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Changes of Organic Solutes and Antioxidative Enzyme Activity in Rice Seedling under Salt Stress

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ABSTRACT: Seedlings of two rice genotypes, cvs. Ilpumbyeo and Gancheokbyeo, were exposed to 0, 50 and 100 mM NaCl in nutrient solution for nine days. Plants were collected at the interval of 3 days and organic and inorganic solutes in leaves and roots and antioxidative enzyme activity in leaves were determined. Under salinity, the accumulation of soluble sugars occurred considerably in the older leaves of stressed seedlings compared to younger leaves and roots. The endogenous Na+ contents markedly increased at higher NaCl concentration in leaves and roots of seedlings, though it was higher accumulated in roots. Salinity resulted in an excessive proline accumulation in the stressed plants. A more pronounced increase was observed in Gancheokbyeo leaves. SOD activity in Impumbyeo cannot found any remarkable change, whereas, in Gancheokbyeo, its activity was rapidly decreased. CAT and POD activities increased with an increase in NaCl concentration in both genotypes. In summary, the high capacity of rice seedlings to overcome an unfavorable growth condition such salt stress appears to be related to an adequate partition of organic solutes between shoots and roots and to changes in absorption, transport and re-translocation of salts.

Keywords: carbohydrate, antioxidants, proline, rice seedling, salt

Abbreviation: CAT; catalase, POD; guaiacol-peroxidase, SOD; superoxide dismutase

Salinity stress is a major problem in agricultural lands throughout the world. Because a plant's ability to cope is critical when determining crop distribution and productivity, it is important to understand the adaptation or acclimation mechanisms to saline environments. Plants under salinity stress accumulate a number of organic solutes which have important roles on plant metabolism (Bohnert *et al.*, 1995; Gilbert *et al.*, 1998). These metabolites include amino acids, polyamines and carbohydrates, e.g., mannitol, sucrose and raffinose oligosaccharides. Earlier experiments have demonstrated that sugars can protect the structural integrity of membranes during dehydration by preventing membrane fusion, phase transition and phase separation (Crowe & Crowe, 1992), and by restroing cell volume and turgor, reducing cell damage induced by free radicals, and protecting and stabilizing enzymes and membrane structure (Timasheff & Arakawa, 1989). The alleviation of oxidative damage and increased resistance to salinity and other environmental stresses is often correlated with an efficient antioxidative system (Scandalios, 1993; Cakmak *et al.*, 1993; Hasegawa *et al.*, 2000; Acar *et al.*, 2001). Dionisio-Sese & Tobita (1998) studied the activities of SOD and POX enzymes under NaCl stress in the leaves of four cultivars of rice exhibiting different sensitivities to NaCl. Their results have indicated that salt tolerance capacity of salt-tolerant species is closely related with the maintenance of specific activity of antioxidant enzymes studied. Comparison of antioxidant defense systems, lipid peroxidation and proline contents in roots of rice cultivars differing in salt tolerance may be helpful in developing a better understanding of tolerance mechanisms to salt stress. Salinity affects plant physiological responses through changes of the water and ionic status in the cells (Sultana *et al.*, 1999; Kashem *et al.*, 2000b; Hasegawa *et al.*, 2000). Ionic imbalance occurs in the cells due to excessive accumulation of Na^+ and Cl^- and reduces the uptake of other mineral nutrients, such as K^+, Ca^{2+} and Mn^{2+} (Cramer & Nowak, 1992; Khan *et al.*, 1997; Lutts *et al.*, 1999). Rapid accumulation of free proline is a typical response to salt stress. When exposed to drought or a high salt content in the soil (both leading to water stress), many plants accumulate high amounts of proline, in some cases several times the sum of all the other amino acids (Mansour, 2000). Sultana *et al.* (1999) have suggested that proline accumulation in both salinized leaves and grains of rice plants is implicated in osmotic adjustment to salinity.

The aim of this work was to better understand changes in early growth, cargbohydrate and proline levels and specific antioxidative enzymes activities for rice cultivars with dif-

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ferent salt resistance.

