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Original Research Paper

Starch Metabolism During Leaf Senescence in Two Rice Varieties on Exposure to Aluminium

M. Muthukumaran and A. Vijaya Bhaskara Rao
Department of Ecology and Environmental Sciences, Pondicherry University, Puducherry-605014, India

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ABSTRACT

Rice *(Oryza sativa)* is an important food crop in India as well as in other Asian countries. It is well known that compounds of heavy metals are known to harm land plants, and plant parts and aluminium is one such an element causing toxic effects in plants particularly in plant growing in marshy and acidic soils. Senescence is characterized by the results of many sequential molecular events and these are influenced by biotic and abiotic factors. The present study was carried out systematically on the toxic effects of aluminium in the detached rice leaves during leaf senescence with reference to starch metabolism and its associated enzymes. In our study reducing and non-reducing sugars were increased and starch content decreased. Significant increases were observed in reducing and non-reducing sugars and their associated enzymes such as starch phosphorylase and sucrose synthase in both Aduthurai 43 (ADT-43) and Pro Agro 6129 (PA 6129) varieties and decreased activity of α-amylase was observed with the increasing periods of exposure and increasing concentration of aluminium in leaves of rice varieties in detached leaves during leaf senescence. However, the shifts in the non-reducing sugars were greater in ADT 43, when compared to PA 6129. The shifted carbon partitioning from non-soluble carbohydrate to soluble carbohydrates significantly contributed to osmotic adjustment in ADT 43 and it indicates that it is tolerant to aluminium toxicity.

INTRODUCTION

Rice (*Oryza sativa.* L) is an important crop in India. It is well known that compounds of heavy metals are known to harm land plants, and plant parts. The components of earth's crust were utilized by various industries, which release toxic substances and are harmful to biota (Ferguson 1990). Many trace metals act as essential micronutrients in higher plants and animals, however, some heavy metals create adverse effects at minor level (Alloway 1995). It is well known that aluminium is a major environmental pollutant and is highly phytotoxic, affecting plant growth and yield (Delhaize & Ryan 1995, Bose et al. 2011, Krstic et al. 2012). The concentrations of soluble sugars particularly non-reducing sugars were increased significantly with the increasing leaf age on exposure to aluminium (Pallavi & Dubey 2008, Balakumar et al. 1992). Aluminium is widely distributed in plants, particularly in vegetation in marshy places and acid soils (Ernest 1972). Aluminium is present in air samples; roadsides sample dusts and water (Rahn 1976). The source of aluminium includes all rocks; particularly igneous rocks contain aluminium in the form of aluminium silicate minerals. Aluminium is one of the heavy metals, widely distributed in environment. It is a problem in plants, particularly in vegetation in marshy places and acid soils affecting plant growth and yield. Carbohydrate metabolism plays an important role in the physiology of a plant. The levels of starch were decreased correspondingly with a decrease in photosynthesis activity on exposure to aluminium (James et al. 1990). Industrialization of 20th century formed the pollution of air, water and soil, which play major global negative impact on the agriculture. Rice is cultivated in almost all the states of India and is used as staple food, hay for cattle feed, and straw for making strawboards, paper and mats. In our studies, two important rice varieties were selected for aluminium toxicity studies. The variety ADT 43 crop cultivation period is 115 days and yields in 7.0 t/ha with medium slender size, seed grains of 1000 having weight of 15.5g. In addition to that ADT 43 was identified as more susceptible crop than seven other high yielding varieties (Radhakrishnan & Ramaraju 2009). Hybrid PA 6129 varieties were selected for studies related to good irrigated, resistant to blast, brown spot diseases from various pests and recommend for irrigated areas of Punjab and Tamil Nadu. Hence, carbohydrates such as starch, reducing sugars and non-reducing sugars and its associated hydrolysing enzymes were studied to know the impact of aluminium during senescence of detached rice leaves.

