Microbiome-based rhizosphere engineering for mitigation of salinity stress in tomato

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Submitted by

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Department of Biochemical Engineering and Biotechnology

In fulfillment of the requirements of the degree of

DOCTOR OF PHILOSOPHY

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DEDICATED

TO THE ALMIGHTY,

PARENTS, BROTHER,

AND SISTER

CERTIFICATE

This is to certify that the thesis entitled “**Microbiome-based rhizosphere engineering for mitigation of salinity stress in tomato**” submitted by Ms. Salila Pradhan has been prepared under my guidance with the rules and regulations of Indian Institute of Technology Delhi, India. The results represented in this thesis have not been submitted for any degree or diploma in any other institute or university.

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ABSTRACT

Soil salinization is a major global constraint that severely hampers crop productivity and threatens agricultural sustainability. Microbiome-based rhizosphere engineering strategies for salinity stress mitigation have emerged as viable and eco-friendly alternatives to conventional methods. This study aimed to develop a salt stress-acclimatized rhizosphere microbiome followed by designing a synthetic microbial community (SMC) capable of enhancing plant growth and physiological resilience under salinity stress. A salt stress-acclimatized rhizosphere microbiome was generated through successive passaging of the rhizosphere soil in a salt-susceptible tomato (*Solanum lycopersicum*) cultivar over multiple plant growth cycles (PGCs) under ramping up of salt concentrations. The efficiency of salt stress-acclimatized rhizosphere microbiome on different plant model systems was evaluated through rhizosphere microbiome transplantation (RMT). It demonstrated a significant enhancement of plant growth in tomato as well as in other plant model systems, *viz.*, brinjal, chilli, bell pepper, and okra. There was an enhancement in salinity stress mitigation across all plant model systems. The prominent effect was observed in chilli and okra. Further, prokaryotic community composition along the process of acclimatization of the rhizosphere microbiome was analyzed. The tomato rhizosphere soil with microbiome+salt (PMS) treatment exhibited a similar prokaryotic community across different PGCs. The phyla *Proteobacteria* (now *Pseudomonadota*) and *Bacteroidota* increased along the process of acclimatization in the PMS set compared to only salt-treated set. In the case of genus, *Pseudomonas* played an important role in mitigating salinity stress in tomato through the acclimatization process. Interestingly, the relative abundance of *Pseudomonas* was also found to be the highest in the rhizosphere soil inoculated with salt stress-acclimatized microbiome of tomato in okra under salt stress compared to other treatment sets. Following this, a culture bank was generated from the salt stress-acclimatized rhizosphere microbiome of tomato. The bacterial strains were screened for salt tolerance and plant growth promoting

(PGP) traits, including 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity, siderophore production, phosphate solubilization, and indole-3-acetic acid (IAA) production, followed by their plant growth promotion activity under salinity stress in controlled conditions. Three salt stress-acclimatized bacterial isolates, *viz.*, *Pseudomonas* sp. SP16.1, *Pseudomonas furukawaii* SP16.16, and *Microbacterium resistens* SP16.19 were shortlisted for designing SMC. Further, whole-genome sequencing of three bacterial strains was performed to elucidate genetic mechanisms underpinning stress adaptation. Genome annotation revealed several biosynthetic gene clusters (BGCs) encoding nonribosomal peptide synthetases (NRPS-like), betalactones, terpenes, and redox cofactors associated with antioxidative defence, osmoprotection, and microbial communication within the rhizosphere. Further, untargeted metabolomics of these three bacterial strains was performed to understand the presence of metabolite features in the presence and absence of salt stress. It was found that the metabolite production was species-specific, irrespective of salt stress. Then, the efficacy of the three-membered SMC for salinity stress mitigation on tomato was evaluated in natural conditions. The SMC treatment significantly improved plant height, dry weight, membrane stability index (MSI), chlorophyll, and carotenoid levels while reducing osmotic and oxidative stress markers such as proline and malondialdehyde (MDA). The observed synergistic effects reflected metabolic cooperation and resource sharing among SMC members, reinforcing the importance of microbial interactions in conferring stress tolerance. Overall, the study provides compelling evidence that the SMC of salt stress-acclimatized rhizosphere microbiome can be effectively integrated to develop biologically robust inoculants to mitigate salinity stress in sustainable agriculture.

