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Salt Stress Causes Acceleration of Purine Catabolism and Inhibition of Pyrimidine Salvage in *Zea mays* Root Tips[1]

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ABSTRACT

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Nucleotide metabolism was studied in apical 5·0 mm root tips of corn plants (*Zea mays* L., cv. Pioneer 3906) hydroponically cultured for 7 d and then salinized for 19 d at a rate calculated to reduce the osmotic potential (ψ_o) of the solutions by 0·1 MPa d^{-1} to a final $\psi_o = -0{\cdot}4$ MPa. Saline treatments with two different molar ratios of Ca^{2+}/Na^+ were employed, viz., 0·03 (2·5 mol m^{-3} $CaCl_2$ + 86·5 mol m^{-3} NaCl) for the NaCl treatment and 0·73 (31·5 mol m^{-3} $CaCl_2$ + 43·1 mol m^{-3} NaCl) for the NaCl + $CaCl_2$ treatment. Both salt treatments reduced root growth by more than 30%. The capacity of roots to provide purine nucleotides either by *de novo* synthesis or by re-utilization of existing bases, e.g. salvage of hypoxanthine to adenine nucleotides, was not affected by either salt treatment. However, catabolism of hypoxanthine was accelerated more than 3·5-fold by both salt treatments, demonstrating an increased capacity for purine catabolism which would shift the normal 1 : 1 ratio of synthesis : degradation of purine nucleotides observed for the roots of healthy control plants to less than 0·2 during salt stress. The ratio of pyrimidine nucleotide synthesis : degradation was also reduced. In this case, the unfavourable shift toward nucleotide degradation resulted because both salt treatments reduced salvage capacity by more than 25%, but had no compensating effect on *de novo* synthesis or catabolism of pyrimidines.

Key words—Salinity, osmotic potential, nucleotide metabolism.

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INTRODUCTION

Salt stress reduces growth and yield of many crop species (Maas and Hoffman, 1977; Maas and Nieman, 1978). This decrease in productivity may be due to ionic effects, changes in

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Abbreviations: ψ_o, osmotic potential; ΣAde, sum of the adenine nucleotides, adenosine, and adenine, obtained by converting the adenine nucleotides and adenosine to adenine by acid hydrolysis at 100 °C; ΣUMP, sum of the total uridine nucleotides converted to UMP by acid hydrolysis at 100 °C.

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osmotic potential resulting in water-deficit stress, or a combination of the two (Bernstein, 1975; Epstein, 1980; Greenway and Munns, 1980). Regardless of the mechanism, salt stress results in an increase in energy expenditure as the plant's metabolic processes work to maintain homeostasis (Ivanovici and Wiebe, 1981). Nucleotides, nucleotide ratios, e.g. adenylate energy charge = ([ATP]+½[ADP])/([ATP]+[ADP]+[AMP],) and sugar nucleotides play an important role in homeostasis, energetics and growth of plants. Previous work by Roberts, Linker, Benoit, Jardetsky, and Nieman (1984) provided evidence that salt stress significantly reduced the pool size of total available nucleotides and sugar nucleotides in the apical root tips of corn plants. In a recent study, Peterson, Nieman, and Clark (1987) identified the specific nucleoside mono-, di-, and triphosphates which were reduced in concentration by salinity. In addition, the latter study demonstrated that UDP-glucose was significantly reduced in apical 5·0 mm root tips excised from salt-stressed corn plants. A smaller pool of available nucleotides during salt stress is consistent with the reduced nucleic acid content observed for citrus rootstocks grown in a saline environment (Kessler and Snir, 1969).

Nucleotide pool size is a function of the rates of synthesis via the *de novo* and salvage pathways which provide nucleotides to the plant cell and the rates of utilization and degradation which remove nucleotides from the pool. In this communication, we report the results of a comparison of the capacity of the roots from healthy control plants (*Zea mays* L. cv. Pioneer 3906) and corn plants salinized for 19 d to synthesize adenine and uridine nucleotides *de novo*. In addition, we measured salvage activity for the re-utilization of purines and pyrimidines in roots grown with and without salt. Utilization of nucleotides was assessed by measuring RNA synthesis. Since catabolism opposes synthesis, we assessed the capacity of salt-stressed corn roots to catabolize hypoxanthine and uridine. Finally, since Maas and Grieve (1986) demonstrated that NaCl salinity causes a sodium-induced calcium deficiency which is relieved by partial replacement of sodium with calcium at iso-osmotic concentrations (Maas and Grieve, 1986), iso-osmotic salt treatments (final $\psi_o = -0{\cdot}4$ MPa) with two different molar ratios of Ca^{2+}/Na^+ (0·03 and 0·73) were employed in this study.

