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Physiology of Osmoregulation and Cell Composition in Salt Li^+ and Na^+Adaptation of *Nostoc muscorum*

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Abstract: *Adaptation to salt in the cyanobacterium Nostoc muscorum, is composed of a few mechanisms which together lead to the generation of a salt-tolerant cell. The initial mechanism combines a stimulation of photosynthetic activity with the accumulation of sucrose as an osmoregulator. The secondary mechanism involves the adaptation of N_2fixationactivity and protein biosynthesis. Under conditions for photoautotrophic growth, significant Na^+ extrusion was observed 30 min after salt shock. Sucrose accumulation reached a maximum value after 16 hours and Li^+ accumulation reached equilibrium after 40 hours. The final concentrations of Li^+ and $Na^+$and sucrose and glucose inside the 0.6 molar Na^+ and Li^+ grown cells indicate that the inorganic ions and organic ;compatible' solutes are the major osmotic species which account for the adaptation of Nostoc muscorum to $Li^+$and Na^+. Thus, in the present investigation microarray data identifies the genes that represent various functional categories needs more intensive research with genetics and physiology to determine gene functions, their chromosomal organization and their mode of regulation.*

Keywords: Nostoc muscorum

I. INTRODUCTION

N. muscorum are important for the nutrient cycling of carbon and nitrogen within the soil ecosystems in which they are found. The process of fixing atmospheric nitrogen contributes plant-available nitrogen to the soil, improving plant growth (Rogers and Burns, 1994).

Soil salinity is an important factor that induces diverse alterations in the growth, photosynthesis, biochemical and physiological characteristics of cyanobacteria (Lee et al., 2021). Substrate pH is another factor that influences the abundance of cyanobacteria (Poza-Carrión et al., 2001). Most cyanobacteria grow in environments that are neutral to alkaline and in laboratory cultures, the optimal pH ranges from 7.5 to 10 (Kaushik, 1994; Shokravi and Soltani, 2011). There is little information regarding the mechanisms of cellular survival, cell stability or growth of cyanobacterial cells under high alkaline conditions (Dwivedi et al., 1994; Jangir et al., 2021). Alkalinity and salinity can affect the structure and function of photosynthetic apparatus (electron transport system, PSI, cytochrome b6f and PSII complexes) and PBS activities. The effects of alkaline-salinity depend on the strain and other environmental conditions (Poza-Carrión et al., 2001; Inoue-Kashino et al., 2005; Abbasi et al., 2019).

Cyanobacteria may improve plant performance under salinity by different mechanisms. Extracellular polysaccharides and proteins produced by *Anabaena sp.* have been found to bind Na^+. This Na^+absorption reduces Na^+ion activity in the culture medium thus lowering the ion toxicity and availability to the rice plants and favouring their growth under saline conditions (Manchanda, 2018). Here we observed that *Nostoc sp.*increased the production of extracellular polysaccharides under saline conditions. Lowering of Na^+ ion activity due to this enhanced binding capacity could be, at least in part, responsible for the amelioration of saline stress without a reduction in Na^+ tissue accumulation observed in rice under the 50% N treatment. The presence of*Nostoc* in the culture medium decreased Na^+ root and shoot concentrations only in plants exposed to 100 mM NaCl in the high nitrogen treatment. Lower Na tissue concentrations in +cyano plants in comparison to -cyano could be responsible for better growth under high salinity and N.

In this work we attempt to describe the dynamic process of adaptation of *Nostoc muscorum* cells to increasing salt concentrations, and to characterize the specific events involved in the process of adaptation at the cellular level. This

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and the accompanying report (Blumwald and Tel-Or 1982) present a general survey of the changes involved in the process of adaptation to salt: cell composition, osmoregulation and cell structure.

II. MATERIAL AND METHODS

Organism and growth conditions:

The cyanobacterium *Nostoc muscorum* used in the present study is filamentous,nitrogen-fixing fresh water strain. The cells of the *Nostoc* will be grown in liquid Chu No. 10 medium for routine as well as for experimental purposes. The culture media will be buffered to pH 7.5 with the addition of 10 mM HEPES-NaOH. The culture will be incubated in the growth chamber at 28oC with a light intensity of 50 µmol m-2 s-1 and temperature of 28^{o}C ± 2^{o}C.