MATERIALS AND METHODS

Rice (*Oryza sativa*. L) seeds of varieties ADT 43 and PA 6129 were procured from PKKVK, Pondicherry district, India, and plants were grown in field conditions. Leaves from 8 weeks old rice plants were used for further studies. Seven cm leaf bits from fully expanded and matured leaves were

washed in distilled water, and surface sterilized with 0.1 per cent mercuric chloride solution for 30 seconds, then washed again with distilled water. Four leaf bits were placed in each Petri dish of 20 cm diameter, containing distilled water as control and aluminium solutions at different concentrations (100µM, 200µM, 300µM) as treated. Six Petri dishes were placed for each concentration of aluminium. Petri dishes were kept under light intensity of approximately 150wm^{-2} and temperature of 27 ± 3°C, the solutions were replaced with fresh one. The samples were estimated for starch metabolism studies at 48, 96, 144, 192 hrs of incubation. The exposed leaf materials were taken for starch estimation by following the method of McCready et al. (1950). The reducing sugars were estimated by Nelson's method (1944) as modified by Somogyi (1952). From the alcoholic extract the non-reducing sugars were estimated by the method of Scott (1960). Starch phosphorylase activity was estimated according to the method of Fiske Subbarow (1925). The sucrose phosphate synthase was extracted by the method of Hubbard et al. (1989) and was assayed according to Miron & Schaffer (1991). Finally, the resulting sucrose formed during reaction catalysed by sucrose phosphate synthase was estimated according to the method of Vassey et al. (1991). α-amylase activity was measured in the leaves of control and aluminium stressed leaf bits according to the method of Sridhar & Ou (1972). All the data obtained per each parameter was analysed for their significance according to the method of Duncans's multiple range test (Duncan 1955). The significance was calculated at 5% level ($P<0.05$).

RESULTS

In the present study the effect of aluminium on some aspects of carbohydrate metabolism during rice leaf senescence was studied. From the data presented in Table 1, it was observed that related to controls, the starch content was decreased in the senescing rice leaves on exposure to aluminium in two rice varieties. In PA 6129 variety the starch content was decreased in the rice leaf with an increase in concentrations of aluminium and period of exposures. ADT 43 also exhibited similar decrease in starch levels with an increase in aluminium concentration and exposure periods. The magnitude of decline in starch content was comparatively more in PA 6129 rice variety than in ADT 43 variety. Reducing sugars levels in the leaves are presented in Table 2; the reducing sugar content was significantly increased in all concentrations of aluminium. The significant increase was also observed in ADT 43 variety in all concentrations and at all exposure periods. However, the percent increase in the reducing sugar levels was relatively more in the variety ADT 43 than in PA 6129 at all concentrations of aluminium and at all periods of exposure. The estimated non-reducing sugars levels in the leaves are presented in Table 3. The non-reducing sugar levels were significantly increased in all aluminium concentrations and periods of exposure. In PA 6129 variety, the non-reducing sugars levels were significantly increased at all aluminium exposure periods. A similar trend was also observed in ADT 43 in the all concentrations of aluminium exposures. It was observed that the degree of increase was dependent on the concentrations and exposure period. The shifts in the non-reducing sugars were greater in ADT 43 than in PA 6129. Relating to the starch hydrolysing enzymes, from the Table 4, it is observed that the levels of starch phosphorylase increased significantly with increasing period of exposure and concentrations of aluminium. Further, from the Table 5, it is noticed that sucrose phosphate activity was also increased with increasing period of exposure and concentrations of aluminium. However, from the Table 6 it is seen that the α-amylase was decreased in both ADT 43 and PA 6129 and the degree of decrease was dependent on concentrations and exposure periods.

