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Short-term Salinity and High Temperature Stress-associated Ultrastructural Alterations in Young Leaf Cells of *Oryza sativa* L.

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Salinity and high temperature stresses adversely affect growth and development of rice plants. To investigate the response of rice cells to these stresses, we have analysed short-term stress-induced subcellular alterations in undifferentiated leaf cells of rice seedlings by transmission electron microscopy. Perturbations noted particularly with respect to plasma membrane, mitochondrial membranes, endoplasmic reticulum, polyribosomes and dictyosomes are highlighted. The subcellular changes evoked by both stresses after 4 h were lysis of the cytoplasm, accumulation of electron-dense granules in the cytoplasm, distension in the ER membranes, enhanced association of ribosomes with the endoplasmic reticulum, reduction in the number of mitochondrial cristae, as well as disorganization of cell wall fibrillar material. Certain changes were found to be unique to either the salinity or high temperature stress. Plasmolysis and increased cytoplasmic vesiculation were seen only in response to salinity stress, while discontinuity in the plasma membrane with close association of the osmiophilic granules were observed only in response to high temperature.

Key words: Electron dense granules, high temperature stress, leaf cells, *Oryza sativa* L., rice, salinity, ultrastructure.

INTRODUCTION

All living organisms are adapted to grow, develop and reproduce in a narrow range of environmental conditions. Adverse effects of environmental stresses have been noted during both vegetative and reproductive growth stages in various crop plants (Katterman, 1990; Mckersie and Leshem, 1994; Pareek, Singla and Grover, 1997*a*; Singla, Pareek and Grover, 1997*a*). Processes leading to seedling emergence, growth of the seedlings, floral development and quality of seeds are critically affected by these stresses. The cellular organelles such as plasma membrane (PM), endoplasmic reticulum (ER) and mitochondria are known to be severely affected in response to adverse environmental conditions (Ciamporova and Mistrik, 1993). Studies on stress-induced membrane perturbations are considered important as membranes represent physical and selective barriers separating cellular activities from the outside environment and further, membranes control compartmentation of metabolites within cells (Santarius, 1980; Caldwell, 1987; Lynch, Lepock and Thompson, 1987; Kandasamy and Kristen, 1989; Brodl, 1990; Palta, 1990). Changes to membranes induced by salinity have been shown to be helpful in elucidating the cellular mechanisms of tolerance to stress conditions (Palta, 1990). Prominent ultrastructural changes in membranes accompanying heat shock (HS) have been reported for the nucleus, ER, mitochondria, plastids and PM (Ciamporova and Mistrik, 1993; Collins, Nie and Saltveit, 1995). In secretory cells of barley aleurone, which have a notably high network of ER lamellae, a principal response to HS is the dissociation of the lamellar structure which causes arrest of α-amylase mRNA translation (Belanger, Brodl and Ho, 1986). Formation of electron dense granules (EDGs) in the cytoplasm can also be promoted by elevated temperatures. In maize root cells, high temperature stress reduces the density of mitochondria, decreases the number of cristae and brings about accumulation of dense inclusions (Ciamporova and Mistrik, 1993). HS-induced formation of granular bodies in the cytoplasm as well as in different organelles has been noted in several plant species (Risueno *et al.*, 1973; Nover, Scharf and Neumann, 1983; Cooper and Ho, 1987; Mansfield, Lingle and Key, 1988; Nover, Scharf and Neumann, 1989; Ciamporova and Mistrik, 1993).

Rice is an important cereal crop. The grain yield in rice is affected by a host of environmental factors amongst which salinity and high temperature are considered agronomically significant (Yoshida, Satake and Mackill, 1981; Khush and Toenniessen, 1991; Singla *et al.*, 1997*a*). Inspite of persistent efforts, genetic improvement of rice for tolerance to abiotic stresses is yet to be fully realized (Grover, Singla and Pareek, 1995). The lack of a full understanding of how plants, in general, cope up with such environmental factors is considered to be the main reason for this failure (Grover, Pareek and Maheshwari, 1993). Previously, we have reported morphological changes as well as alterations to proteins which take place in rice seedlings in response to diverse abiotic stresses (Singla and Grover, 1993, 1994; Pareek, Singla and Grover, 1995; Pareek *et al.*, 1997*b*; Singla *et al.*, 1997*a*). There is, as yet, no information on ultrastructural changes elicited in rice cells in response to abiotic stresses. Accordingly we present data that compares

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short-term high temperature and salinity stress-induced cellular alterations based on electron microscopic observations. This contrasts with several previous reports in which these stresses have been considered separately (Flowers *et al.*, 1985; Kandasamy and Kristen, 1989; Cachorro *et al.*, 1995).

MATERIALS AND METHODS

Plant material and experimental conditions

Rice (*Oryza sativa* L. cultivar Pusa 169, an indica type) seeds were germinated on a thin wet layer of cotton in plastic trays inside a growth chamber (Heraeus, GDR) set at 28 °C, 100% RH, and providing 11 W m^{-2} of light intensity with 16 h daylength. After 4 d, uniform-sized seedlings (1–1·5 cm shoot length) were transferred to 100 ml glass beakers containing a cotton layer soaked with sufficient distilled water to submerge the roots and acclimatized for 24 h under the growth conditions described above. Half of these beakers were then placed in a water bath at 45 °C to subject seedlings to HS as described by Singla and Grover (1993, 1994) and Pareek *et al.* (1995). For recovery after 4 h of HS, beakers containing the seedlings were returned to 28 °C for 16 h. To impose salinity stress (SS), 5-d-old seedlings were transferred to a two-layered sterile piece of cotton floating over 400 mM NaCl solution in 250 ml Erlenmeyer flasks for 4 h. Cotton plugs were placed over the flasks to minimize microbial contamination and water loss. For recovery from SS, NaCl solution from the flasks was replaced with distilled water and seedlings were allowed to recover for 16 h (Fig. 1A).

