Response of Two Indica Rice Varieties to Salt Stress

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Abstract

Salinity is one of the most challenging problems that adversely affects growth and development of plants. Therefore, understanding of the mechanisms that enable plants to adapt to salinity stress will ultimately help in the selection of stress tolerant cultivars for exploiting saline soils. The main objective of this study was to examine the effects of NaCl on some physiological and biochemical characteristics of two rice varieties, IR29 (salt sensitive) and FL485 (salt tolerant), exhibiting different sensitivities to NaCl. NaCl induced a progressive increment in Na^+ concentration of both cultivars, however, it was more marked in the sensitive cultivar IR29. A higher level of sugar and a delay in chlorophyll degradation together with less chlorophyll degradation were observed in the salt tolerant rice. Salt stress may promote sugar accumulation, thus preventing the degradation of chlorophyll. Salinity stress induced an accumulation of starch in cv. FL485. It is possible that adjusted carbon partitioning could have an important implication on salinity tolerance. It is suggested that allocation of sugars into starch may involve in salinity tolerance by avoiding metabolic alteration.

Keywords: Chlorophyll degradation; *Oriza sativa*; Salinity**;** Starch

Introduction

Increasing salinization of agricultural lands is one of the major challenges facing modern agriculture (Kronzucker *et al.* 2008). Considerable progress was made in recent years in understanding of the physiological bases of salt tolerance in rice and in developing salt tolerant genotypes (Ismail *et al.* 2007; Thomson *et al.* 2010). Salt stress injury in rice is mostly caused by the accumulation of Na^+ (Munns and Tester 2008). In rice, substantial variation in uptake and accumulation of sodium between genotypes was repeatedly observed, and tolerant genotypes tend to accumulate less sodium and maintain higher ratios of K^+/Na^+ and Ca^{2+}/Na^+ in plant tissues under salt stress (Ismail *et al.* 2007; Munns and Tester 2008). At the cellular level, plants cope with salinity by osmotic adjustment involving vacuolar sequestration of ions and synthesis of compatible solutes in the cytoplasm (Yancey *et al*. 1982; Garg *et al*. 2002). According

to Cram (1976), sugars contribute up to 50% of the total osmotic potential in glycophytes subject to saline conditions. These compatible solutes, play central roles in the biosynthetic pathways of primary and secondary metabolites, as building blocks of macromolecules, in the control of developmental processes (Gibson 2000; Smeekens 2000; Price *et al.* 2004) and in salt defense mechanisms (Khelil *et al.* 2007; Morsy *et al.* 2007). Under most abiotic stresses, the ability of plants to recover from stress normally increase with increasing concentrations of photosynthetic assimilates in plant tissues during or after stress (Bagheri and Sadeghipour 2009; Naureen and Naqvi 2010). Soluble carbohydrates and starch, which accumulates under normal conditions before the stress, commonly constitute the main resources for plants to supply energy during stress condition, as well as during recovery (Khelil *et al.* 2007). Therefore, higher concentration of carbohydrates

in plant tissue is one of the important adaptive mechanisms as observed under salinity (Khelil *et al*. 2007; Morsy *et al.* 2007; Saeedipour 2014). The objective of this study was to evaluate rice genotypes for physiological characters, emphasizing ion selectivity and sugar accumulation, between two rice cultivars differing in salt tolerance.

Material and methods

Plant materials, growth conditions and stress treatments

Two rice cultivars contrasting in tolerance of salt stress during reproductive stages (Moradi et al. 2003) were selected for this investigation. FL485 is breeding line tolerant of salt stress at both the seedling and reproductive stages, and IR29 is a cultivar sensitive to salt stress during both stages and is commonly used as a sensitive check in breeding nurseries. Salt stress starting at about 10–7 d before panicle initiation and continuing through harvest. The experiment was carried out in a greenhouse with temperature in the range of about 25 to 35 ^{0}C and light intensity in the range of 600–1000 mmol m^{-2} s^{-1}and with 20 pots per cultivar in each replication. Pre-germinated seeds were sown in 1 L perforated plastic pots filled with fertilized (50 N, 25 P and 25 K mg kg^{-1}) Maahas clay soil (43 % clay, 44 % silt and 13 % sand; pH 5.9; Tirol-Padre and Ladha 2004) and were kept in concrete tanks filled with tap water. The level of water was maintained at 3 cm below the soil surface for 2 d. Five seeds of each of the two cultivars were sown in each pot, thinned to one seedling 2 weeks later, and the water level was raised to about 1–2 cm above the soil surface. When the seedlings were 28