Estimation of percentage survival:

For measurement of percentage survival Petri plates of graded concentration of LiCl, NaCl and sucrose were prepared and inoculated with respective control. After the completion of exponential phase Petri plates would be examined in terms of colony forming units (CFU). The CFU appeared on the treated plates would be compared with the Petri plates having no inhibitors. The colonies appeared on the control Petri plates would presumes to shown 100% survival.

Isolation of NaCl and sucrose resistance mutants:

NaCl is known to cause both ionic as well as known ionic stresses; therefore, the direct NaCl resistance mutant is not possible. The next series of experiment we would isolate NaCl resistance mutant and sucrose resistance mutant through LiCl resistance mutants.

Photosynthetic oxygen evolution:

The photosynthetic oxygen evolution was measured with a clark-type oxygen electrode (Hansa-tech instruments Ltd. Uk). Exponetially growing cyanobacterial cells were deposited on a flat platinum cathode that was polarized at 0.6 V with references to a large Ag/Agcl electrode. The electrode wereimmersed in an electrolyte (consisting of 0.05 M phosphate buffer, pH 7.8; 0.1 M kcl). The electrode was separated from the magnetically stirred assay medium by a Teflon membrane. The difference between the output of the electrode in water in equilibrium with pure nitrogen was considered to represent 0.235 mol m¯3 in the assay medium. After injection of the same into the assay medium, the medium was illuminated from the opposite side with a projector lamp. The rate of oxygen evolution was determined from the initial slope of the electrode output as a function of time.

DNA Microarray:

The DNA microarray technology allows monitoring of global gene expression in one single experiment (Harrington *et al.,* 2000; Lucchini*et al*., 2001). Microarrays are small glass slide to which gene-specific DNA fragments, amplified by PCR oroligonucleotide are bound in an ordered manner. Thus, this technology is based on the availability of respective genome sequences.

III. RESULTS

To assess the effects of salinity and alkalinity on the growth of *Nostocmuscorum*, the optical density and Chl a concentration was monitored for 7 days (Table 1). The highest growth was observed under extreme alkaline conditions (pH 11) with 80 mM salinity (Table 1)

In Na^{+}-R mutant maximum up regulated genes were falls in the other category. Next functional category is transport and binding proteins.Similarlydown regulated genes of the regulatory functions showed maximum down regulation next to this is the transport and binding protein.

In Su^{+}-R mutant maximum up regulated genes, belong to the other categories after other categories, transport and binding proteins showed maximum up regulation. Similarly down regulated genes of the regulatory functions showed maximum down regulation and next other categories showed maximum down regulation.

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	pH7			pH 9			pH 11		
	17mM	80mM	160mM	17mM	80mM	160mM	17mM	80mM	160mM
3rd day	0.076± 0.010^{a}	0.078± 0.005^{a}	0.074± 0.016^{a}	0.083± 0.004^{ab}	0.086± 0.031^{ab}	0.047± 0.008^{ab}	0.132± 0.017^{ac}	0.154± 0.037^{ac}	0.036± 0.002^{a} c
4th day	0.143± 0.021^{a}	0.139± 0.019^{a}	0.086± 0.011^{b}	0.202± 0.026^{ab}	0.158± 0.014^{ab}	0.105± 0.029^{ab}	0.274± 0.011^{ac}	0.182± 0.037^{ac}	0.046± 0.008^{a} c
5th day	0.202± 0.035^{a}	0.320± 0.031^{b}	0.179± 0.033^{c}	0.377± 0.017^{ab}	0.425± 0.038^{bc}	0.220± 0.032^{bc}	0.543± 0.089^{ac}	0.552± 0.102^{bc}	0.213± 0.052^{a} c

Table 1. Comparison of growth -Optical density OD 750 nm. Chl a concentration (µg mL-1) of *Nostoc muscorum* at different pHs (7, 9 and 11) and salinity (17, 80, 160 mM). Values are means ± standard deviation (n = 3).