MATERIALS AND METHODS

Plant materials and salt treatment

Seeds of two rice cultivars, cvs. Ilpumbyeo and Gancheokbyeo, were surface-sterilized with a 2% (w/v) solution of sodium hypochlorite, and then placed on an incubator kept at 30 for 3 days with a clean water. After 10 days of rooting, the seedlings were transferred into a growing unit containing an aerated Hoagland solution. Different salt concentrations were obtained by dissolving NaCl in the Hoagland solution to reach a final concentration of 0, 50 and 100 mM. During the 9 days treatment period, the hydroponic medium was renewed every 3 day. Each plant was collected at 0, 3, 6 and 9 days after salt treatment, immediately stored at -70°C for the activities of antioxidative enzymes and proline contents, and others were dried at 80°C for carbohydrate and sodium-ion contents.

Analysis of soluble carbohydrates

Soluble sugars were extracted by heating leaf discs in 80% EtOH according to Roe method (1955). Soluble sugars were analyzed by the reaction of 1.0 ml of the alcoholic extract with 2.0 ml fresh 0.2% anthrone in sulfuric acid (w/v) and placed in a boiling water for 10 min. After cooling, the absorbance at 630 nm was determined. After the extraction of the soluble fractions, the solid fraction was used for starch analysis. Starch was extracted with 9.3 N perchloric acid. The starch concentration was determined by the anthrone method as described above. Glucose was used as standard for both soluble sugars and starch.

Antioxidative enzymes assay

Frozen leaves samples were ground to a fine powder with liquid nitrogen and extracted with ice-cold 100 mM sodium phosphate buffer (pH 7.8). The extracts were centrifuged at 10,000 rpm for 20 min at 4, and resulting supernatants were collected and used for protein content assay and enzyme activities. Protein contents were determined according to Bradford (1976) with bovine serum albumin as the standard. The total SOD activity was determined according to the method described by Beyer & Fridovich (1987). The reaction mixture contained 50 mM sodium phosphate bufer (pH 7.8), 100 mM L-methionine, 50 μM nitro blue tetrazolium, 15 μM riboflavin, 1 mM EDTA, and appropriate volume of enzyme extracts in a 5 ml volume. The tubes were shaken and illuminated. The reaction was allowed to run for 10 min, the light was switched off, and then the absorbance was read at 560 nm. One unit of SOD activity was defined as the amount of enzyme required to cause 50% inhibition of the rate nitro blue tetrazolium chloride reduction. CAT activity was determined by monitoring the decomposition of H_2O_2 (extinction coefficient 39.4 mM cm^{-1}) at 240 nm following the method of Aebi (1974). The reaction mixture contained 50 mM sodium phosphate (pH 7.0), 1 mM EDTA and plant extract in a 1 ml volume. The reaction was initiated by adding 10 mM H_2O_2. One unit of catalase is defined as the amount of enzyme which liberates half of peroxide oxygen from 10 mM H_2O_2 solution per min at 25°C. The activity of POD (EC 1.11.1.7) was determined by monitoring the formation of guaiacol dehydrogenation product (extinction coefficient 6.39 mM cm^{-1}) at 436 nm following the method of Pütter (1974). Three ml of reaction mixture contained 50 mM sodium phosphate buffer (pH 7.0), 0.3 mM guaiacol and plant extracts. The reaction was initiated by adding 10 mM H_2O_2. One unit of peroxidase specific to guaiacol is defined as the oxidation of mmol of guaiacol from 0.3 mM guaiacol and 10 mM H_2O_2 per min at 25°C.

Na-ion concentration

For analyzing Na-ion concentration, plants grown in saline condition were collected and dried at 80°C for 48 hrs. The dried samples (0.3 g) were extracted in 3.3 ml of reaction solution containing 6 g of salicylic acid of 18% H_2SO_4 for 24 hrs, wet-digested on hot-plate. Extracts were cooled down at room temperature, filtered with Whatman No. 6 and made up to 100 ml with distilled water. Na-ion concentration was determined with ICP.

Proline contents

Free proline contents were determined according to Bates *et al.* (1973). Frozen leaf samples (0.5 g) from each group were homogenized in 3 % sulphosalycylic acid (w/v) and the homogenates were filtered through filter paper. After addition of acid ninhydrin and glacial acetic acid, resulting mixture was heated at 100 for 1 hr in water bath. The mixture was extracted with toluene and the absorbance of fraction with toluene aspired from liquid phase was read at 520 nm. Proline contents were determined using calibration curve and expressed as μmol proline per g FW.