d old, water was siphoned out and the pots were drained for 12 h, then flooded with tap water (control) or with a saline solution with EC of 3 dS m^{-1} using NaCl for 3 d, then increased progressively to 4 and 5 dSm^{-1} at 3 d intervals, and finally stabilized at 6+0.3 dS m^{-1} through harvesting. The pots were kept flooded thereafter for the duration of the experiment, and the EC of the water was monitored daily and adjusted when necessary using NaCl and tap water.

Sampling

All parameters were measured on flag leaves of the first two tillers that were tagged 25 d after sowing. Sampling of the flag leaves were removed from anthesis up to full grain maturity at 7 days interval for the various biochemical analyses. For the biochemical assays, samples were cut into small pieces after measuring their fresh weight, frozen in liquid nitrogen, and stored at -80 ^{0}C. Three replicates were maintained for all measurements. The various plant parts were dried in oven at 80 ^{0}C for dry matter analyses and various estimations.

Determination of Na$^+$and K$^+$

Known weight of dried samples were ground to a fine powder and about 0.1 g was transferred to a test tube containing 10 mL of 0.1 N acetic acid, and heated in a water bath at 80 ^{0}C for 2 h. The extracted tissue was cooled at room temperature and left overnight, and then filtered using Whitman filter paper number 40. Sodium and potassium concentrations were then determined using an atomic absorption spectrometer (Perkins Elmer, Norwalk, CT, USA) (Gadallah 1999).

Concentration of starch and soluble sugars

A modified colorimetric method was used for analysis of starch and soluble sugar concentrations (Thakur and Sharma, 2005; Dkhil and Denden 2010). Plant tissues were homogenized in an ice-cold mortar and pestle in a volume of 16 ml 80% (v/v) ethanol. The homogenates were centrifuged at 3000×g, for 10 min at 4°C, and then perchloric acid (HClO$_4$, 6 ml, 30%, v/v) was added to dissolve starch from the pellet. Samples of 0.5 ml starch solution were mixed with 0.5 ml I$_2$-KI reagent, 1 ml 30% (v/v) perchloric acid and vortexed, and then the absorbance of the samples at 620 nm wavelength was then determined using a spectrophotometer. Reducing sugars were determined in the water-soluble fraction, by HPLC (Merck Hitachi). Samples were passed through a Sep-Pak C18 cartridge, preconditioned with methanol (4 ml) and water (10 ml), to remove interfering compounds (Navarro, Martinez, & Carvajal, 2000). The first 2 ml of sample were discarded and the next 1 ml was used for analysis, after filtration through a 0.45-µm Millipore filter. The mobile phase was acetonitrile:water (85:15), with a flow rate of 0.9 ml min^{-1}.

Statistical analysis

The experiment was designed as 2×2×4 (Cultivars × Salinity and Time, respectively) factorials in Completely Randomized Design (CRD) with three replicates. The main effect of factors and their interaction were evaluated by analysis of variance (ANOVA) using IRRISTAT version 92 (IRRI, 1992). The comparison of treatment means was made by least significant difference (LSD) at p= 0.05.