In Li^+-R mutant maximum up regulated genes were falls in the other category. Next functional category is transport and binding proteins. Similarly down regulated genes of the regulatory functions showed maximum down regulation next to this is the transport and binding protein.

Further analysis of the DNA microarray data reveals that even the common up regulated genes have different fold values, likewise the common down regulated genes have different fold value. In addition to this there are certain up regulated and down regulated genes that expressed in both the mutant strains. This analysis suggested that mutant phenotype showing resistant to growth inhibitory action of Na, Su and Li leading to over expression of certain genes and suppression of certain genes.

The basic premise of the present work is to analyze various up regulated and down regulated genes in both the mutant strains. In addition to various up regulated genes belonging to different functional categories we have also, reported common down regulated genes in both the mutant strains and the findings suggested that resistant phenotype resultant in up regulation and down regulation of various genes for acquiring resistant phenotype. This finding suggested that any modification in the genetic material leads to the up regulation and down regulation of various genes for better growth and survival of the organism.

The effect of NaCl and sucrose on the growth of *N. muscorum* was examined. NaCl at a concentration of 100 mM and sucrose at a concentration of 250 mM was found lethal to the diazotrophically grown cultures of the cyanobacterium. Addition of 5 mM K^+ (as KCl) in the growth medium caused recovery in the growth during the initial phase and then no significant growth was observed. The damage caused by the stresses was almost completely recovered when incubation mixture supplied with proline. The growth was further enhanced when the incubation mixture supplied with both K^+ and proline. Therefore, it is suggested that K^+ and proline in combination completely restored the inhibitory effect of NaCl and sucrose.

The cyanobacterial cells were starved for 72 h in K^+-deficient medium. The Km value of the cultures grown under K^+ starved and proline deficient were low as compared to the cultures grown in the medium containing K^+/proline. Addition of K^+ and proline in the growth medium enhanced Km value for proline only.

This finding suggested that presence of K+ in the growth medium accelerate proline uptake under stress conditions. The addition of CCCP in the incubation mixture abolished K^+ and proline uptake (data not shown), therefore it is suggested that both K^+ proline uptake were energy requiring processes.

The uptake of K^+ and proline as a function of NaCl and sucrose stresses were also examined. The addition of NaCl/sucrose in the incubation mixture initially caused no impact on K^+ uptake on the contrary Na^+ uptake was increases during the initial phase followed by K^+ uptake. Further it has been reported that K^+ uptake was more under NaCl stress than sucrose. The intracellular proline contents showed little variation under NaCl and sucrose stresses. On further examination it was found that intracellular proline contents were greatly enhanced when the similar stress cultures were supplied with 1 mM proline. The presence of K^+ in the growth medium further accelerate proline uptake.

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This finding suggested that K^+ ions are necessary for the induction of secondary response under NaCl and sucrose stresses.

As *N. muscorum* is able to perform both oxygenic photosynthesis and oxygen sensitive nitrogenase activity, therefore, the osmolyte role of K^+ and proline on these two vital processes was observed. The result indicates that the presence of K^+ alone in the growth medium has no role as an osmoprotectant. The addition of proline in the growth medium mitigates the adverse effect of NaCl and sucrose stress.

The effect of NaCl on two vital processes of cyanobacterial metabolism, viz. N_2 fixation and oxygenic photosynthesis, was studied in the cyanobacterium *Nostocmuscorum* grown diazotrophically. An increase in NaCl concentration suppressed the formation of heterocyst and adversely affected the nitrogenase activity in the parent, whereas in Li^+-R and Na^+-R mutants NaCl stress did not cause any adverse effect. The rate of photosynthetic O_2evolution was also adversely affected by the NaCl stress, but the magnitude was less than that of nitrogenase activity. L-Proline, the well-known osmoprotectant, provided protection to the cyanobacterium against NaCl stress. The parent strain utilized L-proline as a nitrogen source and suppressed heterocyst formation and nitrogenase activity, while mutants showed normal heterocyst frequency and nitrogenase activity. Therefore, it may be that the proline metabolism is altered as a result of mutation. The intracellular levels of proline in the parent were enhanced about threefold in the medium containing 1 mol xm^{-3} proline, while in mutants there was no significant increase in the intracellular level of proline. In the medium containing both NaCl and proline, the intracellular level of proline was enhanced in the parent as well as in both mutant strains. This suggests that the parent strain possessed both normal proline uptake and salt-induced proline uptake systems, whereas the mutant strains were defective in normal proline uptake and had only salt-induced proline uptake. The over-accumulation of proline in the presence of NaCl stress is due either to the loss of proline oxidase activity or to the accumulation of exogenous proline.