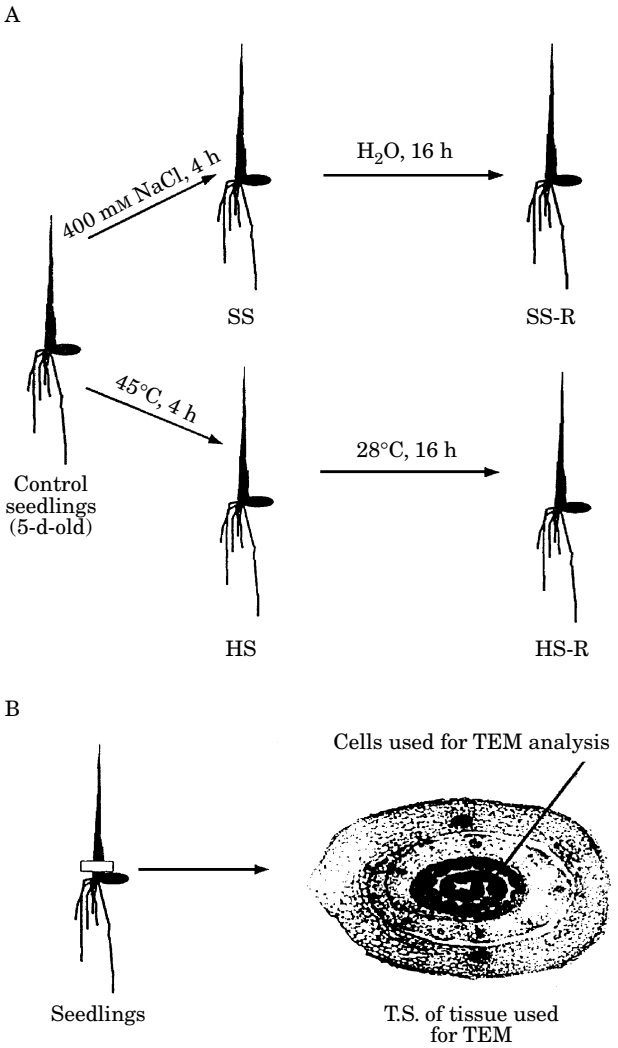

FIG. 1. Diagrammatic representation of salt and heat stresses (SS and HS, respectively) and recovery treatments given to rice seedlings for analysis by transmission electron microscopy. A, Stress treatments and recovery durations. B, Individual seedling from (A) showing the shoot portion used for microtomy (marked by a square). The cellular details of a representative section as seen under light microscope are shown on the right.

Sample processing for transmission electron microscopy (TEM)

Segments (1–2 mm thick) were cut from the basal region of shoots (see Fig. 1B) of seedlings with a sharp blade. The position representing undifferentiated cells from the young leaf analysed in this study is shown in a light microscopic section (Fig. 1B). The shoot segments were immersed in 2% paraformaldehyde while sectioning to prevent entry of air bubbles. Subsequently, tissue sections were fixed in the same reagent followed by Karnovsky fixative containing 8% (v/v) formaldehyde, 12·5% (v/v) glutaraldehyde and 0·1 M phosphate buffer (pH 7·0) (Karnovsky, 1965). Subsequently, samples were washed twice in 0·1 M phosphate buffer (pH 7·0) and post-fixed with 2% osmium tetroxide. The samples were dehydrated in an ascending series of ethanol and propylene oxide. This was followed by infiltration with a series of Epon-Araldite mixtures with propylene oxide. Finally, tissues were embedded in 100% resin according to Mollenhauer (1964). The ultrathin sections (70–80 nm in thickness) were picked-up on copper grids and stained with uranyl acetate followed by lead citrate and observed in an electron microscope (Philips EM-300). Photographs were taken of at least three random sites in three different sections and representative pictures are presented.

RESULTS

Profile of cells from control seedlings

The control cells were filled with cytoplasm. Importantly, no space was seen between the cell wall (CW) and plasma membrane (PM) in control cells, indicating that osmotic damage was not triggered during tissue processing for TEM (Fig. 2A). In these cells, conspicuous cisternae of rough endoplasmic reticulum (RER) were seen, dictyosomes were clearly visible, the nucleus was found to have densely packed nucleolus and mitochondria showed intact membranes and cristae (Fig. 2C and D).

Profile of cells from SS seedlings

Cells from the seedlings subjected to SS showed symptoms of plasmolysis as characterized by the appearance of space

