dry matter production was the lowest. Several annual herbaceous species, although sensitive to salinity, accumulate higher levels of Na+ and Cl- in the shoots without symptoms of leaf injury. In tropical legumes Cl- can exceed 8% dwt (84). Accumulation of Cl- in lamina of cassava was lower than in the stem *or* petiole up to 20 mM; Na+, however, was lower in lamina than in all other tissues up to 50 mM NaCl treatment (37). This at least would support the hypothesis that active mechanisms for selective Na+ restriction or translocation exist in this species. The occurrence of tip burn at 50 mM NaCl supported the supposition that Cl-, rather than Na+, was the cause of this symptom. Thus, important questions may be where are ions located within shoot tissues and what are the mechanisms for ion control within cells and tissues. In tropical legumes, *Macrotilium atropurpureum* and *Neonotonia wightii,* salinity injury has been correlated with chloride accumulation in leaves and mechanisms for restricted Na+ accumulation exist (84). Thus, there is evidence for a central hypothesis that Na+ is the most damaging ion of the two to metabolism and photosynthetic pathways, but at high salinity Cl- accumulation results in leaf burn and subsequent wilting and death. Based on the wide divergence in the salt tolerance between coconut and legumes, it could be assumed that the *ability* to restrict salt uptake into the leaf has a more significant role in salt tolerance than the absolute sensitivity of the leaf tissues to salt accumulation. However, if the *degree of* variation in ion restriction into leaf tissues is not great, as is the case between *Macrotilium* and *Neonotonia, then the* tolerance of the tissue to salt may be a significant contributing factor to differences between species.

Even in salt-sensitive plants, salts must cross biological membranes and their movements are regulated by a *variety* of active and passive transport mechanisms *as water passes* through the plant in response to its potential gradient (30). Some tolerance to salinity has been reported as the result of the enhanced ability of particular genotypes to actively or passively exclude ions. Schubert and Lauchli (73) have attributed high salt tolerance in a maize genotype to the ability of the plasmalemma in the root epidermis and cortex to passively exclude Na$^+$ more effectively than the sensitive genotype.

Inducible Responses

Non-lethal salinity induces molecular biological changes at the level of the genome that are genetically and phenotypically latent, but exist as a result of selective adaptation; these are referred to as inducible responses and may occur at several levels metabolism and development. At one of the most basic levels, stressed-induced changes in gene expression can occur at transcription or post-translational processing and transport. Salt stress reduced total m-RNA in barley roots by 20-30% but 21 new RNA species were induced by the stress while others were inhibited (67). Salt-induced proteins have been described recently in *Nicotiana* (22, 50, 51, 77), barley, *Hordeum vulgare* L. (41, 68), and a hybrid between wheat and *Elytrigia* (35). The physiological significance of the changes that occur as the result of the synthesis of specific new RNA messengers and proteins is generally unknown, but salinity-induced changes related to cell walls, membranes, turgor maintenance, and osmotic adjustment have been documented. In one instance, a re arrangement of the mitochondrial F$_0$-ATPase subunit that is more tolerant to the effects of Cl$^-$ was found in tobacco cell suspension cultures adapted to salt (11). The correlation between transcriptional changes and physiological responses will be an important area for future research.

Structural changes in membranes and their component proteins and lipids may contribute to tolerance in a multitude of ways. Spanswick (78) suggested that salinity may disrupt root growth by decreasing ATP-dependent proton expulsion at the root plasmalemma, thus decreasing cell wall acidification that is normally necessary for wall loosening and subsequent expansion growth. Lower ATPase activities have been reported in membrane vesicles isolated from roots of tomato and Plantago grown in saline media (21, 34). Other evidence indicates that root plasma membrane ATPase activity and proton pumping is not diminished by salt stress (36, 79). Recently, it has been demonstrated that salinity levels that inhibit maize (Zea *mays* L.) root growth do not prevent cell wall acidification in the growing zone of the root (90). Salt-adapted cells from tobacco (*Nicotiana tabacum* L.) tissue cultures were found to exhibit slow growth due partially to changes in the structural components of the cell walls (11).