The parent *N. muscorum* when grown in 1 mol m^{-3} NH_4Cl medium did not produce heterocyst and nitrogenase activity. The ammonium-grown filaments remained non-heterocystous, and when such a non-heterocystous culture was transferred to diazotrophic medium, it started producing heterocysts within 24–30 h of such transfer and reached a heterocyst frequency of 7–8% in 48- to 60-h-old cultures. The experiments were planned to examine the effect of NaCl on diazotrophic growth, heterocyst frequency, nitrogenase activity, photosynthetic O_2 evolution, percentage survival, and proline contents.

The NaCl stress was given to the ammonium-grown cultures for 12 h before their transfer to diazotrophic medium under photoautotrophic growth conditions. The doses for inducing increasing salinity stress were 30, 60, and 90 mol m^{-3} NaCl. All parameters were measured in 6-day-old, diazotrophically grown cultures. Such treated cultures along with their respective controls were incubated under diazotrophic growth conditions and then examined for diazotrophic growth, heterocyst frequency, nitrogenase activity, photosynthetic O_2evolution, percentage survival, and proline contents. The spontaneously occurring mutant clones of the cyanobacterium resistant to the growth-inhibitory action of LiCl and NaCl arose with a frequency of 0.7–0.8 $*10^{-7}$, which is characteristic of single mutational events.

The effect of NaCl on the survival of parent *N.muscorum* and its Li^+-R and Na^+ -R mutant strains cultured in N_2 medium was studied. NaCl at a concentration of 100 mol m^{-3} completely arrested the growth of the parent strain; however, this concentration of NaCl did not have any effect on the growth of both Li^+ -R and Na^+ -R mutant strains.

In order to see the impact of exogenously supplied proline on NaCl-caused inhibition in the parent and its Li^+ -R and Na^+-R mutants, the growth of the parent as well as the Li^+ -R and Na^+

-R mutant strains in NaCl- stressed conditions were measured in the presence and absence of proline. NaCl in the absence of proline completely arrested the growth of the parent strain; however, it could slightly inhibit the growth (only 14%) in the presence of proline. Thus, exogenously supplemented proline provides protection to the cyanobacterium against NaCl stress. In contrast, the percentage survival of both the mutant strains was found to be similar in the presence as well as in the absence of proline.

In the parent, growth decreased with the increasing concentration of NaCl stress. Further, there was a progressive lag in the differentiation of the N_2 -fixing heterocyst with increase in NaCl stress, and a dose of 100 mol m^{-3}NaCl for 12 h resulted in complete prevention of the formation of the N_2 fixing heterocyst. Similarly, the effects of increasing concentration of NaCl on photosynthetic O_2 evolution in the parent strain were also examined. Nitrogenase activity of

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the cyanobacterium was completely inhibited at a dose of 100 mol m^{-3} NaCl. In comparison, oxygenic photosynthetic activity, though reduced, was still significant even at this concentration.

Thus, the photosynthetic O_2 evolution was also adversely affected by NaCl stress; however, the magnitude of NaCl-caused inhibition on the rate of photosynthetic O_2 evolution was comparatively less than that of the heterocyst frequency and nitrogenase activity.