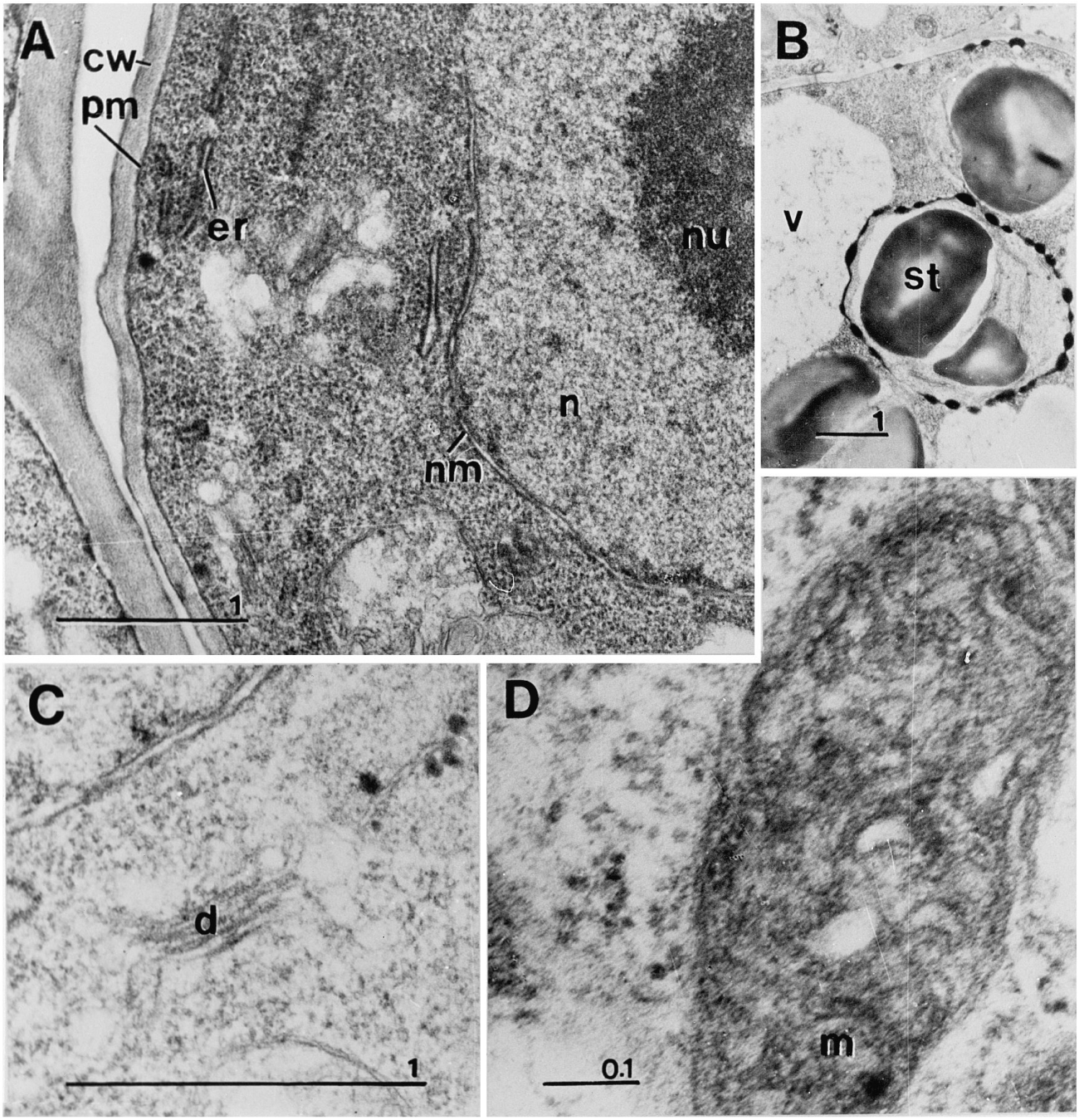

FIG. 2. Electron micrographs showing the ultrastructure of control (non-stressed) cells of rice shoots. A, Single cell from control unstressed tissue. B, A portion of the cell showing the solubilization of starch. C, A magnified portion of the cell showing the presence of dictyosomes. D, A portion of cell showing normal mitochondria. The bars represent the linear size in μm. cw, Cell wall; d, dictyosome; er, endoplasmic reticulum; n, nucleus; nu, nucleolus; nm, nuclear membrane; pm, plasma membrane; st, starch; v, vacuole.

between the CW and PM (shown by arrows in Fig. 3A). Vacuoles were prominent in these cells and were found to contain electron dense inclusions (shown by arrowheads in Fig. 3A). The shape of the nucleus was altered and mitochondria were globular with dilated cristae (Fig. 3B). An enlarged portion of the cell showing clustering of mitochondria is shown in Fig. 3C. The ER membranes were highly distended with pronounced association of ribosomes (Fig. 3D). Intact starch granules were seen in salinity-stressed cells (Fig. 3E), unlike control cells where active solubilization was noticed at certain places (Fig. 2B). Discrete circular electron dense granules (EDGs), probably representing plastoglobuli, were also found in these cells (shown by arrows in Fig. 3E). The PM was associated with deposition of EDGs (shown by small arrows in Fig. 3F). The enlarged view of a portion of the cell showed lysed regions (as indicated by open squares) present in cells near the site of accumulation of EDGs (shown by arrows in Fig.

