

THEORETICAL APPROACH TO LIFE PROCESSES

Part IV. Plant Growth/Aging in Saline Environment

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The hypothesis holding dehydration as one of the major processes governing aging has been examined by considering plant processes viz. cell growth, turgor pressure, hydraulic conductivity of tissues, water potential of system and expanding leaf, and hydrogen bondability of solutes in plant fluids in terms of Lockhart's equation, and the process of dehydration which leads to aging. The process of aging is deduced directly from Lockhart's equation, from which it is inferred that ionic and/or hormonal interaction in a water deficit environment in leaves results in the introduction of cross-linkages.

The property of the cell wall to keep hydrated by extending the hydrogen bonding network in a given micro-environment and time frame and the role of hydrogen bondable organic solutes, and inorganic ions whose degree of hydration and osmotic potential is low has been described. Ionic imbalances are created due to excess supply over demand which finally give rise to apoplasmic ion concentration. The resultant salt damage creates an imbalance in water relations of the neighbouring cells. Water is withdrawn from the protoplast and the consequent loss in the degree of hydration, loss of turgor and cellular desiccation lead to the death of the plant. Accordingly, the hypothesis suggests that cells can grow only if an optimum degree of hydration prevails to allow maintenance of turgor. It further points towards the continuous need for the uptake of hydrated ions and hydrogen bondable solutes through the roots and their despatch to the shoots.

Ions are required for maintaining turgor and cell expansion and their supply is deterministic of growth. The expanding leaf has to compete for the available sodium chloride which provides the cross-linkages necessary for its maturity.

Key words: Aging, Plant process, Life, Dehydration, Cell wall.

INTRODUCTION

Dehydration has been hypothesised earlier as one of the major processes governing aging [1]. It has been suggested that formation of hydrophobic substances as a result of intramolecular dehydration, such as formation of cellulose from glucose and their deposition at selective sites in the microcapillaries of the transportation system of the plant leads to aging. Polymer and cross-linkage formation would accordingly constitute an aging process and thus formation of cellulose from glucose should be regarded as one of its initial stages. It has also been proposed that small changes in pH and ionic concentration alter the buffer capacity of the solution and the ionic balance. The changes therefore aid either the flushing or the deposition process. In this context it is already known that damages caused to plants growing in a saline environment are due to ion accumulation and ionic imbalances as a result of osmotic adjustments [2]. The excessive ion concentration in leaves gives rise to dehydration and ultimately to death of the plant. This paper examines the hypothesis by considering plant processes such as cell growth, turgor pressure, hydraulic

conductivity of tissues, water potential of xylem and expanding leaf and hydrogen bondability of solutes in the plant fluids, in terms of Lockhart's equation, and the process of dehydration, which leads to aging.

METHODS

Cell growth, turgor pressure and dehydration. Aging could be quantitatively related to cell growth and cell turgor since the same becomes apparent whenever there is a lowering in cell water potential induced by water deficit or dehydration. In this connection the equation proposed by Lockhart shows that cell growth or expansion with respect to time (or aging), dv/dt , has a linear dependence on turgor pressure (ψ_p) above the threshold turgor γ in the following manner.

$$\frac{dv}{dt} = m (\psi_p - \gamma)$$

Where m is the factor determining cell extensibility or yielding capacity [3]. Aging or reduction in growth induced by ionic and/or hormonal interaction can thus be quantitated to a decrease in the cell wall extensibility (m) or

decrease in the turgor pressure (ψ_p) or else in the increase in γ , the cell wall yield threshold. Accordingly, low water potential in leaves induces their poor growth and it is, in general, true that growth would be retarded whether it is low moisture content of the soil, the air or the plant itself [4].