DISCUSSION

Senescence is programmed changes in many metabolic and morphological aspects of flora. Such senescence can be induced by various environmental stresses and aluminium is one of the environmental stresses. Metabolism of starch and sugars are influenced by a variety of stressful conditions. Starch is a high molecular weight polysaccharide and the chief storage carbohydrate in higher plants consisting of about 80 % water soluble amylopectin and 20% water soluble amylose. In plant metabolism the starch first appears as an assimilation product in chloroplasts. It is then degraded, the products of degradation are translocated and starch is resynthesized as storage starch in storage organs. Further sugars such as reducing sugars, non-reducing sugars and their associated hydrolysing enzymes play an important role during plant metabolism and development. Acid invertase or sucrose synthase (Pfeiffer & Kutschera 1996) enzymes involve in sucrose breakdown. Starch phosphorylase breaks down the starch molecule at non-reducing end. In the present study a decrease in the starch content and an increase in sugar levels in the two varieties of rice was observed at all exposure periods and at different concentrations of aluminium. The increased sucrose phosphate synthase activity was correlated with significant increasing levels of non-reducing sugars. The results demonstrate that the increased hydrolysis of starch and increased carbon mobilization were attributed to the enhanced starch phosphorylase and the significant increase in the activity of sucrose phosphate synthase. However, in our study it was found that the activity of α-amylase enzyme which is also a starch hydrolysing enzyme was decreased. In spite of the decline in the α-amylase the

Table 1: Starch (mg/g dry wt.) in the leaves of rice verities of control and on exposure to different concentrations of aluminum at 24, 48, 72 and 96 hours.

Exposure	ADT 43				PA 6129			
periods (hrs)	Control	100µM	200µM	300µM	Control	100µM	200µM	300µM
24	52.406^{a}	48.611^{b}± 0.17 (-0.724)	49.197^{c}±0.14 (-6.123)	44.833^{d}±0.11 (-14.450)	54.496^{a}	49.595^{b}±0.15 (-8.992)	48.988^{c}±0.12 (-10.107)	46.421^{d}±0.04 (-14.816)
48	56.934^{a}	53.421^{b}±0.15 (-6.710)	48.359^{c}±0.11 (-15.061)	44.386^{d}±0.09 (-22.039)	56.231^{a}	51.940^{b}±0.09 (-7.631)	44.180^{c}±0.01 (-21.431)	40.238^{d}±0.17 (-28.440)
72	59.610^{a}	52.813^{b}±0.05 (-11.402)	45.579^{c}± 0.09 (-23.538)	39.506^{d}±0.02 (-33.725)	59.423^{a}	51.296^{b}±0.01 (-13.675)	42.220^{c}±0.17 (-28.950)	33.520^{d}±0.11 (-43.590)
96	64.672^{a}	49.164^{b}±0.11 (-23.625)	41.588^{c}±0.04 (-35.394)	35.127^{d}±0.09 (-45.431)	64.890^{a}	50.623^{b}±0.04 (-21.985)	43.203^{c}±0.05 (-33.421)	28.148^{d}±0.06 (-56.621)

Each value is a mean of six replicates estimations; Percent decrease / increase over control is given in parentheses.
Means within a row followed by the same letter are not significantly different (P>0.05) from each other according to Duncan's multiple range tests.

Table 2: Reducing sugar (mg/g dry wt.) in the leaves of rice varieties of control and on exposure to different concentrations of aluminum at 24, 48, 72 and 96 hours.

Exposure	ADT 43				PA 6129			
periods (hrs)	Control	100µM	200µM	300µM	Control	100µM	200µM	300µM
24	6.294^{a}	7.239^{b}±0.02 (+13.140)	8.089^{c}± 0.03 (+16.654)	8.957^{d}±0.05 (+30.435)	6.083^{a}	7.812^{b}±0.11 (+12.270)	9.265^{c}±0.05 (+36.150)	9.981^{d}±0.02 (+47.923)
48	6.350^{a}	9.108^{b}±0.12 (+18.511)	9.353^{c}±0.05 (+22.355)	9.741^{d}± 0.09 (+28.470)	6.542^{a}	8.861^{b}±0.02 (+21.425)	10.351^{c}± 0.05 (+44.217)	12.756^{d}±0.05 (+80.269)
72	7.911^{a}	10.068^{b}±0.16 (+20.455)	10.723^{c}± 0.13 (+28.730)	11.074^{d}±0.07 (+33.175)	7.821^{a}	10.505^{b}±0.06 (+33.907)	14.474^{c}±0.15 (+84.315)	15.503^{d}± 0.09 (+97.815)
96	8.235^{a}	10.994^{b}±0.11 (+24.639)	11.574^{c}±0.04 (+31.681)	12.852^{d}±0.15 (+47.207)	8.321^{a}	11.821^{b}±0.16 (+43.111)	15.811^{c}±0.07 (+91.106)	18.244^{d}±0.15 (+120.375)