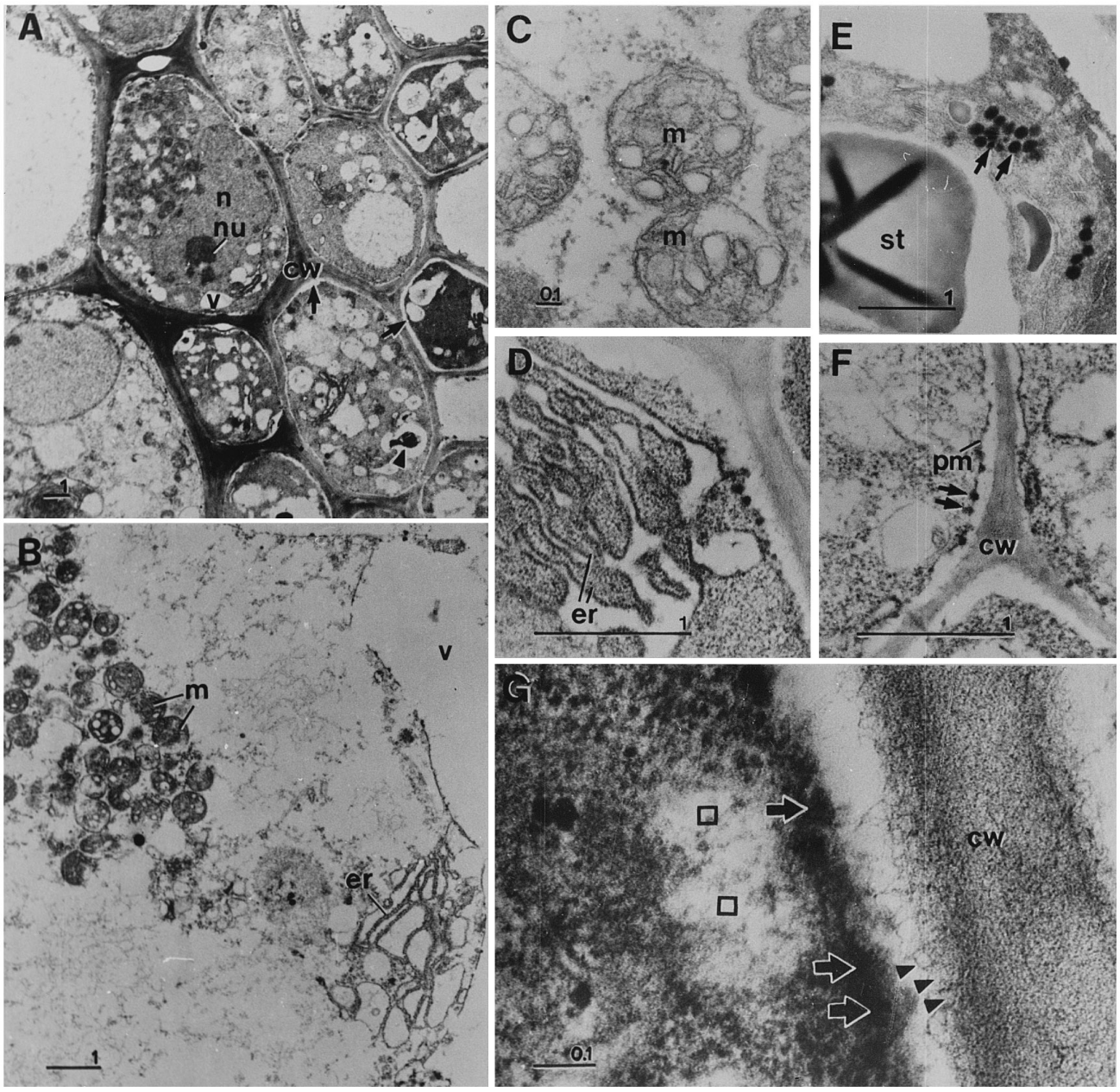

FIG. 3. Electron micrographs showing the effect of 400 mM NaCl (4 h) on cells of rice shoots. A, An overview of a representative cell. The cell appears plasmolysed (arrow). Some vacuoles show electron dense inclusions (arrowhead). B, A portion of the cell showing clustering of mitochondria. Bulbous endoplasmic reticulum can also be seen. C, A magnified view showing the effects of salt stress on mitochondria. D, A magnified portion of the cell showing the distended endoplasmic reticulum. E, A portion of the cell showing an intact starch grain. Electron dense granules (arrows) can also be seen. F, An intercellular junction showing the accumulation of electron dense bodies near the cell wall (arrows). G, A portion of cell enlarged to show the damage caused to cell wall and plasma membrane. Disorganized fibrils of cell wall can be seen (arrowheads) along with lysed regions in the cytoplasm (□). The bars represent the linear size in μm. cw, Cell wall; er, endoplasmic reticulum; n, nucleus; nu, nucleolus; pm, plasma membrane; st, starch; v, vacuole.

3G). Fibrils of the CW were found to be highly disorganized (shown by small arrowheads in Fig. 3G).

Profile of cells representing seedlings recovering from SS

After 16 h of recovery, cells showed several alterations which were seen during salt-stress. These included the presence of lysed regions (shown by open squares in Fig. 4A). As in control cells (Fig. 2B), starch granules were found in a partially-metabolized state (labelled 's') in cells recovering from stress. The nuclear membrane of recovering cells appeared intact, while mitochondria in such cells showed partially damaged cristae (Fig. 4B). A portion of Fig. 4B is enlarged in Fig. 4C in which fragments of the cristae which were not fully formed (shown by arrows) and