Decreases in tissue K$^+$ content with increasing Na$^+$ concentrations in saline media is one of the most universal effects of salinity. In some species selective uptake of K$^+$ into the cytoplasm combined with extrusion of Na$^+$ into the vacuole may be one mechanism of salt tolerance (44). Proton-pumping ATPases may create concentration gradients that mediate or drive antiport systems responsible for sequestering Na$^+$ in vacuoles (29). Recently, we have found evidence in tomato of a Na$^+$/H$^+$ antiporter that transports Na$^+$ across the plasma membrane; this type of antiporter has been demonstrated previously in Dunaliella *salina*, a highly salt-tolerant alga (48). Mechanisms of tolerance involving pot-ret-s and antiporters have certain limitations and drawbacks. The vacuole is finite, movement of ions into this compartment and maintenance of transmembrane gradients of ions and water require a significant energy commitment that would detract from optimum growth. Exporting Na$^+$ across the plasma membrane increases the ion and osmotic problems already present due to high salt, but this strategy could be beneficial if the root zone is frequently flushed by irrigation or some natural condition, such as tides.

Changes in membrane function that are inducible by salt stress also may occur due to structural changes in membrane lipid or fatty acid components. In response to drought. total polar lipid and lipid phosphorus contents of maize seedlings decrease (64). Simonds and Orcutt (76) hypothesized that modifications of sterols may reflect initial events that lead to destabilization of membranes in stressful environments. In roots of salt sensitive Plantago *media* L., phospho-, galacto-, and sulpholipids decreased significantly with increasing NaCl concentration, indicating increased permeability of membranes (21). In the salt-tolerant species, *P. muritima* L., the lipid levels were maintained. Likewise, lipid and fatty acid variations in a drought-resistant cotton (*Gossypium hirsutum* L.) variety was less pronounced than in a sensitive variety (66). Brown and DuPont (9), however, recently found very little change in the mole fraction composition of various membrane components isolated from barley roots exposed to 100 mM NaCl.

Composition changes in membranes may affect membrane fluidity, membrane surface charge or potential, and ion discrimination. Our data demonstrate that the root cell modulates the electrostatic properties of the plasma membrane in response to high external salt levels. Average membrane surface potentials of tomato roots increased from -26.0 to -13.7 mV as the result of the plants being grown in 75 mM salt solutions (79). A large positive shift in plasma membrane surface potential would result in a decrease in the surface concentrations of monovalent and divalent cations by 40% and 62% respectively; whereas, monovalent anion concentrations may increase by 60%. A more positive membrane surface would serve to attract more anions, thus increasing their likelihood of transport into the cell where they could be useful in osmotic adjustment and charge compensation. The modulation of the electrostatic properties of the plasma membrane could represent a mechanism by which the cell limits the stimulation of ATPase activity by monovalent cations when potentially high intracellular concentrations of these ions have accumulated during salt stress. A potentially detrimental effect of a more positive surface potential is the predicted decrease in calcium ions at the membrane surface. A decrease in membrane-bound calcium can affect membrane permeability. Adequate calcium levels supplied to the nutrient solutions of hydroponically grown plants have been shown to improve the apparent tolerance to salt. Leaf Na$^+$ content of rice and corn varieties decrease in salinized iso-osmotic nutrient solutions with varying Na$^+$/Ca$^+$ ratios as the ratio decreases; whereas. the Ca^{2+} content increases (33, 60).

Osmotic adjustment. Plants may synthesize metabolically-compatible cytoplasmic solutes in response to either drought or salt stress (7). As discussed, ions that would be detrimental to metabolism might be sequestered in the vacuole; therefore lower salt concentrations within the cytoplasm would be augmented osmotically by organic solutes at a significant energy cost. Efficiency would be dependent upon turnover rates. Organic solutes which accumulate to high concentrations occur in a wide variety of alga and higher plants and include varied forms of polyols, glycerol, mannitol, sucrose, proline and glycinebetaine (S6). Osmotic stresses can cause significant yield reductions in most crops before foliar injury is apparent. Reports that reductions in citrus fruit yields occur without excessive accumulations of Cl- or Na^+ and without any apparent toxicity symptoms indicate that the dominant effect is osmotic (4,13,20,56).