Each value is a mean of six replicates estimations; Percent decrease / increase over control is given in parentheses.
Means within a row followed by the same letter are not significantly different (P>0.05) from each other according to Duncan's multiple range tests.

enhanced activities of starch phosphorylase and sucrose phosphate synthase activities contributed the higher concentrations of soluble sugars particularly non-reducing sugars increased significantly with the increasing leaf age during leaf senescence on exposure to aluminium stress. Probably, the accumulated soluble sugars might have inhibited the amylase expression in feedback mechanism. In support of our results, earlier researchers exhibited that glucose and fructose exert a repression on the α-amylase synthesis similar to that of sucrose and also explained that the induction of α-amylase synthesis is by carbohydrate starvation in suspension cells of rice (Yu et al. 1991, 1992). In support of our results, earlier researchers exhibited that glucose and fructose exert a repression on the α-amylase synthesis similar to that of sucrose and also explained that the induction of α-amylase synthesis is by carbohydrate starvation in suspension cells of rice (Yu et al. 1992). Dubey & Singh (1999) exhibited that under salinity stress the starch contents in roots decreased whereas the content of reducing and non- reducing sugars and the activities of sucrose phosphate synthase increased more in the sensitive rice cultivars.

During stress and in senescing leaves, sugars often accumulate and the accumulation and stress can induce leaf senescence (Wingler & Roitsch 2008). In our study, a decrease in starch levels and an increase in reducing and non-reducing sugar content levels were observed in both senescing rice leaves varieties on exposure to aluminium at different concentrations and at different exposure periods. The degree of decline in starch content was relatively less and the magnitude of elevation of reducing and non-reducing sugars was comparatively more in the variety ADT 43 than in PA 6129. Earlier studies reported that sucrose and hexoses are highly sensitive to environmental stresses and serve as substrate for cellular respiration as well as osmolytes to maintain cell homoeostasis under stress (Gupta & Kaur 2005, Pallavi & Dubey 2008). Further, antioxidant and free radical scavenging properties were also attributed to the accumulated sugars (Greger & Lindberg 1986). Hence, the variety ADT43 that could be able to accumulate relatively higher levels of sugars and could mitigate the oxidative stress more efficiently than the variety PA 6129 which accumulated lesser levels of sugars. A conclusion could be drawn in the present investiga-

Table 3: Non-reducing sugar (mg/g dry wt.) in the leaves of rice verities of control and on exposure to different concentrations of aluminum at 24, 48, 72 and 96 hours.

Exposure	ADT 43				PA 6129			
periods (hrs)	Control	100µM	200µM	300µM	Control	100µM	200µM	300µM
24	28.435[a]	33.657[b]±0.16 (+11.277)	39.082[c]±0.07 (+30.358)	40.579[d]±0.15 (+35.620)	24.519[a]	29.395[b]±0.07 (+16.485)	39.138[c]±0.054 (+56.221)	7.026[d]±0.07 (+88.391)
48	30.562[a]	39.530[b]±0.07 (+22.458)	45.051[c]±0.09 (+40.525)	47.749[d]±0.11 (+49.352)	26.618[a]	35.933[b]±0.07 (+31.395)	46.087[c]±0.05 (+69.545)	57.576[d]±0.07 (+112.705)
72	32.734[a]	44.086[b]±0.07 (+32.79)	53.128[c]±0.05 (+60.412)	57.763[d]±0.07 (+74.571)	30.490[a]	42.792[b]±0.11 (+37.395)	54.341[c]±0.07 (+75.275)	64.135[d]±0.05 (+107.39)
96	34.510[a]	47.656[b]±0.08 (+35.881)	58.615[c]± 0.07 (+67.639)	62.660[d]± 0.03 (+79.361)	33.785[a]	50.557[b]±0.08 (+47.597)	66.374[c]± 0.07 (+94.415)	75.849[d]± 0.03 (+122.461)

Each value is a mean of six replicates estimations; Percent decrease / increase over control is given in parentheses.
Means within a row followed by the same letter are not significantly different (P>0.05) from each other according to Duncan's multiple range tests.