MATERIALS AND METHODS

Chemicals

All radiolabelled chemicals were purchased from ICN Pharmaceuticals, Inc. Liquiscint (liquid scintillation cocktail) was purchased from National Diagnostics. Mineral salts for hydroponic culture were of analytical reagent quality and were purchased from Mallinckrodt and Fisher Scientific Co. All other chemicals were purchased from Sigma Chemical Co.

Determination of radioisotope content

To determine the content of radioisotope, samples were prepared as described in the text. In all cases, the samples (4·0 cm^3 final volume) were subsequently diluted with 13 cm^3 Liquiscint and the activity of radioisotope measured using a Beckman LS 100 liquid scintillation spectrometer.

Plant material

Corn seeds (*Zea mays* L., cv. Pioneer 3906) supplied through the courtesy of Pioneer Hi-Bred International, Inc. were imbibed in vigorously-aerated distilled H_2O for 30 h at room temperature. They were then spread evenly on paper towelling placed in a plastic box (33 cm × 33 cm × 9·5 cm) and moistened with 0·25 mol m^{-3} $CaSO_4$. The covered box was kept in the dark at room temperature for 72 h. After germination, uniform seedlings were placed on cheesecloth supported between two plastic grids with 1·7 cm^2 openings. The seedlings, separated by the grid partitions, were covered with moist vermiculite. The grid assemblies were transferred to the glasshouse and supported over plastic pots containing 28 dm^3 of aerated nutrient solution [2·5 mol m^{-3} $Ca(NO_3)_2$, 3·0 mol m^{-3} KNO_3, 1·5 mol m^{-3} $MgSO_4$, 0·17 mol m^{-3} KH_2PO_4, 0·05 mol m^{-3} Fe (as sodium ferric diethylenetriamine

pentaacetate), 23 mmol m^{-3} H_3BO_3, 5·0 mmol m^{-3} $MnSO_4$, 0·4 mmol m^{-3} $ZnSO_4$, 0·2 mmol m^{-3} $CuSO_4$, and 0·1 mmol m^{-3} H_2MoO_4]. The average maximum and minimum values for glasshouse temperature and relative humidity, respectively, were 37·3 and 22·6 °C and 68·7 and 37·1%. The average total daily photosynthetically active radiation was 46·7 mol m^{-2}. Glasshouse shade screens were not used.

Seven days after germination the seedlings were thinned to 35 per pot. Salination to $-0{\cdot}4$ MPa ψ_o was initiated at a rate of 0·1 MPa d^{-1}. Three treatments included a non-saline control and two saline treatments, both with $\psi_o = -0{\cdot}4$ MPa but one with low calcium (2·5 mol m^{-3} $CaCl_2$ + 86·5 mol m^{-3} NaCl) and one with high calcium (31·5 mol m^{-3} $CaCl_2$ + 43·1 mol m^{-3} NaCl) to prevent sodium-induced calcium deficiency. The pH of the culture solutions was adjusted to pH 5·0 with H_2SO_4 whenever it increased to pH 6·5. All solutions were changed four times during the 26-d culture period. Each treatment was replicated by three pots.

Root growth and cell number

Total root biomass was determined. Apical 5·0 mm root segments were harvested and immersed in 2·0 cm^3 5% chromic acid (w/v) in 1 N HCl and stored at 4 °C. Immediately before counting, the cells were separated by repeatedly forcing the sample through a No. 22 needle. A sample was withdrawn and placed in a Levy-Houser deep well (0·2 mm) counting chamber with a Fuchs-Rosenthal grid. The number of cells in an area 0·2 × 1·0 × 1·0 mm was counted at × 400. Cell number was determined for eight samples for each root tip and six root tips were examined per treatment.