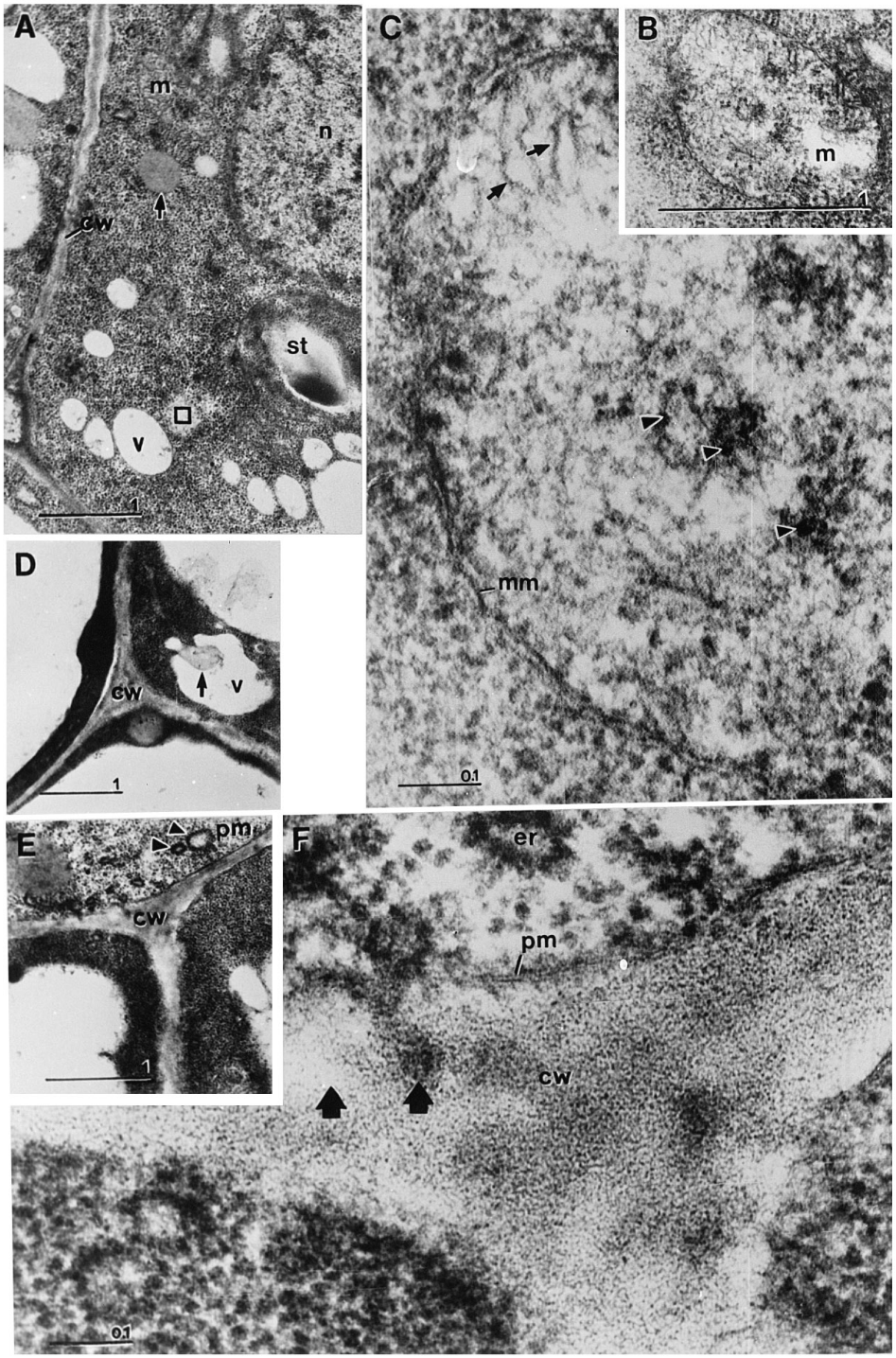

FIG. 4. Electron micrographs showing the details of rice cells allowed to recover for 16 h following 4 h of 400 mM NaCl stress. A, A portion of cell showing the presence of injury symptoms. Lysed regions (□) and fluid-filled microbodies (arrow) are evident. B, A single mitochondria showing damaged cristae. C, Portion of mitochondria revealing details of membrane and cristae (arrows). Electron dense inclusions are visible (arrowheads). D, An intercellular junction and secretion of an unknown metabolite into the vacuole (arrow). E, An intercellular junction of cell showing damage to the cell wall and the bulbous nature of the endoplasmic reticulum (arrowheads). F, An enlarged portion of the intercellular junction. Note the patchy appearance of the wall (the two types of region in the cell wall are marked with arrows). The bars represent the linear size in μm. cw, Cell wall; er, endoplasmic reticulum; m, mitochondria; mm, mitochondrial membrane; n, nucleus; pm, plasma membrane; st, starch; v, vacuole.

which contained electron dense inclusions (shown by arrowheads are shown). In some of the cells, vacuoles with an inclusion were noted (shown by arrows in Fig. 4D). The ER cisternae were found to be distended with ribosomes covering their surface (shown by arrowhead in Fig. 4E). A magnified view of these cells indicates that the CW has a