Results

Effect of salinity on Na$^+$, K$^+$ uptake and Chlorophyll content

The interaction among treatments was significant in regard to Na$^+$, K$^+$ and Chlorophyll content (Table1). Na$^+$ content in the salt-stressed leaves was directly related to salt exposure times (Fig. 1). NaCl induced a progressive increment in Na$^+$ concentration of salt-sensitive and tolerant one which was more marked in sensitive cultivar IR29. Salt-stressed IR29 showed a slow initial increase of Na$^+$ reaching a maximum up to 21 days, and then showed a pronounced increment, reaching to value of 5.37 mg g^{-1}DW until the end of the experiment. By contrast, in salt-tolerant FL485 Na$^+$ content showed a rapid increase until the 7 day and then slowly decreased up to 14 days reaching a value of 3.04 mg g^{-1}DW. After that, Na$^+$ content showed a gradual increment until the end of the experiment. Opposite to that observed in Na$^+$ salt-stressed leaves of the cultivars, the K$^+$ concentration sharply decreased during all stages of sampling to compare those control treatment in both cultivars (Fig. 1). A trend of changing pattern was similar in both cultivars and under both regime, as slow increment took place up to 7 days, and then gradually decreased up to 14 days. From this point onwards, K$^+$ content showed a progressive rising until the end of the experiment.

Chlorophyll content is often measured in plants in order to assess the impact of environmental stress, as changes in pigment content are linked to visual symptoms of plant illness and photosynthetic productivity. Data in Fig. 1 indicate that the contents of chlorophyll a and chlorophyll b in flag leaves of both cultivars

Table 1: Analysis variance of data for different physiological attributes of two rice (Oriza sativa L.) cultivars subjected to salinity 6 dSm-1 or control during reproductive stage.

Variation source	Degree freedom	Na+	K+	Chl a	Chl b	Soluble sugars	Glucose	Fructose	Sucrose	Starch
Rep.	2	ns	ns	ns	ns	ns	ns	ns	ns	ns
Cultivar A)	1	×	××	××	××	××	××	××	ns	××
Salinity (B)	1	××	ns	××	××	ns	ns	×	×	××
Time (C)	3	××	ns	×	××	×	ns	×	×	××
A×B	1	×	×	ns	ns	××	ns	×	×	××
A×C	3	ns	ns	×	××	ns	ns	ns	ns	ns
B×C	3	×	ns	××	××	××	ns	×	×	××
A×B×C	3	×	×	××	××	××	ns	×	×	××
Error	30	0.032	6.345	0.001	0.001	0.788	844.14	0.967	829.69	18714.6
CV%		10.84	9.1	4.04	6.39	6.71	7.34	2.47	7.02	8.21

s :Insignificant, ××, ×: Significant differences at the p = 0.01 and 0.05 levels, respectively

decreased under salt stress. However, this decrease was more pronounced in IR29 than FL485 cv. (Fig. 1). On the other hand, Chl $_{a:b}$ ratio was increased markedly on day 14 onwards in IR29 cultivar, represented that the change in pigments composition and the degradation of Chl b at a higher rate than chl a in susceptible cultivar (Fig. 1).

Changes in Soluble Sugars and starch on leaves
The endogenous content of soluble carbohydrates (sucrose, glucose and fructose) and starch was influenced by the treatments (Table1). Soluble sugars and starch showed similar patterns in both salt-stressed and unstressed plant of both cultivars (Fig. 2). Soluble sugar concentration was significantly higher in stressed plant than in unstressed ones (Fig. 2). The highest value, 37.19 mmol g^{-1} DW, was observed on day 21 in FL485 and thereafter remained practically unchanged until the end of the experiment. By contrast, sucrose content of salt-stressed IR29 showed an

initial similar trend, reaching a maximum value of 35.33 mmol g^{-1} up to 21 days. From this point on, sucrose content showed a progressive decrease, since the value reached to 19.49 mmol g^{-1} DW at the end of the experiment (Fig. 2). Results showed that sucrose content was higher in unstressed plants than in salt-stressed ones (Fig. 2). Of interest, in unstressed salt sensitive IR29 and salt tolerant FL485 the content of sucrose was nearly 53.1% and 35.9% more than in stressed ones respectively. In non-stressed plants no significant difference was recorded between cultivars at the end of experiment. NaCl induced a progressive decrease in sucrose concentration of both cultivars which was more marked in salt-sensitive than tolerant one (Fig. 2). Glucose content showed a different pattern between control and treated plants and the highest value was observed in salt-stressed ones. There was a sustained increase up to 7 days in salt-stressed FL485, reaching a maximum value of 750.1 µmol g^{-1} DW. After that, glucose content gradually decreased until the end of the experiment (Fig. 2). Regarding salt-stressed IR29 the glucose