RESULTS AND DISCUSSION

Non-structural carbohydrates for providing energy are required for maintenance metabolism of seedlings after germination. Soluble sugars concentrations increased in the

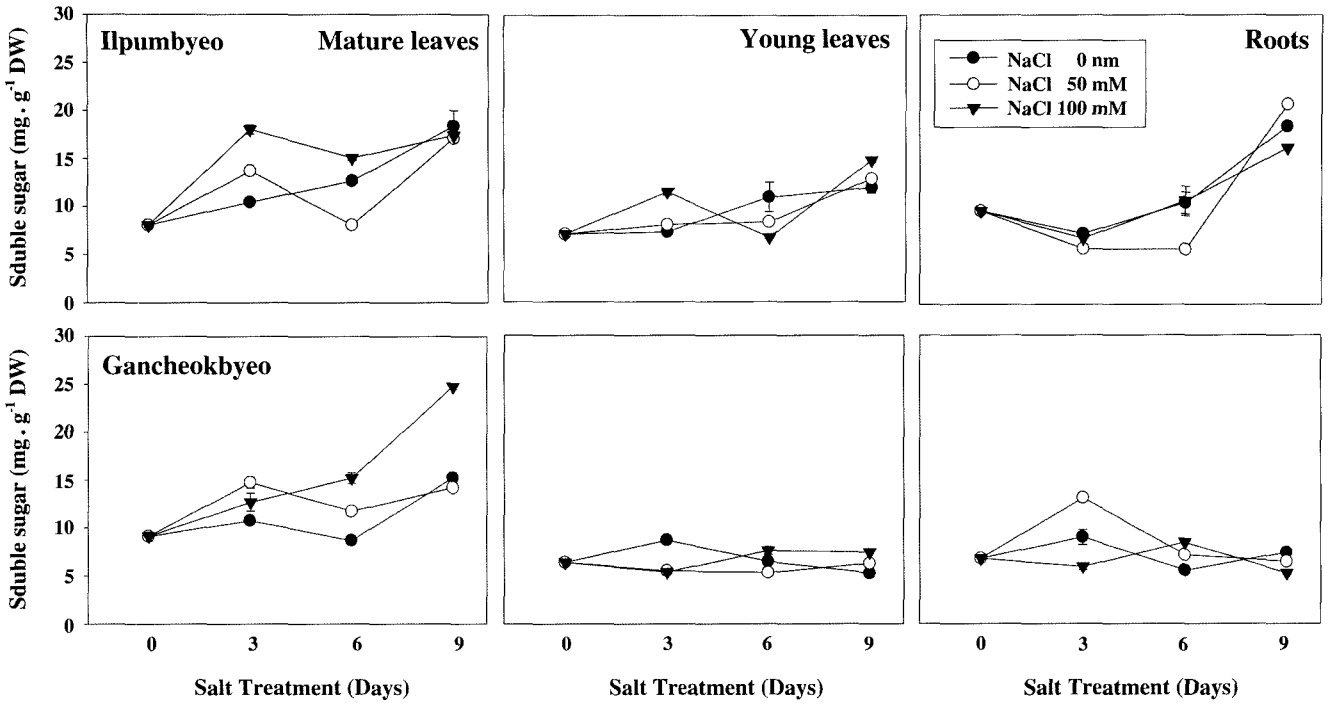

Fig. 1. Time course soluble sugars concentrations in each part of two rice genotypes exposed to different salinity. Error bars represent standard deviation of the replicates ($p<0.05$, $n=3$).