Measurement of de novo *biosynthesis, salvage and catabolism of adenine and uridine nucleotides*

Metabolic activities were assessed routinely in the intact cells of apical 5·0 mm root tips excised 26 d after germination (19 d after salination). Those from the same treatment were pooled and then divided into three samples, each weighing 300 ± 20 mg and containing approximately 40 root tips. In all cases, the root samples were pre-incubated for 2 h at 30 °C in their respective hydroponic culture solutions adjusted to pH 7·4. At the end of the pre-incubation, the nutrient solution was decanted and discarded and the roots were immediately transferred to fresh hydroponic culture solution of the appropriate salinity, adjusted to pH 7·4 and supplemented with the desired radiolabelled precursor and incubated for 3 h at 30 °C. Incorporation is linear for the 3 h incubation period at 30 °C (Lovatt, Albert, and Tremblay, 1979; Lovatt, 1983).

The activities of the pathways for the *de novo* biosynthesis of adenine and uridine nucleotides were assessed by measuring the incorporation of $NaH^{14}CO_3$ (10 mol m^{-3}, 4000 dpm $nmol^{-1}$) into ΣAde or ΣUMP. The 3 h incubation was terminated by injecting 1·0 cm^3 6 N $HClO_4$ into the main chamber of the flask. Unincorporated $NaH^{14}CO_3$ was precipitated as $K_2{}^{14}CO_3$ with KOH on a filter paper wick in a plastic centre well suspended over the main chamber from the stopper sealing the reaction flask. Total adenine nucleotides and adenosine were converted to adenine and total uridine nucleotides were converted to UMP by acid hydrolysis of the acid-soluble fraction at 100 °C for 1 h. [^{14}C]Adenine or [^{14}C]UMP were isolated from the neutralized acid-soluble fraction by cocrystallization with carrier adenine or UMP and recrystallized to a constant specific activity (Lovatt *et al.*, 1979; Lovatt, 1983). The capacity for salvaging preformed purine or pyrimidine bases or nucleotides was assessed by measuring the incorporation of [$^{14}C_8$]hypoxanthine (1·0 mol m^{-3}, 800 dpm $nmol^{-1}$) into ΣAde and of [$^{14}C_2$]uridine (1·0 mol m^{-3}, 800 dpm $nmol^{-1}$) into ΣUMP with total adenine nucleotides and adenosine being converted to adenine and with total uridine nucleotides being converted to UMP by acid hydrolysis and isolated with carrier as in the measurements of *de novo* activity described above (Lovatt *et al.*, 1979; Tomlinson and Lovatt, 1987). RNA synthesis was assessed simultaneously with the salvage of [$^{14}C_2$]uridine. RNA synthesis by root tips was estimated from the incorporation of [$^{14}C_2$]uridine into the acid-insoluble fraction (Cohen and Ennis, 1965). Catabolic activity was measured simultaneously with salvage activity by determining the amount of $^{14}CO_2$ generated from the degradation of [$^{14}C_8$]hypoxanthine or [$^{14}C_2$]uridine; the $^{14}CO_2$ was released upon acidification and precipitated as $K_2{}^{14}CO_3$ in 20% KOH on a filter wick in a plastic centre well suspended from the stopper sealing the reaction flask (Lovatt, Albert, and Tremblay, 1981; Tomlinson and Lovatt, 1987). The uptake of [$^{14}C_8$]hypoxanthine or [$^{14}C_2$]uridine by root tips was also measured simultaneously with catabolism. When precursor uptake was being assessed, roots were immediately removed from the incubation medium at the end of 3 h, rinsed with a copious amount of distilled H_2O, transferred to 4·0 cm^3 distilled H_2O and homogenized. The radioactivity in the homogenate plus the label released as $^{14}CO_2$ equals the total uptake of the precursor.

Statistical analyses

Analysis of variance was used to analyse the effects of salt stress on root weight, cell number, uptake of hypoxanthine and uridine, and RNA synthesis. Statistical Analysis System (Cary, NC) was used to generate l.s.d.'s to test for treatment effects on purine and pyrimidine metabolism.

RESULTS

Purine and pyrimidine metabolism

Salt stress did not significantly affect the capacity of roots for either *de novo* synthesis or salvage of purine nucleotides, but accelerated catabolism 3·5- and 4·0-fold for the two salt treatments, NaCl and NaCl+$CaCl_2$, respectively ($P < 0·05$) (Table 1). Uptake of [$^{14}C_8$]hypoxanthine, which is the sum of the [$^{14}C_8$]hypoxanthine in the root tissue and the $^{14}CO_2$ released by catabolism, was increased to the same degree as catabolism, 3·5- and 4·0-fold by the two salt treatments, respectively ($P < 0·05$) (Table 1). The tissue levels of [$^{14}C_8$]hypoxanthine were similar for root tips from all treatments (Table 1).