Reduction in growth due to ionic or hormonal interaction could be viewed as introduction of cross-linkages and formation of polymer units of size smaller than before. Such formations of small units involve elimination of water molecules from the site of reaction of the ionic moiety in the micro-environment and the events of dehydration and introduction of cross linkages are considered as the main processes concerned with disease [5] and aging [1]. Furthermore, according to Lockhart's equation the introduction of cross-links reduces the cell wall extensibility and this according to the present hypothesis suggests a correlation with aging. The higher the quantity of ionic species, the higher would be the cross-linkages in the micro-environment and the lower would be the degree of hydration. Since turgor pressure is related to the quantity of water present in the leaf cell, any reduction in the degree of hydration would show up as a reduction in ψ_p and in the form of reduced growth of the leaf or leaves and consequently in dv/dt or as aging. Conclusions based on this equation have been found to be valid in several cases such as oat coleoptiles, pea roots, radish cotyledons and leaves of several other species [6, 7].

Cell walls contain cross-linked polymers in parallel, as also observed in the case of leather. Introduction of cross-links brings in rigidity in the collagen matrix [5] and the same is true about the cell walls. Metabolic processes create chemical or hydrostatic forces which act on cell wall to form new bonds. Formation of new bonds or cross links results in irreversible damage to cell wall. Accordingly, the value of m , the cell wall extensibility factor in Lockhart's equation decreases, suggesting that the process of aging has set in.

Hydraulic conductivity and water deficits in the micro-environment. Plant cell enlargement occurs entirely through the uptake of water which is in sharp contrast with cell growth in bacteria and animals where protein synthesis is mainly involved and that is why this hypothesis is being applied initially to plant processes. Expansion in the cell dimension takes place when a force is applied and depends on the incorporation of new material within the existing cell wall matrix. Supply of water to the growing cells to raise their degree of hydration is related to aging by another version of Lockhart's equation.

$$dv/dt = L_p (\psi_x - \psi_e)$$

Where L_p is the hydraulic conductivity of the tissues and ψ_x and ψ_e are the water potentials of the xylem and expanding regions, respectively. The latter equation suggests that ag-

ing would proceed at a fast rate if large differentials are created by reducing the hydraulic conductivity of the tissues and/or the water potential of the xylem and by increasing the water potential of the expanding leaf. Support for this argument comes from the observation that water deficits in the environment reduce leaf expansion in maize [8, 9] by restricting the rate of water supply to the growing areas and that it limits soybean stem growth by reducing water uptake as well as cell wall extension [10]. In both cases large differentials are created between the supply from the xylem and demand by the growing cells. The process of dehydration is thereby induced and the consequent aging leads to the death of the plant.

The process of physical dehydration accounts for most of the water losses, and only a small proportion of it is available for growth [11]. The flux of water is two to three times higher than that of CO_2 [12]. The largest proportion of nutrients is utilized for growth while the remaining, mainly the ions, such as calcium, accumulate in leaves as excretory products of the transpiration stream. Some nutrients are circulated back into the soil but ions like potassium and nitrogen being mobile in the phloem are recirculated into the plant.

Leaf transpiration declines with aging of plant, its sodium content increases while the influx to the leaf does not decline with time [13]. The increase in sodium concentration in leaf has a linear relation to that in the xylem supply to the leaf [14]. The balance between ion accumulation into leaf cells and their supply from roots is critical to aging of individual leaves.

Water storage depletion within the plant decreases leaf-gas exchange and gives rise to premature aging of leaves. The reduction in availability of water modifies growth and if nutrients are also not available in quantities sufficient for maintaining the growth of new leaves, assimilation of carbon dioxide is seriously affected [15].

The degree of hydration is determined by the water uptake by plants which is influenced by hydraulic conductivity during its flow. Low hydraulic conductivity between soil and shoots induces low differentials and hence the lower water potential in leaves than in roots. Hydraulic conductivity has been noted to vary not only among different species [16], but also on altering the root xylem diameter [17]. These variations, however, emanate mainly from the roots and in certain species also from stems and leaves [16]. Leaf turgor rather than root turgor is decreased by an axial resistance to flow in plants, having an overall low degree of hydration. Plants with low hydraulic conductivity would be more sensitive to dehydration as a result of aerial stresses and vapour pressure deficits in the immediate environment and are less sensitive to soil water stress, than those having high hydraulic conductivity [17]. This is attributed to dehydration due to large decrease in the degree of hydration and hence in leaf water potential in plant spe-

cies with low hydraulic conductivity.