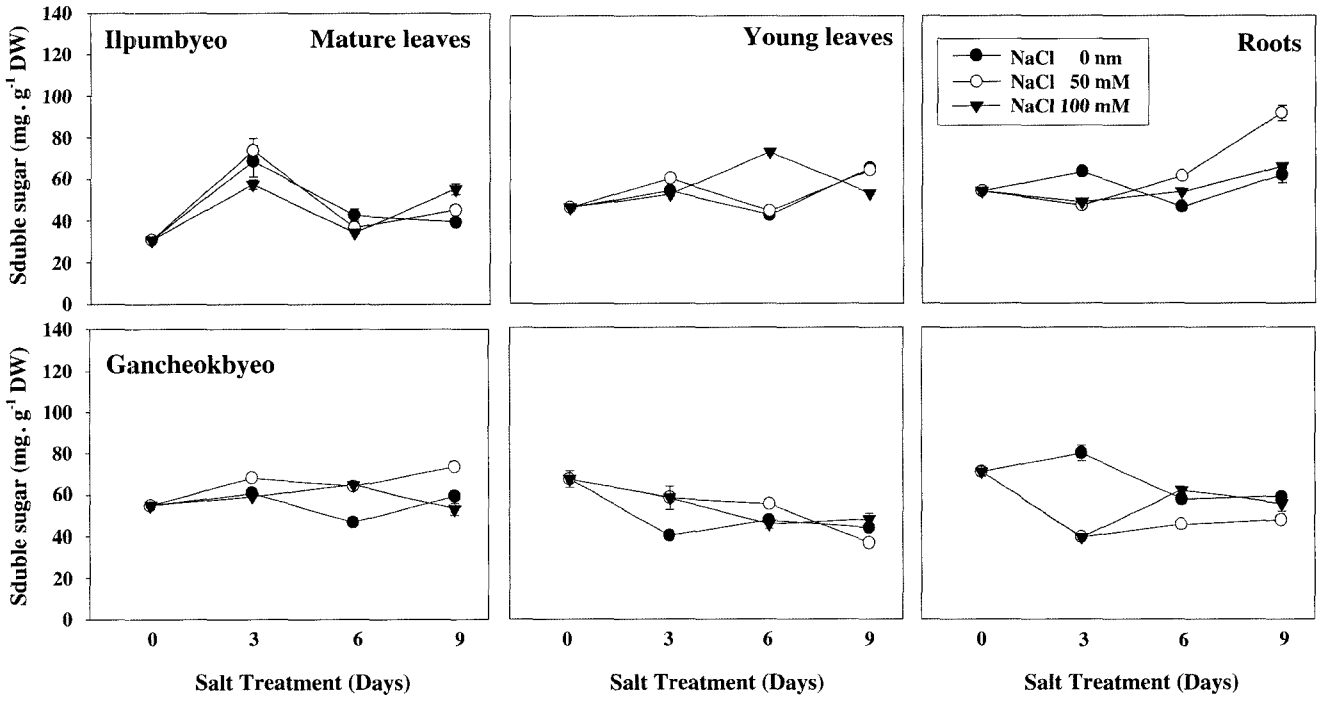

Fig. 2. Starch contents in each part of two rice cultivars subjected to NaCl treatment. Error bars represent standard deviation of the replicates ($p<0.05$, $n=3$).

older leaves of stressed seedling of both genotypes, especially at a salt concentration of 100 mM (Fig. 1). Changes in the soluble sugars in younger leaves were not remarkable compared to the older leaves, however, their levels in Ilpumbyeo were slightly increased during salt stress. Soluble sugars concentrations in roots were rapidly accumulated after 3

days of salt treatment. There were no changes in the soluble sugars in the younger leaves and roots of Gancheokbyeo. Starch concentrations in both genotypes were higher accumulated in all parts of seedlings than soluble sugars (Fig. 2). Under our experiment, starch concentrations varied from 25 to 180 g^{-1} DW, and were higher accumulated in Ilpumbyeo than in Gancheokbyeo. Starch concentrations in younger leaves and roots of Ilpumbyeo showed a slight increase during salt treatment, whereas, in Gancheokbyeo (salt-tolerant), were gradually reduced. Our results found that salt-tolerant genotype, cv. Gancheokbyeo, acclimated favorably at higher salt concentration. Therefore, soluble carbohydrates, especially soluble sugars, were preferably utilized except the mature leaves. However, carbohydrate metabolism of the seedlings, cv. Ilpumbyeo, were very sensitive to changes in plant status, showing alterations in soluble sugars concentrations when stress intensity was more pronounced. A severe salt stress caused with a higher accumulation of Na^+ ion would lead to a reduction in the photosynthetic area of the plants (Munns & Turmaat, 1986) and, consequently, an insufficient carbohydrate production to support growth, as described by our results. Additionally, since the growth of younger leaves is dependent on photosynthates produced by mature leaves (Munns, 2002) and these leaves were more severely injured in salt sensitive genotype. Excessively high concentration of carbohydrates in mature leaves by a feedback mechanism may inhibit photosynthesis (Munns, 1993) causing a reduction of leaf growth, as it was observed in the salt sensitive genotype. Also, Kerepesi & Galiba (2000) reported early that the content of sugars such as glucose, fructose, sucrose and fructan increases by NaCl exposure in a number of plants. However, Alamgir & Ali (1999) reported that sugar content increases in some genotypes of rice, but also decreases in some genotypes. As shown in Fig. 3, the endogenous Na^+ contents markedly increased at 50 and 100 mM NaCl in shoots and roots of rice seedlings,