content decreased slowly to the 7 day and then strongly increased until 14 days, reaching a maximum value of 678.43 µmol g^{-1} DW. From this point on, glucose content showed a progressive decrease. From day 14 onward glucose content showed a similar trend in both cultivar and under both regimes (Fig. 2). In the case of the fructose concentration, NaCl induced a progressive decrease which was more marked in salt tolerant

FL485 than salt sensitive cultivar IR29 in compare to those control treatments (Fig. 2). The fructose pattern of salt-stressed FL485 showed an initial increase up to 21 days followed by a gradual decrease reaching a minimum of 71.78 µmol g^{-1} DW at the end of experiment. The fructose level in susceptible cultivar showed to increase at a later exposure time on day 14 and reach to maximum of
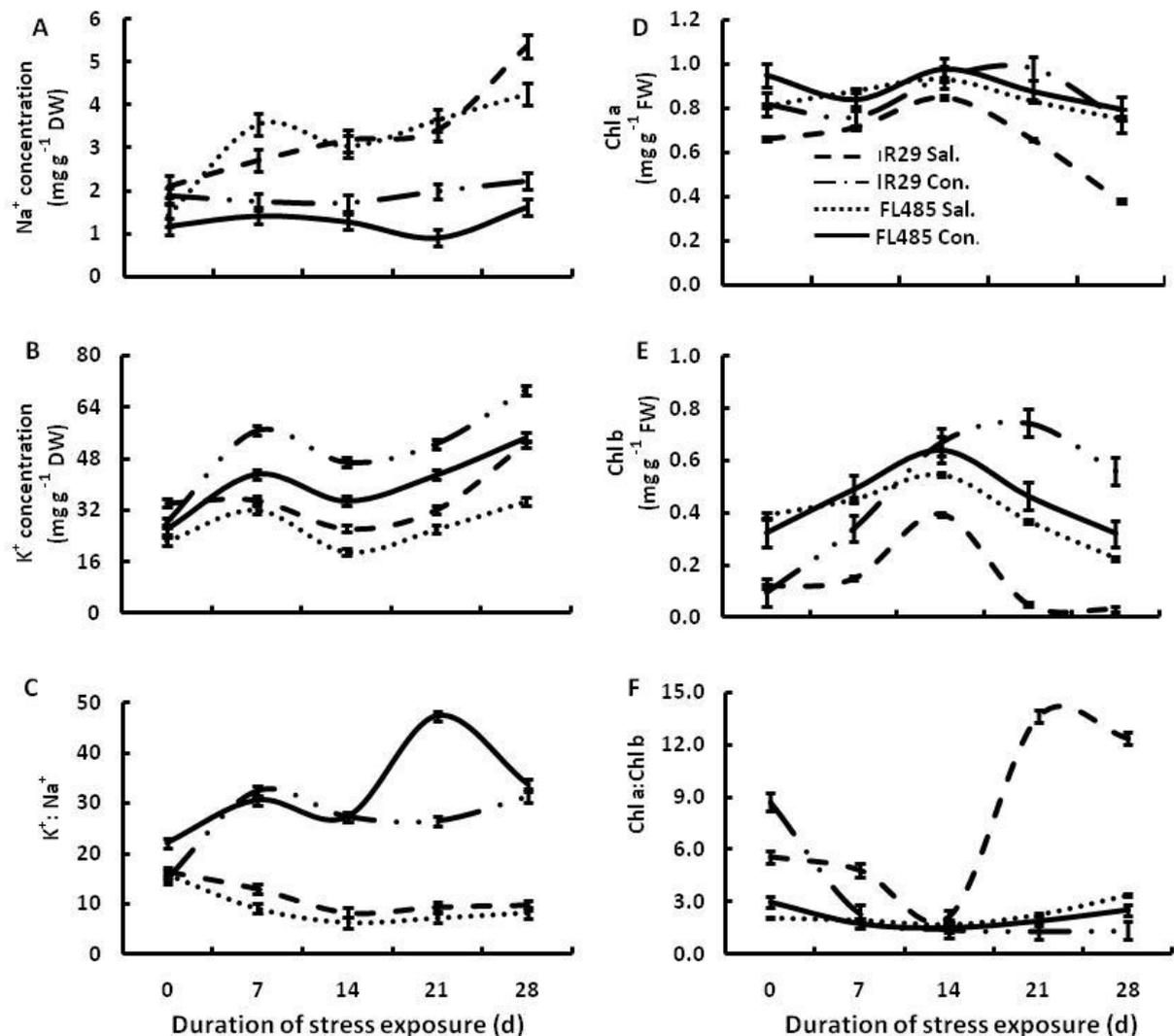