Cell growth needs the following main substrates for, 1) uptake of ions and synthesis of solutes so that osmotic potential could be generated to facilitate transport of water, 2) supply of nitrogen for the synthesis of proteins, (3) supply of carbohydrates for building up cell wall and (4) synthesis of ATP. Expansion takes place only when a force is applied and depends on the incorporation of new material i.e. new bond within the cell wall material. Cross-links are thus introduced and the process of aging gets initiated.

Hydrogen bondability and cell wall extensibility. Consideration of the uptake of ions and the supply of various ingredients for the synthesis of solutes, leads to yet another interpretation of Lockhart's equation which could be in terms of the hydrogen bonding, dominant in plant fluids. Water is an essential component of plant life and in fact it starts with the hydration of the germ plasm. However, it is not just water that is required for the life processes but a mix of solutes forming a buffer solution with a predetermined pH and ionic concentration. Support to these processes is possible if the solutes in the fluid are hydrogen bondable. Glucose formed as a result of photosynthesis is ideal in this respect and so are the proteins forming the backbone of the cells.

Hydrogen bonds are of structural importance in holding groups in proteins where they are encountered as a result of interaction between oxygen of the carbonyl and hydrogen of the amide group. They are formed when the folding of polypeptide chains either on themselves or on the neighbouring chains reduces the interatomic distances of the interacting atoms to less than 2\AA . The groups which form hydrogen bonds are of necessity required to be polar and hence they tend to orient themselves towards an aqueous environment. In case of predominance of the latter, the hydrogen bonds of the proteins are destabilized in favour of water in the micro-environment.

Electron mobility, or polarizability of bonds is induced by the close approach of ionized or strongly polar groups. A partial charge of opposite sign is created on the close approach of an ionized or strongly polar groups towards polarizable groups in molecules such as hydroxyls on steroids, amino acid side chains in proteins and portions of fatty acid side chains. The attraction energy involved in interaction is of small order amounting to 0.002 kcal/mole for a CH_2 group for a charge separation of 5\AA .

The amino acid side chains e.g. the carboxyl group of glutamic or aspartic acid, the ϵ -amino group of lysine, the amino group of phosphatidyl-ethanolamine, the quaternary nitrogen of the phosphatidylcholine and the phosphate group of the phospholipids comprise some of the charged portions of the proteins and lipids which are ionized at physiological pH. The ions so generated can attract two unit charges of opposite sign involving an energy of $4\text{--}5$ kcal/mole and a distance of approximately 5\AA of closest

approach.

London-van der Waals forces which are short range weak attractions, are caused by instantaneous charge density fluctuations in molecules. They produce electric moments in adjacent molecules even if they are nonpolar. The attractive forces between two CH_2 groups at a distance of 5\AA is estimated at 0.1 kcal/mole.

Electrostatics forces, polarization or induction forces and London-van der Waals dispersion forces, besides the hydrogen bonds, may be considered to constitute the major components of forces leading to interaction, cohesion and stability of associated complexes among proteins, lipids and their different groups. However, it may also be suggested that hydrogen bonding and electrostatic forces should comprise the dominant attractive/cohesive systems and the others viz. polarization and London-van der Waals forces constitute weak interactions. Hydrogen bonds, because of their tendency to interact with other water molecules and polar groups give rise to an ordered macromolecular framework. If such a system has to work as a solvent it would introduce cross-links among the hydrogen bondables. The presence of hydrocarbons and other non-hydrogen bondable molecules like the lipids and fatty acids in the vicinity of the proteins or lipoproteins would alter the arrangement of the solvent system. The non-polar groups would give rise to stable configuration by withdrawing from the polar environment, and by combining with other hydrophobic moieties of the molecule, they would be enclosed into an associated mix of various cohesive forces. The London-van der Waals forces bring about a strong cohesion among lipids which are separated by a distance of much less than 5\AA . The macromolecular framework emerging out of these interactions suggests open areas or pores, due to non-uniform attractions, which are loose and large enough to allow for passage of water, and at times even large molecules such as glycerol.