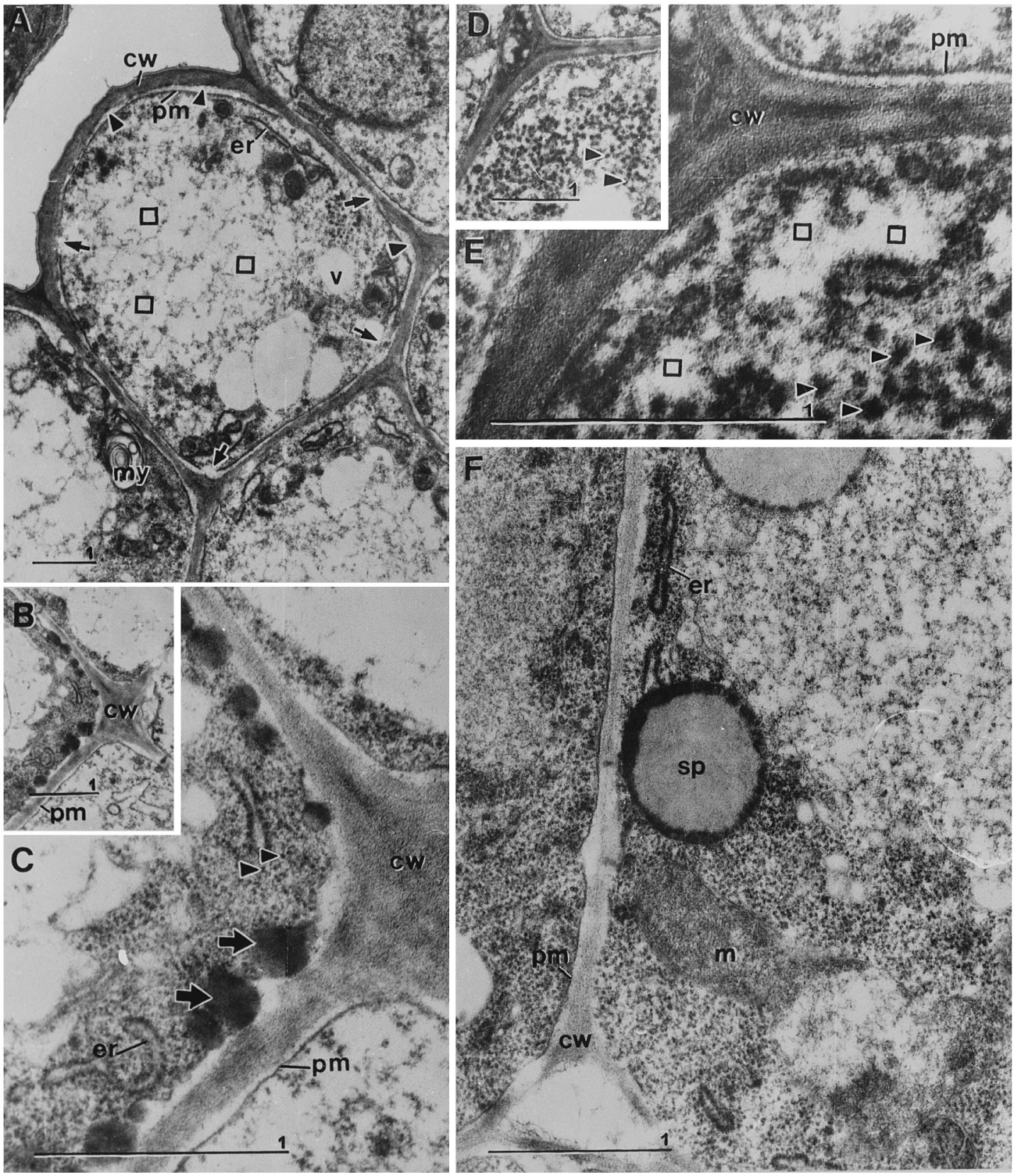

FIG. 5. Electron micrographs showing details of cells of rice shoots subjected to 45 °C for 4 h. A, An overview of cell showing the injury caused by elevated temperature. Discontinuities in the plasma membrane (arrows) as well as space between the cell wall and the plasma membrane (arrowhead) were noted. The lysed regions in the cytoplasm are also seen (□). B, An intercellular junction showing deposition of electron dense bodies near the damaged plasma membrane. C, Enlarged view of (B) showing the two types of electron dense bodies near the cell wall (marked by arrows and arrowheads). D, An additional view of the intercellular junction showing the accumulation of electron dense bodies (arrowheads). E, Enlarged view of the cell wall junction shown in (D). F, A portion of the cell showing damage to the cell wall, plasma membrane and mitochondria. The bars represent linear size in μm. cw, Cell wall; er, endoplasmic reticulum; m, mitochondria; mm, mitochondrial membrane; my, myelin-like body; n, nucleus; pm, plasma membrane; v, vacuole.

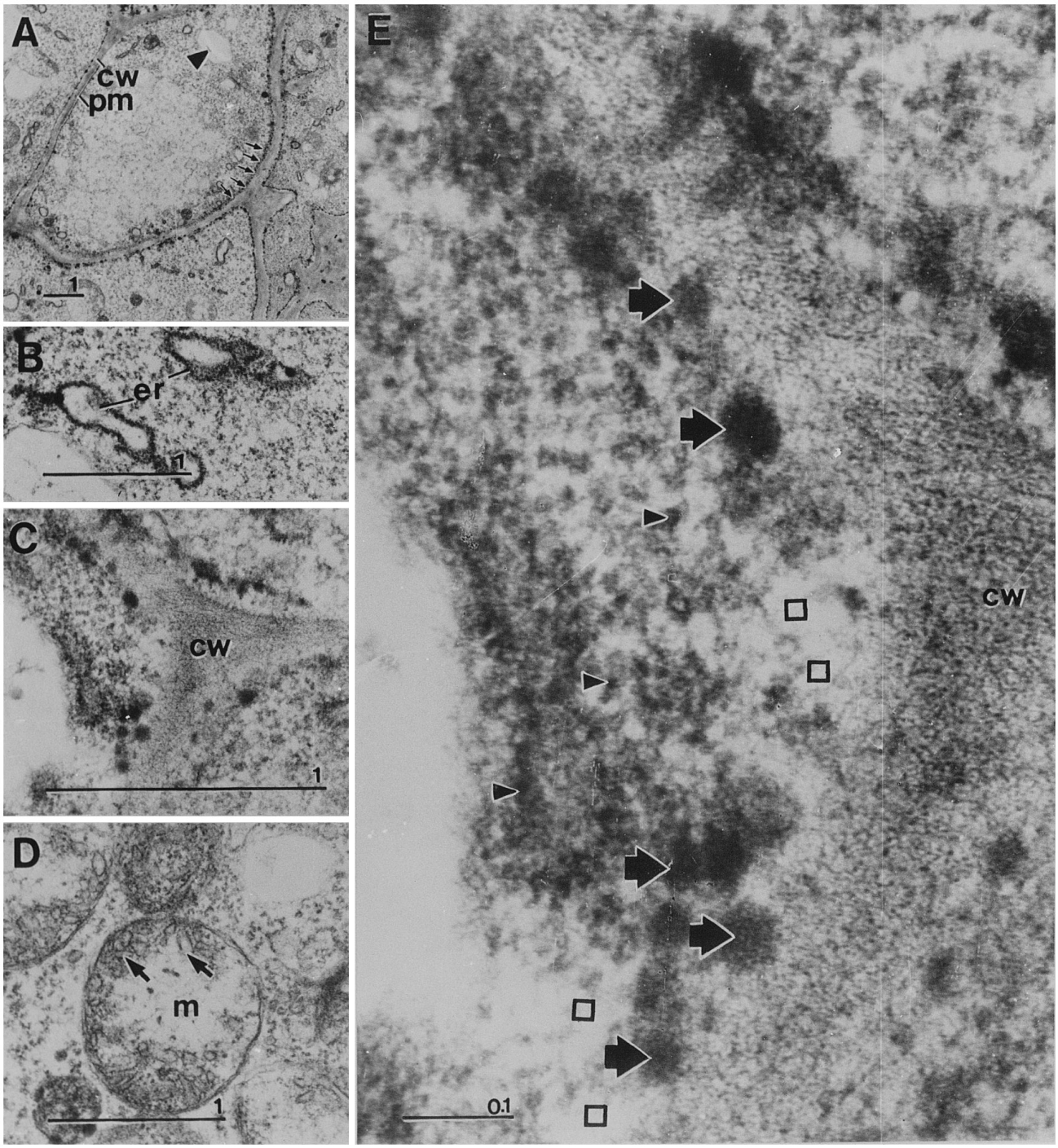

FIG. 6. Electron micrographs showing details of rice cells allowed to recover for 16 h following 4 h of high temperature stress. A, A view of cell showing the presence of injury symptoms. The lysed cytoplasmic regions (arrowhead) are visible. Electron dense bodies, heavily deposited along the cell wall (arrows) are also evident. B, Distended ER membrane is visible. C, An intercellular junction of cells showing discontinuous plasma membrane and damaged cell wall. D, Mitochondria showing damaged cristae as well as the formation of new cristae (arrows). E, A portion of the intercellular junction shown in (C) magnified to show the accumulation of electron dense bodies (shown by arrow and arrowheads) along the damaged cell wall. The lysed regions in the cytoplasm can be seen (□). The bars represent linear size in μm. cw, Cell wall; er, endoplasmic reticulum; m, mitochondria; pm, plasma membrane.

non-homogenous appearance (different regions in the CW are represented by arrows in Fig. 4F).