Table 4: Starch phosphorylase (µmol (pi)/mg (protein) s^{-1} in the leaves of rice verities of control and on exposure to different concentrations of aluminum at 24, 48, 72 and 96 hours.

Exposure	ADT 43				PA 6129			
periods (hrs)	Control	100µM	200µM	300µM	Control	100µM	200µM	300µM
24	0.24[a]	0.31[b]±0.08 (+ 29.16)	0.33[c]± 0.04 (+37.5)	0.34[d]± 0.03 (+41.66)	0.37[a]	0.48[b]±0.08 (+29.72)	0.54[c]± 0.07 (+45.94)	0.55[d]± 0.03 (+48.84)
48	0.36[a]	0.47[b]±0.09 (+30.55)	0.52[c]± 0.13 (+48.96)	0.53[d]±0.17 (+47.22)	0.45[a]	0.60[b]±0.04 (+33.33)	0.66[c]±0.12 (+46.66)	0.67[d]±0.09 (+48.88)
72	0.47[a]	0.64[b]±0.09 (+36.17)	0.70[c]±0.13 (+48.93)	0.71[d]±0.17 (+51.06)	0.52[a]	0.71[b]±0.09 (+36.53)	0.77[c]±0.17 (+48.07)	0.80[d]0.01 (+53.84)
96	0.55[a]	0.78[b]±0.08 (+47.16)	0.82[c]±0.13 (+54.7)	0.82[d]±0.06 (+56.48)	0.55[a]	0.81[b]±0.12 (+47.27)	0.82[c]±0.19 (+49.09)	0.87[d]±0.11 (+58.41)

Each value is a mean of six replicates estimations; Percent decrease / increase over control is given in parentheses.
Means within a row followed by the same letter are not significantly different (P>0.05) from each other according to Duncan's multiple range tests.

tion based on sugar accumulation, supporting the aluminium tolerant nature of ADT 43. Further, a better level of reducing sugar content on exposure to aluminium in ADT 43 can also be explained by relatively a better rate of photosynthesis when compared to PA 6129. The variety ADT 43 had maintained relatively better levels of starch, which was due to better photosynthetic efficiency under stress conditions, over the variety PA 6129. The data on starch content also support the relative tolerance of ADT 43. Chaves (1991) reported that increased concentrations of reducing and non-reducing sugars might have resulted from increased starch hydrolysis, synthesis by other pathway or decreased conversion to other products or from a reduced rate of export of sugars from leaf. Increased level of heavy metal like cadmium stress could induce the decreased level of starch and an increase in proline content in ADT 43 (Vijayarengan 2012). Similarly, our findings exhibit that coincident of similar results on aluminium toxicity also when compared with cadmium toxicity.

CONCLUSIONS

The analysis of carbohydrate fractions, especially sugars provide information in the contribution of sugars in osmotic adjustments during aluminium toxicity stress in senescing rice varieties. Reducing and non-reducing sugars increased whereas, the starch content decreased, in the leaves in both rice varieties on exposure to aluminium. Further, the starch hydrolysing enzymes like starch phosphorylase and sucrose phosphate synthase were increased in association with breakdown of starch resulting reducing and non-reducing sugars in senescing rice leaves on exposure to aluminium. Therefore, it is suggested that aluminium enhanced the leaf senescence at faster rate in rice leaves. Since, greater magnifications in reducing and non-reducing sugars were observed in ADT 43, supporting the aluminium tolerant nature, the shifts in carbon partitioning from non-soluble carbohydrate to soluble carbohydrate could greatly contribute to osmotic adjustments in ADT 43 rice variety.