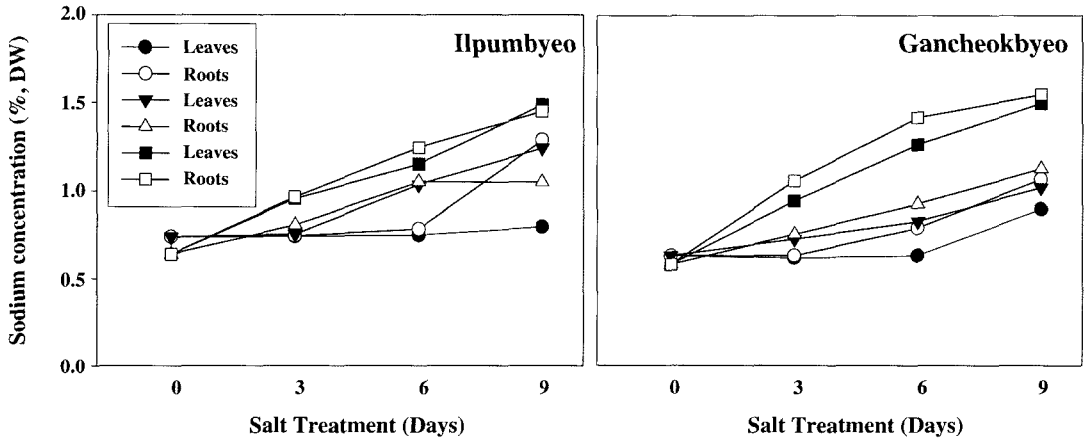

Fig. 3. Effect of salinity (0, 50 and 100 mM NaCl) on Na^+ concentration in seedlings of two rice genotypes after the subjection for 9 days. Each symbol, circle, triangle and square, means 0, 50 and 100 mM of sodium chloride concentration, respectively. Error bars represent standard deviation of the replicates ($p<0.05$, n=3).

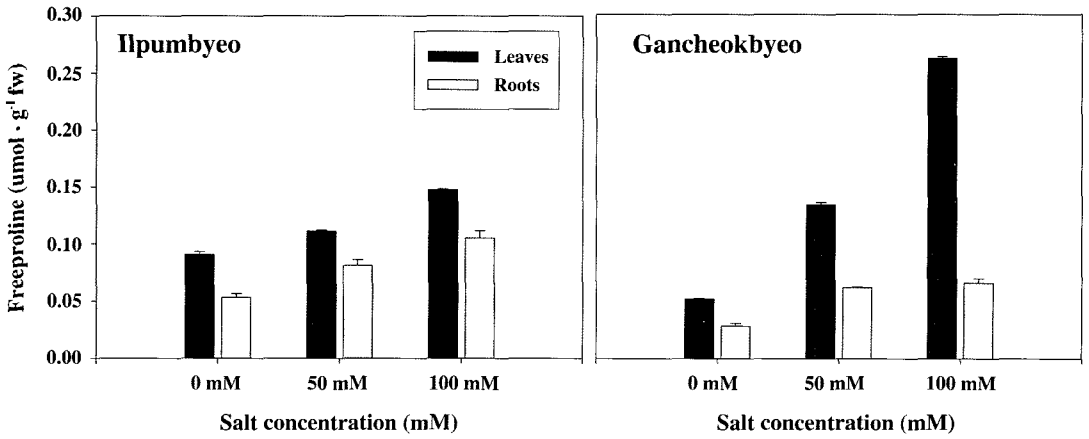

Fig. 4. Free proline contents in leaves and roots of salt-stressed rice seedlings on 9th day after salt treatment. Error bars represent standard deviation of the replicates ($p<0.05$, n=3).