Profile of cells from seedlings subjected to HS

In response to HS, the cells showed symptoms of cellular injury (Fig. 5A). Myelin-like formation was prominent in these cells (labelled 'my'). The cytoplasm was found to have several lysed regions (shown by open squares) similar to those seen in SS. Importantly, the PM showed discontinuity (shown by arrow) which was not observed under SS (Fig. 5A). EDGs of two sizes, large (shown by arrows in Fig. 5C) and small (shown by arrowheads in Fig. 5C, D and E) were found to have accumulated in the cytoplasm of these cells. The smaller-sized EDGs were distributed throughout the cytoplasm, while the larger-sized bodies were concentrated towards the periphery of the cell in close proximity to the PM (Fig. 5C and E). Similar to SS samples, ER membranes were found to be distended and were associated with polyribosomes. Importantly, the ER membranes were organized around the cell periphery (see Fig. 5A–F). Mitochondria in these cells were much damaged as distinct cristae were no longer visible (Fig. 5F). In certain cells, structures resembling spherosomes were found (labelled 'sp' in Fig. 5F). These bodies had an enriched covering of osmiophilic granules.

Profile of cells representing seedlings recovering from HS

Cells appeared normal in shape, but were found to be covered with EDGs along the PM (shown by arrows in Fig. 6A). Lysed regions in the cytoplasm were observed in these cells (shown by arrowhead in Fig. 6A) at reduced frequency compared to seedlings subjected to HS. The ER cisternae were highly distended and densely associated with ribosomes (Fig. 6B). The PM appeared to be damaged in these cells, indicating that the recovery was partial. Figure 6C shows the intercellular junction of three cells. The enlarged view of this junction showed clear indications of PM as well as CW injury. Certain EDGs were visible near the damaged membrane (shown by arrows in Fig. 6E). The cells recovering from HS showed fewer EDGs (shown by arrowheads in Fig. 6E) as compared to HS samples. Lysed sites in the cytoplasm were seen in these cells (shown by open squares in Fig. 6E) and mitochondria showed a reduced number of cristae compared to controls (Fig. 6D).

DISCUSSION

The aim of this study was to characterize ultrastructural alterations brought about by high temperature and salinity stresses in leaf cells of rice shoots, and to compare the effects triggered by these two stresses. Ciamporavo and Mistrik (1993) have suggested that similar types and ages of cells must be compared in such studies. We focused on undifferentiated leaf cells from the basal portion of shoots throughout this analysis. Furthermore, the same time interval of 4 h was followed for both high temperature (45 °C) and salt stress (400 mM), as well as same length of recovery phase (16 h). This allowed comparisons which were not affected by differential development of seedlings. In essence, this study describes changes triggered by short-term high temperature and salt stress levels. It is debatable whether stress-associated cellular changes are consequences of the damaging effect or adaptive responses (Cachorro *et al.*, 1995). Exposure of tissues to sublethal stress prior to lethal levels often induces tolerance against a range of abiotic stresses, indicating that metabolic changes taking place during sublethal stresses might have a role in adapting the system to lethal stress levels (Singla *et al.*, 1997*a*). With this viewpoint, we highlight cellular alterations caused by sublethal levels of high temperature and salinity stresses. With respect to high temperature stress, we showed earlier that 4 h of 45 °C is sublethal to 5-d-old seedlings of rice (cv. Pusa 169) based on the pattern of recovery (Singla *et al.*, 1997*a*). In a similar type of experiment here, we noted that 4 h of 400 mM salt treatment is sublethal for rice seedlings.

There is a possibility that the processing of samples for TEM analysis may have generated artifacts in subcellular structure. To reduce this possibility, samples were supplied with a combination of paraformaldehyde and glutaraldehyde in a buffered regime to ensure maintenance of a neutral pH and favourable osmolarities. This was done to minimize extraction of proteins and other solutes and to maintain the structures as close as possible to their native form (Karnovsky, 1965; Jernstedt, Jones and Rost, 1993). Further, unstressed control cells were compared with stressed cells to specifically pinpoint differences arising due to the imposition of stress conditions. However, there remains a possibility that water relations of the stressed samples may be affected differently to controls due to fixation and other processing steps.

The principal cellular alterations noted in this study were as follows: (1) in response to salt stress, the plasma membrane was separated from the CW at several points indicating plasmolysis (Figs 2B and 3A). It is important to note here that 4 h exposure of seedlings to 400 mM NaCl stress may have constituted a predominantly osmotic stress rather than merely ionic effects caused by excess Na^+ (as described later in this section). The ultrastructural effects caused by the salt treatment may therefore possibly represent those associated with osmotic stress. Previous studies have established that the ability to plasmolyse in response to osmotic shock is a ubiquitous feature of walled plant cells (Lee-Stadelmann and Stadelmann, 1989). It is noteworthy that plasmolysis was not evoked in response to high temperature in this study (Figs 2 and 5), indicating that the temperature stress imposed in this study may not have been sufficiently high or prolonged to elicit plasmolysis. (2) The ER lamellae became bulbous in response to salinity and high temperature stresses. Further, ribosomes were prominently attached to ER lamellae (Figs 3D, 4F, 5C, F and 6B). Such prominent ER-ribosome complexes have previously been noted in response to water deficit, cold stress and oxygen deficiency in various plant species which may possibly reflect induction of stress proteins often seen in response to stress conditions (Mistrik, Holobrada and Ciamporova, 1992; Ciamporova and Mistrik, 1993; Singla *et al.*, 1997*a*). To explain why such prominent complexing of ribosomes with endoplasmic reticulum was not seen in