Cell growth is related to the capability of the cell wall to get hydrated and stretched and to maintain it in the meantime by extending the hydrogen bonding network. This characteristic is aided by hydrogen bondable organic solutes and inorganic ions like sodium, magnesium and chloride since their degree of hydration and osmotic potential is high. Thus cell growth given by dv/dt , in effect, suggests the extension and/or maintenance of a hydrogen bonding network in a given micro-environment and time frame. If the extent of hydrogen bonding in the micro-environment is reduced for reasons such as the presence of hydrophobic substances, there would be a tendency to restrict the growth. The extensive hydrogen bonding network could then be considered as a polymeric macromolecule and the introduction of ions or other molecules may be treated as a depolymerization phenomenon. The cell extensibility or m in Lockhart's equation would thus be related to the degree of hydrogen bonding and the amount of hydrogen

bondable ions or organic substances present. As suggested earlier, the presence of ions and organics depolymerizes the hydrogen bonded structure and generates one water molecule per cross link by dehydration. It thus ages the cell by reducing its extensibility and reduces the turgor pressure in the meantime.

Cell wall extensibility depends on the amount of water surrounding the proteinous wall. The water already present as a helical chain around the proteinous wall keeps it wet and hence the extensibility would be low if the water spiral dries up or the protein is denatured, which in essence suggests that the hydrogen bondability of the cell wall is reduced, m would then depend both on the degree of hydration of the cell wall and its hydrogen bondability. Likewise, the turgor pressure would depend on the amount of water in the cell. In case of dehydration due to water deficiency, the degree of hydration would be reduced in the cell suggesting decline in growth or dv/dt or an enhancement in the rate of aging. In case of ion accumulation in the cell, the degree of hydration would again be lowered both with regard to concentration and the depolymerization effect which the ions have on the macromolecular framework of water. Such a situation would also reduce the hydrogen bondability of cell wall and this would not allow the turgor pressure to increase.

Plant growth regulators and the hydration process. Leaf growth is controlled by plant growth regulators or hormones like abscisic acid, cytokinins and gibberellins which directly or indirectly influence the hydraulic conductivity of cell membranes, and/or wall loosening factor [18]. Abscisic acid, for example, is an inhibitor of leaf growth [19] and it is produced or released as a consequence of loss of turgor in the expanded zone of leaf or leaves and leads to reduced growth of the expanding leaf [20]. The mechanism involved in the formation of these regulators is apparently related to the dehydration of cells as a result of the less extensive hydrogen bonding network due to a water deficit.

Plant hormones fully take part in the growth process, they regulate the hydration process by modulating the shoot response to water stress. By depolymerizing the water macro-molecule they decrease the value of m in Lockhart's equation or the cell wall extensibility factor, influence the turgor pressure as well as the capability of the cells to take up osmotic solutes and thus help maintain the turgor pressure. The hormone abscisic acid is known as a potent stomatal regulator [21]. It is formed under low degrees of hydration, rather under desiccation conditions and its accumulation in the roots is found to increase in response to water deficits [22, 23] during repeated episodes of low turgor. It acts within cells or at the plasma membrane but the ultimate response is of extracellular nature. In order to communicate between the cell and the wall, the former is suggested to excrete a wall loosening factor which may be proton [24] or an ion like Ca^{++} [25] which is known to be a

biological excretory product [1]. The ion acts as a wall loosening factor when it is removed from the walls and is taken up in cells by forming cross-linkages or by inhibiting cell wall-loosening enzymes [26].