Table 5: Sucrose phosphate synthase (µmol (sucrose)/mg (protein) s^{-1} in the leaves of rice verities of control and on exposure to different concentrations of aluminum at 24, 48, 72 and 96 hours.

Exposure	ADT 43				PA 6129			
periods (hrs)	Control	100µM	200µM	300µM	Control	100µM	200µM	300µM
24	1. 184^{a}	1.542^{b}±0.13 (+ 30.23)	1.612^{c}± 0.22 (+36.14)	1.706^{d}± 0.63 (+44.08)	1.267^{a}	1.666^{b}±0.24 (+31.49)	1.814^{c}± 0.37 (+43.17)	1.933^{d}± 0.61 (+52.56)
48	1.207^{a}	1.626^{b}±0.76 (+34.71)	1.761^{c}± 0.44 (+45.89)	1.789^{d}±0.15 (+48.21)	1.395^{a}	1.903^{b}±0.29 (+36.41)	2.018^{c}±0.42 (+44.65)	2.088^{d}±0.20 (+49.67)
72	1.455^{a}	2.004^{b}±0.39 (+37.73)	2.148^{c}±0.11 (+47.62)	2.220^{d}±0.27 (+52.57)	1.526^{a}	2.127^{b}±0.56 (+39.38)	2.262^{c}±0.17 (+48.23)	2.367^{d}0.54 (+55.11)
96	1.647^{a}	2.439^{b}±0.34 (+48.08)	2.546^{c}±0.15 (+54.58)	2.600^{d}±0.45 (+57.86)	1.655^{a}	2.471^{b}±0.14 (+49.30)	2.527^{c}±0.22 (+52.68)	2.608^{d}±0.61 (+57.58)

Each value is a mean of six replicates estimations; Percent decrease / increase over control is given in parentheses.
Means within a row followed by the same letter are not significantly different (P>0.05) from each other according to Duncan's multiple range tests.

Table 6: α- amylase (µg reducing sugar formed per mg protein min^{-1}) in the leaves of rice varities of control and on exposure to different concentrations of aluminum at 24, 48, 72 and 96 hours.

Exposure	ADT 43				PA 6129			
periods (hrs)	Control	100µM	200µM	300µM	Control	100µM	200µM	300µM
24	2.147^{a}	2.131^{a}±0.09 (-0.745)	2.099^{a}±0.04 (-2.328)	2.140^{a}±0.09 (-2.921)	1.960^{c}	1.944^{b} ±0.04 (-0.816)	1.926^{a}±0.08 (-1.734)	1.920^{a} ±0.07 (-2.040)
48	2.260^{c}	2.154^{b}±0.13 (-4.69)	2.141^{a} ±0.12 (-5.265)	2.112^{a}± 0.13 (-6.548)	2.083^{c}	1.988^{b}± 0.12 (-4.560)	1.965^{a}± 0.06 (-5.664)	1.910^{a} ±0.05 (-8.305)
72	2.642^{c}	2.138^{b}±0.01 (-19.076)	2.078^{a} ±0.06 (-21.347)	1.998^{a} ±0.17 (-24.375)	2.175^{c}	1.726^{b} ±0.07 (-20.464)	2.128^{b}± 0.04 (-21.461)	1.691^{a}± 0.09 (-22.240)
96	2.695^{c}	1.966^{b}±0.14 (-30.50)	1.856**a**±0.11 (-31.856)	1.814^{a}±0.03 (-32.690)	2.228^{c}	1.660^{a}±0.16 (-20.649)	1.749^{b}±0.10 (-21.499)	1.710^{b} ±0.07 (-23.240)

Each value is a mean of six replicates estimations; Percent decrease / increase over control is given in parentheses.
Means within a row followed by the same letter are not significantly different (P>0.05) from each other according to Duncan's multiple range tests.

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