TABLE 1. *Ultrastructural changes in cell organelles in response to salinity and high temperature stress in shoot tissues of rice* (O. sativa L. *cv. Pusa 169*) *seedlings*

Ultrastructural change	Salinity stress	Salinity stress recovery	High temp. stress	High temp. stress recovery
Cell wall damage	+	+	+	+
Electron dense granules (EDGs)	+	+	+	+
Plasmolysis	+	−	−	−
Cytoplasmic lysis	+	+	+	+
Vesicles near damaged plasma membrane	+	−	+	+
Endoplasmic reticulum distended	+	+	+	+
Mitochondria damage	+	+	+	+
Plasma membrane discontinuous with EDGs deposition	−	−	+	+
Spherosomes seen	−	−	+	−

control cells, it is suggested that the control cells have an elaborate network of active membranes which together carry out the protein biosynthesis function. As the stresses cause drastic rearrangement of endoplasmic reticulum lamellar structure (see Fig. 5 and also Ciamporova and Mistrik, 1993), increased association of ribosomes may specifically enhance the synthesis of stress proteins from those few lamellae which remain metabolically active despite the stressful conditions. (3) Cellular bodies corresponding in size to heat shock granules were noted in this study both in response to high temperature and salinity stresses (Figs 5 and 6). In yeast cells, heat shock granules are considered to be the denatured proteins (Parsell *et al*., 1994). It has further been noted that heat shock granules are disaggregated in yeast cells after the stress is relieved. This is brought about by the action of a specific 104 kDa heat shock protein (HSP) called ScHSP 104 (Parsell *et al*., 1994). Importantly, proteins equivalent to ScHSP 104 have recently been shown in plants, including rice (Singla and Grover, 1993; Lee, Nagao and Key, 1994; Schirmer, Lindquist and Vierling, 1994). Furthermore, it has been found that a rice equivalent of ScHSP 104 protein (i.e. OsHSP 110) is accumulated in response to salt and to high temperature stress (Singla, Pareek and Grover, 1997*b*). It is possible that protein aggregation is a common feature of salt and high temperature stresses in plant cells and, as in yeast, specific plant HSP helps to solubilize the HS granules in the cells in the post-stress period. (4) Mitochondria showed dilated cristae and increased matrical density in response to stress conditions (Figs 3C, 4C and 6D). These changes in the ultrastructure of mitochondria are probably indications of stress-associated alterations in mitochondrial energy status resulting in decline of ATP levels (Barlow, Ching and Boersma, 1976; Kandasamy and Kristen, 1989). (5) Osmiophilic granules were noted in close proximity to the high temperature-damaged plasma membrane (Figs 5C and 6E). Such granules have also been noted in close proximity to the plasma membrane of the stressed cells in other studies (McKersie and Lesham, 1994). This may be considered as an important cellular activity because osmiophilic granules have been proposed to play a role in re-establishing the integrity of the plasma membrane (Brodl, 1990; McKersie and Lesham, 1994).

It has been shown previously that high temperature and salinity stresses share certain common physiological determinants (Harrington and Alm, 1988). Cross-adaptation in plants, in the sense that tissues which are preadapted to salinity show enhanced thermotolerance and *vice versa*, has been observed in a few instances (Borkird *et al*., 1991). At the molecular level, certain changes in gene expression can be co-triggered by salinity or high temperatures (Borkird *et al*., 1991; Pareek *et al*., 1995). It was noted in this study that cellular changes evoked in response to HS and SS were also similar to a large extent (Table 1). These include traits such as lysis of the cytoplasm, accumulation of EDGs in the cytoplasm, distension in the ER membranes, enhanced association of ribosomes with the ER, reduction in the number of mitochondrial cristae, as well as disorganization of the cell wall fibrillar material. At the other extreme, certain changes were found to be unique to either the salinity or high temperature stress. For instance, plasmolysis and increased cytoplasmic vesiculation were seen only in response to salinity stress, while discontinuity in the plasma membrane as well as close association of the osmiophilic granules with damaged plasma membrane were observed only in response to high temperature. Such stress-specific traits might represent reactions unique to the given stress i.e. those caused by excess ions or osmotic stress in case of salt stress and supra-optimal temperature in case of high temperature stress.

Both salinity as well as high temperature-induced cellular perturbations persisted in rice shoot cells for at least 16 h after withdrawal of stress conditions. However, recovery from plasmolysis induced by salt stress appeared to be a rapid response. Likewise, disappearance of osmiophilic granules from high temperature-exposed cells during the recovery phase was also a relatively quick response. The cellular changes brought about by such short-term stress treatments might be different from longer-term stress effects. According to Yeo *et al*. (1991), the initial growth reduction

in rice caused by salinization (50 mM) is due to a limitation of water supply and is reversible. On the other hand, long-term effects result from the accumulation of salt within the system which have long-lasting effects. Similar findings have recently been made in wheat and barley systems by Munns, Schachtman and Condon (1995). According to these workers, decrease in growth rate in the initial phase of the salt response could be an osmotic response. The synthesis of HSPs in response to high temperature stress is shown to be differentially-modulated in response to short- and long-term temperature stress levels (Singla *et al*., 1997*a*). In the light of these arguments, it will be rewarding to make time-course studies of the stress- and recovery-associated changes after longer periods of stress treatment. We are currently attempting to correlate stress-induced alterations to ultrastructure and to molecular events for a better understanding of the mechanisms evoked in rice by environmental perturbations such as salinity and high temperature.

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