Hydrogen bondability and osmotic adjustment. Cell wall loosening has been mentioned above to be the result of lowering in hydrogen bondability which decreases the turgor pressure unless there is an immediate counteraction by way of osmotic adjustment. Accordingly, dehydration in plants can be avoided or reduced either by turgor maintenance through osmotic adjustments and decrease in cell size or by desiccation tolerance which depends on the capability of the membranes as well as cytoplasm to resist denaturation of proteins [27]. Desiccation can be tolerated by the inherent capacity of cells to overcome mechanical injury and of the membranes to withstand degradation.

Water deficit or a low degree of hydration creates a situation whereby osmotic adjustment by the accumulation of solutes resulting in the decrease of osmotic potential in the expanding region and in the increase of turgor pressure ψ_p of the cells. Osmotic adjustment naturally follows maintenance of stomatal opening and photosynthesis at low leaf water potential so that leaf rolling and leaf death could be deferred till such time that lower leaf water potentials are reached by further adjustments

Osmotic adjustments could be viewed as a means to maintaining a reduced degree of hydration by attaining a less extensive hydrogen bonding system thus prolonging the process of aging by dehydration. This aspect is supported by the study of plant life under the stress of salinity since increasing concentration of salts increases the cross-linkages and correspondingly lowers the plant water potential. The free energy of water available to the plants, though lower than that of pure water [13], can still provide useful work under the stated conditions. The water potential of the symplast needs to be adjusted in order to desiccate the plant and this is possible with the available free energy which can provide a high value to the turgor pressure.

Plants of diverse families, both monocotyledonous and dicotyledonous, can live in saline conditions [28]. However, the former halophytes grow under low degrees of hydration i.e. with a less extensive hydrogen bonding system. They are users of ions having a low degree of hydration viz. to the extent that they have a Na/K ratio of less than one [29]. They therefore, have a tendency to accumulate hydrogen bondables such as sugars. They are not succulent i.e. they do not increase the size or volume per unit of surface area of the mature cells of the leaf by hydration. The dicotyledons, in contrast, can sustain high degrees of hydration. They utilize sodium and chloride ions mainly and lower their water potential in this manner. They have a Na/K ratio of 10 and are succulent. The ions, which are important in osmotic adjustment of the halophytes are sodium, potassium and chloride. They are restricted largely to the

vacuoles and the adjustments of osmotic potential of the cytoplasm is effected with compatible organic solutes [30]. The differences in the Na:K ratio are perhaps due to hydrogen bondability of organic solutes as well as the capability of sodium and chloride ions to get hydrated. They speak of the relative volumes of vacuole and cytoplasm in species of different water content.

Xylem supplies the ions to the leaf cells directly in the apoplast or indirectly through the symplast depending on the pathway adopted by the flow of the solution in the leaf [31]. The origin of ions in the apoplast is in the xylem vessels. The quantity of the ions supplied depends on the product of the xylem ion concentration i.e. the degree of hydration and the transpiration rate, both of which vary with the age of the plant as well as time in the 24 hours cycle and on their external concentration. Ions accumulate in the compartments of the cells within the plasma membranes depending on the hydrogen bondability of the cell wall or the protoplasm after they have been supplied to the leaf. They remain either in the apoplast or are re-exported. The accumulation of ions in the leaf is governed by the storage capacity of various compartments which is determined by their volume and ionic concentration. The leaf volume is dominated by the protoplast and vacuoles while the cytoplasm has a small fraction of the protoplast volume (5 to 10 percent) [32] and hence dehydration in the former and cross-linkages in the latter are deterministic of aging.

Re-export of ions is possible either through the phloem or through excretion by salt glands. While the former has only a limited capacity to remove ions because of the lower degree of hydration, the latter may be important in certain species only since a large number of halophytes do not have glands [33]. The phloem of salinised plants contains sodium ions just like the cytoplasm of their cells. The re-translocation of sodium is lower in salt resistant species if this ion is applied to the leaf apoplast. This suggests that ions have to be excluded from the cytoplasm for tolerance [34] since their exclusion alone can reduce the cross-links and provide some cell wall extensibility.