Fig. 1 Changes in concentrations of, Na$^+$ (A), K$^+$ (B), K$^+$:Na$^+$ (C), Chl a (D), Chl b (E), and Chl a:Chl b in control (Con.) and salt-stressed (Sal.) in flag leaf during grain filling in two rice cultivars (Salt-Sensitive cv. IR29 and Salt-Tolerant cv. FL485). Vertical bars represent ± SE of the mean (n=3)

101.35 μmol g^{-1} DW to the end of the experiment (Fig. 2). Opposite to that observed for fructose concentration, the starch content increased in salt stressed tolerant genotype, during all stages of sampling. Starch content of FL485 leaf showed a gradual increment up to 14 days, reaching a maximum value of 3764.3 mmol g^{-1} DW. From this point on, starch content showed a progressive decrease up to 21 days and then increased again until the end of the experiment (Fig. 2). The starch content in salt stressed sensitive genotype IR29 was contrary to that observed in unstressed plant. By contrast, starch content of salt stressed FL485 was 2.4 fold more than salt sensitive IR29 at the end of experiment (Fig. 2).

Discussion

The uptake of Na$^+$ and K$^+$ or the ratio of K$^+$/Na$^+$ have been associated with salinity tolerance in some plant species (Dasgan and Koc 2009; Azadi et al. 2011). The tolerant wheat genotypes maintained low Na$^+$ and high K$^+$ and high K$^+$/Na$^+$ in the leaf blade (Munns et al. 2000). However, concentration of Na$^+$ and K$^+$ were not associated with the degree of salinity tolerance in other species (Munns and James 2003). Our results indicated that K$^+$/Na$^+$ may not well represent salinity tolerance. However, the tolerant FL485 had less accumulation of Na$^+$ under salinity, compared to the sensitive IR29, suggesting that avoiding excessive accumulation of Na$^+$ or tolerance to accumulated Na$^+$ facilitated salinity tolerance in rice plant. The inconsistent results of salinity tolerance in relation to K$^+$ or Na$^+$ accumulation found in different studies may be due to variations of salinity level, duration, species or

cultivars (Marcar, 1987; Munns and James, 2003). Plants often accumulate carbohydrates under salinity stress (Heidari and Jamshid 2010; Nemati et al. 2011). Accumulation of sugars has been associated with drought and salinity tolerant responses in many species. It is generally accepted that the increase in cellular osmolarity which results is accompanied by the influx of water into, or at least a reduced efflux from cell, thus providing the turgor necessary for cell expansion. In the present study, increased concentration of soluble sugars in response to salinity stress were found in both salt-sensitive and tolerant one. The high sugars accumulation observed in salt-treated plants, principally in salt-tolerant one, could imply that the metabolic carbon flux was mainly used for sugar accumulation, necessary to counteract the osmotic imbalance imposed by salt (Fig. 2). In agreement with this assumption in unstressed plants, sugar content was significantly lower than in salt-stressed ones. On the other hand, the relatively high glucose observed between 0 and 7 days in salt-stressed FL485 could be explained by a higher demand of soluble sugars for osmotic adjustment (Fig. 2). Rosa et al. (2004) have demonstrated that saline stress induces accumulation of glucose rather than fructose in embryonic axes of quinoa seedlings. In contrast, salinity tolerance was unrelated to sugar accumulation in cowpea (*Vigna unguiculata*) cultivars (Praxedes et al. 2011) and in salt tolerant and sensitive lines of safflower (*Carthamus tinctorius* L.) (Ashraf and Fatima 1995). Water-soluble carbohydrate also decreased (Zhang et al. 2012) or remained unchanged (Heidari 2012) in plants under salinity stress. Dubey and Singh