In cyanobacteria,a Li^+-R mutant is possible by generating a mechanism that effluxes out Li+ much faster than the system causing Li^+influx. Since Li^+ is an analogue of Na^+, it can enter the cyanobacterial cells by all transport systems transporting Na+. Cyanobacteria have a Na^+/H^+ antiporter which effluxes out Na^+as well as Li^+. It is possible that a cyanobacterial *N. muscorum*single step mutantovercomes Li^+toxicity by generating a mutant with a Na^+/H^+antiporter which is more efficient in the efflux of intracellular Na^+/ Li^+. This inter-pretation for the cyanobacterial mutant resistant to Na^+/ Li^+agrees with the interpretation of resistance to Na^+/ Li^+ in *N. muscorum*. Li^+ has been used in E. coli to study the genetics of Na^+/H^+antiporter by generating a Li^+-R mutant to understand the molecular mechanism of the bacterial Na^+/H^+antiporter activity. Our interpretation of the cyanobac-terial Li^+-R and Na^+-R mutant are in agreement withthe concept already established on *N. muscorum*. Mutational analysis of the bacterial Na^+/H^+antiporter has already demonstrated that this anti-porter exhibits physiological pleiotropy, promoting pH homeostasis, alkalophily and resistance to Li^+/ Na^+stress. The present studies on Na^+-R mutant are consistent with the cyanobacterial Na^+-Rmutant as a mutant of the cyanobacterial Na^+/H^+antiporter permitting the mutant to grow under Li^+stress and Na^+stress.

Thus, in the present investigation microarray data identifies the genes that represent various functional categories needs more intensive research with genetics and physiology to determine gene functions, their chromosomal organization and their mode of regulation.

IV. DISCUSSION

Cyanobacteria occur in environments with different salinities. Usually, high salt means an increase in the external concentration of NaCl, the quantitatively dominant salt in seawater, which is therefore most used in laboratory experiments.

There are many reports showing that the different ion composition of alkaline lakes or hypersaline environments, where other ions predominate, may pose additional challenges to their inhabitants; therefore, only highly specialized organisms, including some specialized cyanobacteria, can live in such extreme environments (Oren et al., 1999; Nübel, 2000). Here, processes will be described that are involved in acclimation to elevated $Na^+$and Cl^- concentrations and the role of K^+, which is an important monovalent cation inside the cell, where it is preferentially accumulated and exchanged with the toxic Na^+. Theoftenobserved toxicity of the alkaline ion $Na^+$and the compatibility of the alkaline ion K^+ are not well understood (Maathuis & Amtmann, 1999). Both ions show similar physicochemical structures, as the smaller ion Na^+together with its rather large hydration shell mimics the size of K^+. Therefore, uptake systems for K^+ have difficulties discriminating between these ions, and high Na^+contents in the medium may result in K^+deficiency. Inside the cell, Na^+ competes for K^+binding sites [e.g. K^+ is often found in proteins stabilizing and defining three-dimensional (3D) structures], resulting in the inhibition of K^+-dependent metabolic processes. Therefore, all organisms tend to ensure a defined K^+/ Na^+ ratio in the cytoplasm (Maathuis & Amtmann, 1999).

Of the published data on the Na^+ content of salt-treated cyanobacterial cells, the most reliable values were obtained using tracer experiments with radio-labeled Na^+, as this strategy allows the distinction of internal and external Na^+ (Reed et al., 1984a, 1985a, b; Ritchie, 1992a). These data show that cells grown in basal medium (e.g. BG11) contain about 5–10 mM Na^+, whereas salt-acclimated cells have sodium ion contents of 10–20% of the external Na^+concentration. These values are supported using in vivo nuclear magnetic resonance (NMR), another noninvasive technology that allows ion quantification in the cytoplasmic space without washing (Nitschmann & Packer, 1992). Using silicone oil centrifugation and flame photometry, we found a stronger increase of Na^+ in salt-acclimated cells of *Synechocystis* 6803, which can be attributed to the difficulty in completely removing external sodium ions (Hagemann et al., 1994). Nevertheless, all datasets show clearly that cyanobacteria [even when grown under hypersaline conditions as shown by Reed et al. (1984) contain significantly lower internal sodium concentrations compared with the external medium, suggesting active extrusion of this toxic ion from the cytoplasm.

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