though it was higher accumulated in roots in response to salt treatments. The response on Na^+ accumulation showed differently: Gancheokbyeo (salt-tolerant) roots accumulated higher concentrations of Na^+ ion to reduce the translocation to shoots compared with Ilpumbyeo (salt-sensitive). In Roots, the highest Na^+ content was observed on 6th day after 100 mM NaCl treatment. Salt stress, induced by increasing NaCl in the nutrient solution, resulted in reduction in K^+ and Ca^{2+} concentrations and increase Na^+ concentration resulting in Na+/K+ and Na^+/Ca^{2+} ratios inadequate for plant growth (Lacerda *et al.*, 2001). In fact, roots are reported to be among the first organ affected by a salt stress and are most sensitive (Lewitt, 1980; Okusanya & Ungar, 1984; Zidan *et al.*, 1990). It was presumed that an interfering Na^+ mobilization into leaves from roots, especially cv. Gancheockbyeo, minimized the photosynthetic malfunction which can be caused by salt stress. Free proline contents in leaves and roots of control and NaCl stressed plants of both cultivars were measured at day 9 of NaCl stress, and results are presented in Fig. 4. The free proline content was significantly increased in the stressed plants over control plants of both genotypes at all stress regimes during NaCl treatment.

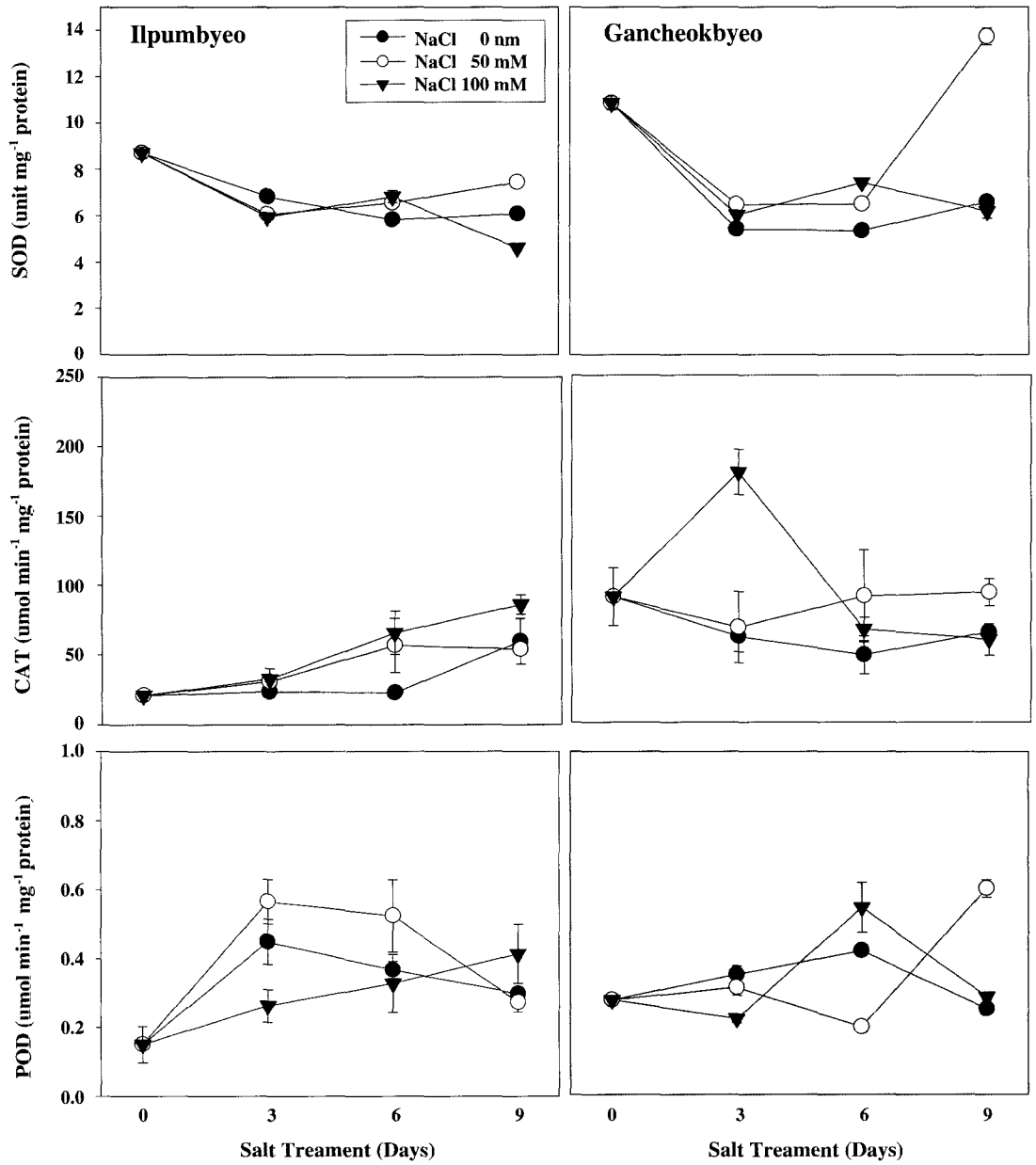

Fig. 5. The activities of antioxidant enzymes in leaves of rice seedlings exposed to different NaCl concentrations. Error bars represent standard deviation of the replicates ($p<0.05$, $n=6$).

There was a linear increase in free proline accumulation with increasing concentration of salt. A more pronounced increase was observed in Gancheokbyeo leaves compared to Ilpumbyeo. Proline contents increased by about 2.5-and 5.0-fold in the leaves of Gancheokbyeo at a salt concentration of 50 an 100 mM, respectively, on day 9. The accumulation of proline under stress protects the cell by balancing the osmotic pressure of cytosol with that of vacuole and external environment (Gadallah, 1999; Greenway & Munns, 1980). Many workers found accumulation of proline in plants exposed to salt stress. Proline accumulation may contribute to osmotic adjustment at the cellular level (Perez-Alfocea *et al.*, 1993). Genotypic differences in proline accumulation during salt stress have been noticed in a variety of crop species. A positive correlation between magnitude of free proline accumulation and salt tolerance has been suggested as an index for determines salt tolreance potentials between cultivars (Madan *et al.