(1999) also reported that the sugar contents increased more in the sensitive than in the tolerant rice cultivars. In tomato, salt-sensitive cultivar was able to accumulate hexoses and sucrose under salinity stress while their concentration remained unchanged or decreased in salt-tolerant cultivar

(Balibrea et al. 2000). It is worth noting that the increment of total sugars was unrelated with fructose, glucose and sucrose concentration. Therefore, present results agreed with the previous reports on the differences in sugar accumulation in
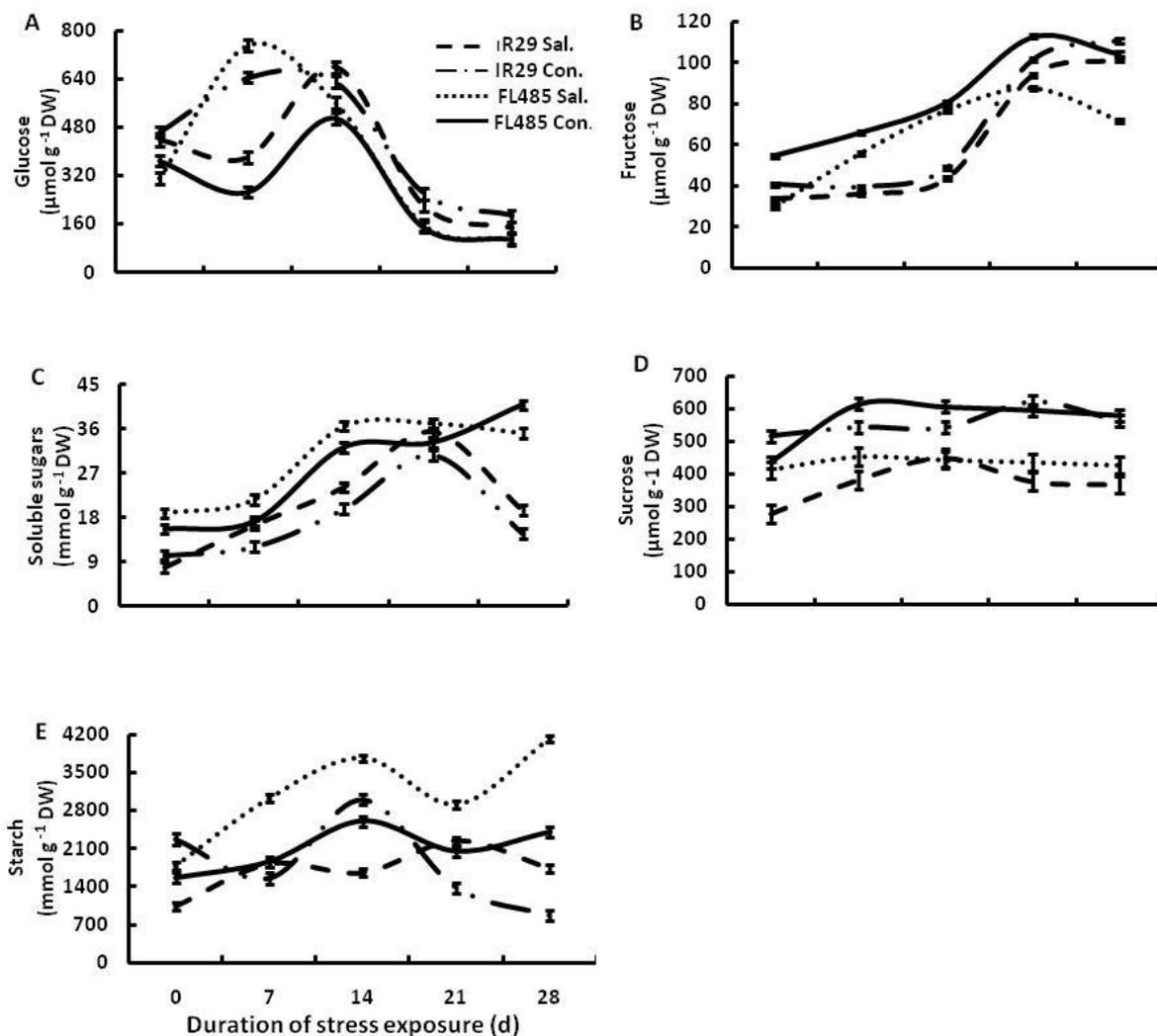