The halophytes, like other plants, use the phloem for re-export, it is now established that halophyte tissues which are fed by phloem and which grow in sodium chloride, receive very little sodium compared to potassium, which is also true in the case of the seeds, developing leaves, and root species [35]. This, according to the present hypothesis, is due to the depolymerization of the water macromolecule effected by a large number of ions and the consequent lower degree of hydration of the phloem fluid. It could be generalized that healthy phloem of the halophytes, just mentioned, has a low degree of hydration by nature and hence transports ions having a high K:Na ratio to the growing area. Accordingly, the metabolism in these plants is adapted to function with an ionic imbalance in a less hydrated environment due to K rather than Na ions. The ionic

imbalance in the plant accumulates in the older leaves and creates a low Na:K ratio in young growing tissues. It is, therefore, apparent that the imported Na and Cl ions are taken up by the cells or else they remain in the apoplast [13].

The apoplast volume is fixed in a mature leaf while the protoplast volume increases with time and age. The plants with salt glands can excrete excess ions while those without glands transport them into the vacuoles. In the former case i.e., cells with a fixed volume, the concentration within the leaf would rise if the degree of hydration is reduced and in spite of this condition, the ion import continues. In the latter, however, increasing concentration would be osmotically compensated by increase in the volume because they possess the desired open structure mentioned earlier. In both cases, ionic imbalances can be created due to the excess supply over uptake which would result in an increase in the apoplastic ion concentration [13]. The consequence of the excessive accumulation of ions in the apoplast is the effect observed on the water relations of the neighbouring cells; there is withdrawal of water from the protoplasm, a loss in the degree of hydration, and hence a loss of turgor followed by cellular desiccation and finally death of the plant. The life span of the leaves depends on the ionic balance between the supply and uptake into the vacuoles which are the only compartments within the protoplasm with any significant storage capacity since it is observed that when the tissue of the plant is incised, a massive quantity of ions is released from the vacuoles [13].

The consequences of the imbalance in the maintenance of turgor in response to the ionic concentration or salinity was outlined by Oertli in 1968 [2] and it was suggested that salt damage is a result of ionic accumulation in apoplast. It is being hypothesised here that cells can grow only if an optimum degree of hydration exists so that turgor is maintained. This demands a continuous need for the import of hydrated ions and hydrogen bondable solutes through the roots and their onward transport to the shoots. It is known from the study on *Suaeda maritima* that unit area ion fluxes in the leaf cells decrease with time as the cells expand and therefore it follows that membrane fluxes fall below their capacity. The growth of the cell consequently cannot be restricted by the transport properties and hydrogen bondability of the membranes during the lifetime of the cell. It has been observed that the net transport of sodium at high external concentration of NaCl, namely 340 mol m^{-3} , is the maximum which is possible through the root system. It is therefore, reasonable to suggest that the root supply and not the shoot ion transport capacity is the limiting factor for the growth rate in halophytes [13].

The natural consequence of the above suggestion is that if an adequate level of hydration is not maintained the net requirement for Na and Cl ions would decline as the leaves age and the net import of ions would fall substan-

tially. A reduced supply of ions is possible if the transpiration rate per leaf decreases with time. Although such measurements for the halophytes have not been reported, yet it is known that transpiration from the whole plant falls as the external and hence the internal salinity rises. It is also expected from the succulent nature of the plant where there is a decrease in the surface to volume ratio that the transpiration per unit volume of leaf would decline as the leaf ages; there would then be a reduction in the delivery of ions in the transpiration stream per unit volume of the leaf.