TABLE 1. *Purine and pyrimidine metabolism in intact cells of apical 5·0 mm root segments excised from healthy and salt-stressed corn plants*

Means of horizontal rows followed by different letters are significantly different at ($P < 0·05$),[a] ($P < 0·01$),[b] and ($P < 0·001$).[c]

	Treatment		
	Control	−0·4 MPa NaCl	−0·4 MPa NaCl+$CaCl_2$
Biosynthesis *de novo*[b] (nmol $NaH^{14}CO_3$ incorporated into ΣAde or ΣUMP g^{-1} root tips h^{-3})			
Purine	106·2 a	86·7 a	91·2 a
Pyrimidine	13·2 a	24·0 a	17·7 a
Salvage[b] (nmol [$^{14}C_8$]hypoxanthine or [$^{14}C_2$]uridine incorporated into ΣAde or ΣUMP g^{-1} root tips h^{-3})			
Purine	313·5 a	342·9 a	355·5 a
Pyrimidine	191·7 a	145·5 b	134·1 c
Catabolism[b] (nmol [$^{14}CO_2$] generated from [$^{14}C_8$]hypoxanthine or [$^{14}C_2$]uridine g^{-1} root tips h^{-3})			
Purine	582·0 a	2081·7 b	2499·6 c
Pyrimidine	543·0 a	574·2 a	609·6 a
Uptake and tissue retention[a] (nmol [$^{14}C_8$]hypoxanthine or [$^{14}C_2$]uridine g^{-1} root tips h^{-3})			
Purine	172·0 a	178·2 a	161·0 a
Pyrimidine	133·1 a	142·8 a	141·5 a
Total uptake[a]—amount taken up and lost through catabolism, plus amount retained by the tissue (nmol [$^{14}C_8$]hypoxanthine or [$^{14}C_2$]uridine g^{-1} root tips h^{-3})			
Purine	754·8 a	2259·9 b	2660·6 b
Pyrimidine	676·1 a	717·0 a	751·1 a
RNA synthesis[c] (nmol [$^{14}C_2$]uridine incorporated into RNA g^{-1} root tips h^{-3})			
	10·6 a	23·8 b	31·9 c

TABLE 2. *Root biomass per plant and fresh weight and cell number per root tip for healthy and salt-stressed corn plants*

Values are means ± standard errors for 50 root tip weights and 8 cell counts on each of 6 roots per treatment. Values in a column followed by different letters are significantly different ($P < 0.05$).

	Treatment
	Root biomass ± s.e. g^{-1} fr. wt. plant
Control	10·1 ± 0·4 a
−0·4 MPa NaCl	6·6 ± 0·7 b
−0·4 MPa NaCl + $CaCl_2$	6·5 ± 0·3 b
	Root tip fr. wt. ± s.e. mg^{-1} apical 5·0 mm
Control	7·6 ± 0·3 a
−0·4 MPa NaCl	6·8 ± 0·3 a
	Root tip cell number ± s.e. × 10^{-4} apical 5·0 mm
Control	11·17 ± 1·84 a
−0·4 MPa NaCl	9·46 ± 0·96 a
−0·4 MPa NaCl ± $CaCl_2$	8·73 ± 1·17 a

Salt stress influenced pyrimidine metabolism in a different manner. The capacity for catabolism was not significantly affected by salinity, but the provision of pyrimidine nucleotides to salt-stressed root cells was reduced by inhibition of uridine salvage (25% and 30% by the two salt treatments, respectively) ($P < 0.05$) (Table 1). Uptake of [$^{14}C_2$]uridine was not influenced by salinity ($P < 0.05$) (Table 1). Thus, altered uptake does not provide a mechanism to explain inhibition of pyrimidine salvage or the increased incorporation of [$^{14}C_2$]uridine into RNA caused by salt stress ($P < 0.001$) (Table 1). *De novo* biosynthesis of pyrimidine nucleotides was not affected by either salt treatment (Table 1).