Fig.2 Changes in concentrations of nonstructural carbohydrates, Glucose (A), Fructose (B), Total Soluble sugars (C), Sucrose (D), and Starch (E), in control (Con.) and salt-stressed (Sal.) in flag leaf during grain filling in two rice cultivars (Salt-Sensitive cv. IR29 and Salt-Tolerant cv. FL485). Vertical bars represent ± SE of the mean (n=3)

Cultivars differing in salt tolerance which may explain tolerance differences between these cultivars and may provide detail about the sugar

components possibly involved in salt tolerance. Starch accumulate in leaves as a temporary reserve form of carbon in the leaves and is the principal

component of dry mass accumulated in mature leaves, whereas sucrose is transported to different organs it is used by plants. During periods of active photosynthesis, excess carbohydrates produced are temporarily stored as starch in the leaves for subsequent remobilization to other developing tissue when there is little or no photosynthesis (Basu and Minhas, 1991; Lorenzen and Ewing, 1992). Opposite to that observed in sucrose leaf concentration, starch accumulation was noticed in salt-tolerant cultivar exposed to stress. Starch accumulation perhaps resulted from the increased activity of alkaline invertase activity which hydrolyzes sucrose and convert into simpler sugars. Starch maybe synthesized from such sugars. High starch accumulation in mature leaves of salt-tolerant cultivar of tomato was reported earlier (Balibrea et al. 2000). Although starch may not play a crucial role in salt-tolerant mechanism, it was suggested that the ability of plant to partition sugars into starch may help to avoid metabolic alterations by lowering feedback inhibition caused by excess amount of sucrose in cytoplasm (Krapp and Stitt 1995). Thus, starch synthesis may be a reflection of the need to produce an internal metabolic sink for soluble sugars in the leaves. It has also been suggested that starch synthesis in cotyledons can represent the formation of a secondary pool of carbon to prevent the increase of sugar concentrations to inhibitory levels (Santos and Buckeridge 2004).

Leaf yellowing is the first step in senescence associated programmed cell death. The most convenient assay for the chloroplast senescence is the measurement of chlorophyll loss. In leaves exposed to stress not only was the chlorophyll a content drastically reduced, but the $Chl_{a:b}$ ratio increased showing that chl b was degraded at a higher rate than chl a (Fig. 1). This can be explained by the fact that the first step in chlb degradation involves its conversion to chl a (Fang et al. 1998). The increase in the ratio of $Chl_{a:b}$ has been linked with the change in pigment composition of photosynthetic apparatus that possesses lower levels of light harvesting chlorophyll proteins; LHCPs (Loggini et al. 1999).

Conclusion

In summary, salinity stress alters carbohydrate metabolism differently in salt-tolerant and salt-sensitive rice cultivars. Salinity stress induced accumulation of total sugars in leaves of both cultivars without a concomitant increase in glucose, fructose and sucrose concentration. Therefore, it is suggested that accumulation of total sugars related to other sugar component involved in salt tolerance. On the other hand, starch concentration increased markedly in salt-tolerant cultivar when grown under salinity stress. Probably, starch accumulation may play a role in salt-tolerant cultivar, it is possible that adjusted carbon partitioning and allocation could have an important implication on the overall plant growth under salinity.

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