*, 1995; Ramanjulu & Sudhakar, 2001). In contrast, it has been also reported that the salt sensitive cultivars accumulated significantly higher levels of proline compared to the tolerant ones (Lutts *et al.*, 1999; Vaidyanathan *et al.*, 2003). In this paper, we report on a positive correlation between compatible solute accumulation and salt tolerance in rice genotypes. There were striking differences in superoxide dismutase activity between the two cultivars with increasing salt concentration (Fig. 5). SOD activity in leaves of Ilpumbyeo could observe no remarkable change during salt treatment. However, SOD activity in Gancheokbyeo rapidly declined on 3rd day regardless of salt concentration treated, whereas its activity at 50 mM NaCl resulted in a sudden elevation on 9th day. CAT activity showed a gradual increase in both genotypes, though was higher in Gancheokbyeo. It was supposed that salinity have a direct effect and, particularly, higher NaCl concentration seemed to trigger the activation of catalase. Like catalase, POD activity increased with an increase of NaCl concentration in both genotypes. For Ilpumbyeo, POD showed very sensitive responses at the intial period of NaCl treatment, and then slowly decreased. Contrary to Ilpumbyeo, POD in Gancheokbyeo bluntly responded on salt stress. These results are in good agreement with those of Shalata *et al.* (2001) who found that SOD and CAT activities decreased in roots of a salt-sensitive tomato cultivar but increased in roots of a salt-tolerant tomato cultivar under salt stress. Singha & Choudhuri (1990) reported that H_2O_2 accumulation in the leaves of *Vigna* and *Oryza* seedlings under salinity stress was related to a decrease in CAT activity. Their results are consistent with ours in that with increased salinity, there was an increase in peroxidase activity in leaves irrespective of salt resistance. Peroxidases are involved not only in scavenging of H_2O_2 produced in chloroplasts but also in growth and developmental processes (Dionisio-Sese & Tobita, 1998). Mittal & Dubey (1991) compared two sets of rice cultivars differing in salt tolerance to determine a possible correlation between peroxidase activity and salt tolerance of rice cvs. Increase CAT activities have promoted H_2O_2 decomposition in both rice leaves, which could result in a Haber-weiss reaction to form hydroxyl radicals (Bowler *et al.*, 1992).

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