Root growth and cell number

NaCl inhibited root growth by 30% ($P < 0.05$) (Table 2). Increasing the Ca^{2+} concentration at the same ψ_o also resulted in a 30% decrease in root biomass ($P < 0.05$) (Table 2) suggesting that inhibition of root growth is an osmotic, rather than a specific ion effect.

The observed changes in nucleotide metabolism, hypoxanthine uptake and RNA synthesis brought about by salinity cannot be explained on the basis of differences in cell number in the excised root tips. Apical 5·0 mm root segments from healthy control plants and salt-stressed plants did not differ significantly in fresh weight ($P < 0.05$) (Table 2). Thus, a 300 mg sample did not contain more roots for one treatment versus another. In addition, the number of cells in apical 5·0 mm root segments from healthy control plants and salt-stressed plants were not significantly different ($P < 0.05$) (Table 2). Hence, a 300 mg sample did not contain more cells for one treatment versus another.

DISCUSSION

Research to determine the actual mechanism by which salinity reduces the supply of nucleotides available to root apices has been minimal. To our knowledge, the present study is the first to investigate the impact of salinity on the pathways of purine and pyrimidine metabolism. The current study was undertaken in an attempt to identify the underlying cause of the smaller pool size and reduced availability of nucleotides in salinized root apices and inhibition of root growth during salt stress. The results provide evidence to suggest that the normal ratio of nucleotide synthesis to degradation observed for root apices of healthy corn

plants may be shifted toward degradation of both purines and pyrimidines in the root tips of salt-stressed plants through increased capacity for purine catabolism and decreased capacity for pyrimidine salvage.

The markedly enhanced capacity of salt-stressed roots to degrade purines may account for the reduction in adenine nucleotide pools observed by Peterson *et al.* (1987) and the decrease in total available nucleotides reported by Roberts *et al.* (1984). It is interesting to note that the significantly increased uptake and catabolism of hypoxanthine in salt-stressed roots was not accompanied by a concomitant increase in the salvage of the purine base. Clearly the metabolism of the roots does not simply reflect substrate availability. This is supported further by the demonstration of inhibition of uridine salvage in salt-stressed root apices despite the fact that uridine uptake remained unperturbed. Any further significance should not be attached to the observed similarity in pool size of [$^{14}C_8$]hypoxanthine or [$^{14}C_2$]uridine in root tips from the three salt treatments as the pools result from exogenous supply of purine and pyrimidine, not endogenous conditions and thus can only be used to assess capacities.

It is tempting to speculate about the relationship between pyrimidine salvage and root growth which were inhibited similarly (30%) by the two salt treatments. A decreased capacity to re-utilize existing pyrimidine bases and nucleotides due to inhibition of uridine salvage would be expected to reduce the pool size of total available nucleotides and to account specifically for the loss in UMP, UDP, UTP, and UDP-glucose observed previously in salt-stressed corn roots by Peterson *et al.* (1987).

Our results suggest a substantial increase in RNA synthesis in corn root tips during salt stress, consistent with recent evidence that salt stress induces the transcription of specific mRNAs in the roots of barley (Ramagopal, 1987) and wheat (Gulick and Dvorak, 1987). However, caution is urged in interpreting the estimates of RNA synthesis in this study. The increased incorporation of [$^{14}C_2$]uridine into RNA in response to salt stress may simply reflect decreased isotope dilution due to the reduced size of the uridine nucleotide pool brought about by salt stress (Peterson *et al.*, 1987). The results provide evidence that the machinery for RNA synthesis is not impaired by salt stress.

In conclusion, salt stress was selective in its effects on cell processes and specifically on nucleotide metabolism. Despite the fact that the two iso-osmotic salt treatments had very different Ca^{2+}/Na^{+} ratios, i.e. 0·03 and 0·73, for each parameter measured the effect of the two treatments were nearly the same. This suggests that the effects of salinity on nucleotide metabolism and growth were more likely to be osmotic than ionic.

The capacity of intact cells of root apices to synthesize purine and pyrimidine nucleotides *de novo* was unaffected. Despite this, the ratio of synthesis : degradation may be shifted during salt stress toward degradation of available nucleotides through acceleration of purine catabolism and reduced capacity for pyrimidine salvage. Whether an increased capacity for purine catabolism or decreased capacity for pyrimidine salvage cause significant perturbations in the pool size of specific purine or pyrimidine nucleotides, which in turn influence growth, is not known, emphasizing the need for further research in this area.

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