Macroscale changes. There are a number of fairly large scale changes in plant metabolism and development that occur as a result of salt stress. Some of the most dramatic salinity-induced responses include changes in basic metabolism, increases in root/shoot ratio, changes in yield components and time to anthesis, and the development of succulence.

Salinity stress changes basic metabolism from C-3 to CAM (Crassulacean acid metabolism) in species of ***Kalanchoe, Mesembryanthemum, Portulacaria*** and ***Peperomia (17).*** The ability to fis carbon at night as accumulated malate and to reduce daytime losses of leaf moisture through stomata1 control can be important features in both salt and drought tolerance and may contribute to the high salt tolerance in many tropical CAM species such as pineapple, ***Ananas comosus*** (L.) Merrill. CAM is found predominantly, but not exclusively, in succulent plants. High succulence can dilute cytoplasmic Cl- concentrations and contribute to salt tolerance. Some succulent species, like ***Kalanchoe,*** are very salt tolerant; other species develop a degree of succulence under salt stress. Wilson (84) noted that ***Macrotillium*** had higher growth rates than Neonotonia despite having higher leaf Cl- levels, but ***Macrotillium*** also was more succulent.

A point that is not typically addressed in relation to salt stress, but is discussed relative to drought stress, is whether decreased plant growth ***per se is*** actually an effective salt tolerance adaptation. Under low to moderate salinity, root/shoot ratio can increase due to stimulation of root growth and/or nonconcommitant inhibition of shoot growth. Genotypic differences in salt tolerance in crop species have been correlated with higher root-shoot ratios. Decreased shoot growth also results in less vegetative dry weight production prior to reproductive growth. In some species the duration of the vegetative stage is reduced; although in other species the reproductive stage is delayed. The net result of a reduced vegetative stage is that fruit is produced much more efficiently with regard to conservation of resources, and, as noted, sometimes sooner as well. Often there is a shortening of internodes; a response similar to short daylength and low temperature effects. The characteristic of shortened internodes is an esample of both an inducible trait and a constitutive character that may exist in the absence of salinity as a prendnptation. The ultimate constitutive expression of this character is found in plants that. normally exhibit rosette growth. Rosette growth minimizes the amount of osmotic and water potential that must be developed bv the plant to transport water and nutrients to the shoots.

Perennial species may take one to several years of salt stress before symptoms such as reduced growth and leaf burn due to Na^+ or Cl- accumulation are manifested, but increases in reproductive growth may occur more quickly. With tree crops where the buds and fruit develop over two seasons, e.g. citrus. folisr injury and leaf loss during both years will be more detrimental than injury that occurs only the second year. Of course continued salt stress can cause complete defoliation and even death of the tree (2, 40). It is also worth noting that salts tend to accumulate in woody tissues over several years before toxic symptoms appear; consequently, leaf injury and loss can occur suddenly years later when the salts reach the leaves.

A tremendous amount of evidence from many diverse species supports the contention that plants partition accumulated inorganic salts away from the most active photosynthetic tissues. What is not known, is whether this is an active process in most species, or the cumulative result of normal plant growth processes. Low salt accumulation normally associated with growing apices, for instance, could be a natural result of undeveloped xylem tissues. High salt accumulation in older leaves, a phenomenon characteristic of many species, may be result of their role as transpiration sinks over a long and continuous period.

Conclusion

A number of physiological mechanisms are associated with plant salt tolerance and additional research is needed in several areas. A vast array of salinity-induced responses are known to occur within the plant kmgdom in response to an equally diverse range of saline environments. Despite our ever-increasing understanding of these responses, the morphological, physiological and genetic characteristics that provide the crop plant with the best possible adaptations in the saline cultivated environment cannot be determined at the present time. Future advances in three areas of endeavor are necessary for the development of highly salt tolerant crop species. First, increased efforts should be focused on the understanding of the inter-relationships between various salinity-induced responses and crop plant metabolism. Second, the inevitable advancement of molecular biology will one day create new potential to isolate and transfer complex physiological characters for salt tolerance across conventional genetic barriers. Finally, the development of physiological process models that accurately predict salinity responses would make the process for evaluating potential transgenic plants more efficient and practical.

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