Leaves of different ages in the dicotyledonous plants transpire at different rates obviously because of the different levels of hydration and the ionic balances which characterise the plants individually. The differences may also be due to the nature and number of cross-linkages introduced that influence the internally regulated changes in stomatal and water flow resistance to leaf blades. Yet another possibility is that since the concentration of ions delivered to different leaves on the plant varies, the nature and number of cross-links introduced would vary. Thus the ionic concentration of solution being transported through the xylem to the old leaves would be lower in Na than that supplied to the younger leaves. Since turgor pressures have been noted to be higher and osmotic potentials lower in young leaves, it is suggested that this is due to a high salt load in the apoplast of the mature cells which in turn is related to the low turgor and hence low growth rate [13].

Ions being in demand for maintaining turgor pressure and hence cell expansion, their supply would determine the growth. This would suggest that the expanding leaf would compete for the available sodium chloride since this would be able to provide the cross-links needed for maturity. This is supported by the observation that ion concentration in the xylem supply to different leaves varies from species to species. The constancy of shoot ion concentration is possibly not much due to regulation of net sodium chloride transport by the root as higher plants do not usually regulate net sodium chloride uptake. The halophyte with salt glands excretes the excess ions which are delivered to the shoots and are not demanded for growth and this process maintains the constancy.

The transport capacity of the leaf cell plasmalemma does not limit the growth of the cell and in case of ionic imbalances it may be inferred that the failure of the cells to remove the ions from the apoplast has serious consequences in the regulation of turgor and, therefore, the life of the cell. For plants growing in 340 mol m^{-3} sodium chloride, for example, a one percent imbalance between the arrival of Na ions in leaf apoplast and their rate of removal to the protoplast would lead to an accumulation of 80 ml m^{-3} sodium chloride in the apoplast and within a week there would be a 560 mol m^{-3} apoplastic salt load accumulation. Similarly, the salt sensitive rice species (*Oryza sativa*) is not able to tolerate a salt level of 50 mol m^{-3} so far as the

seedlings of dwarf varieties are concerned [13].

The processes which decrease productivity are related to factors governing postponement of dehydration by reducing water losses e.g. a decrease in stomatal conductance, leaf rolling and decrease in leaf areas. Such factors increase water use efficiency by a reduction in water loss at the critical periods during the day when there may be large deficits in water vapour pressure. They, however, allow photosynthesis to continue in the morning and towards the evening. Stomatal closure and leaf wilting or leaf rolling at midday and reduction in photosynthesis and water usage in the early life cycle of the plant may increase the grain yield by conserving water.

Reduction of water loss by stomatal closure is controlled by growth regulators like abscisic acid and cytokinin. The sensitivity to water vapour deficit induces midday stomatal closure independent of the bulk leaf turgor giving rise to improved water use efficiency, delayed soil water deficit, and any occurrence of imbalance in plant growth regulators and electrolytes in the plants. A reduction in leaf area is a result, in many cases, of alteration in soil-water or soil-mineral-matter-water status and is affected by root hydration [37].

Leaves of a non-halophyte, when exposed to saline conditions grow slowly and the root:shoot ratio decreases. While root growth may not be affected at a low salinity, the shoot growth does decline. In the long run, prolonged transpiration brings over large quantities of salts into the shoots, specially the old leaves, and kills them. This process limits the supply of assimilated matter to the growing areas and becomes deterministic of the yield.

CONCLUSION

It is borne out from the foregoing discussion that aging would be rapid in a water-deficit micro-environment if large differentials are created by reduction in hydraulic conductivity of tissues on the one hand and increase in water potential of expanding leaf on the other hand.

Ionic imbalances created due to excess supply over demand give rise to salt damage which disbalances the water relations of the neighbouring cells. Water is withdrawn from the protoplast and the consequent loss in the degree of hydration, loss of turgor and cellular desiccation lead to the death of the plant. Cells can grow only if an optimum degree of hydration prevails to allow maintenance of turgor and there is a continuous need for the uptake of hydrated ions and hydrogen bondable solutes through the roots and their despatch to the shoots.

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