सार/सारांश

मृदा लवणीकरण एक प्रमुख वैश्विक बाधा है जो फसल उत्पादकता को गंभीर रूप से बाधित करती है और कृषि स्थिरता को खतरा पहुंचाती है। लवणता तनाव (salt stress) न्यूनीकरण के लिए माइक्रोबायोम-आधारित राइजोस्फीयर इंजीनियरिंग (microbiome-based rhizosphere engineering) रणनीतियाँ पारंपरिक तरीकों के व्यवहार्य और पर्यावरण-अनुकूल विकल्प के रूप में उभरी इस अध्ययन का उद्देश्य लवण तनाव के प्रति अनुकूलित राइजोस्फीयर माइक्रोबायोम का विकास करना था, जिसके पश्चात् एक कृत्रिम सूक्ष्मजीवी समुदाय (SMC) का निर्माण किया गया, जो लवणता तनाव की स्थिति में पौधों की वृद्धि और शारीरिक सहनशीलता को बढ़ाने में सक्षम हो। लवण सांद्रता में वृद्धि के तहत कई पादप विकास चक्रों (PGCs) में लवण-संवेदनशील (salt-susceptible) टमाटर (*Solanum lycopersicum*) की किस्म में राइजोस्फीयर (rhizosphere) मिट्टी के क्रमिक मार्गन के माध्यम से एक लवण तनाव-अनुकूलित राइजोस्फीयर माइक्रोबायोम (salt stress-acclimatized rhizosphere microbiome) उत्पन्न किया गया था। विभिन्न पादप मॉडल प्रणालियों पर लवण तनाव-अनुकूलित राइजोस्फीयर माइक्रोबायोम की दक्षता का मूल्यांकन राइजोस्फीयर माइक्रोबायोम प्रत्यारोपण (RMT) के माध्यम से किया गया। इसने टमाटर के साथ-साथ अन्य पादप मॉडल प्रणालियों, जैसे बैंगन, मिर्च, शिमला मिर्च और भिंडी में पादप वृद्धि में उल्लेखनीय वृद्धि प्रदर्शित की। सभी पादप मॉडल प्रणालियों में लवणता तनाव (salt stress) न्यूनीकरण में वृद्धि देखी गई। मिर्च और भिंडी में इसका प्रमुख प्रभाव देखा गया। इसके अलावा, राइजोस्फीयर माइक्रोबायोम (rhizosphere microbiome) के अनुकूलन की प्रक्रिया के साथ प्रोकैरियोटिक समुदाय संरचना का विश्लेषण किया गया। माइक्रोबायोम (microbiome)+नमक (PMS) उपचार वाली टमाटर राइजोस्फीयर (rhizosphere) मिट्टी ने विभिन्न PGCs में एक समान प्रोकैरियोटिक (prokaryotic) समुदाय प्रदर्शित किया। केवल लवण-उपचारित सेट की तुलना में PMS सेट में अनुकूलन की प्रक्रिया के साथ प्रोटियोबैक्टीरिया (*Proteobacteria/Pseudomonadota*) और बैक्टीरॉइडोटा (*Bacteroidota*) संघों में वृद्धि हुई। जीनस के मामले में, स्यूडोमोनास (*Pseudomonas*) ने अनुकूलन

प्रक्रिया के माध्यम से टमाटर में लवणता तनाव (salt stress) को कम करने में महत्वपूर्ण भूमिका दिलचस्प बात यह है कि स्यूडोमोनास (*Pseudomonas*) की सापेक्ष प्रचुरता अन्य उपचार सेटों की तुलना में नमक तनाव के तहत टमाटर के नमक तनाव-अनुकूलित माइक्रोबायोम के साथ टीका लगाए गए राइजोस्फीयर (rhizosphere) मिट्टी में सबसे अधिक पाई गई। इसके बाद, टमाटर के नमक तनाव-अनुकूलित राइजोस्फीयर माइक्रोबायोम (rhizosphere microbiome) से एक संस्कृति बैंक तैयार किया गया था। 1-एमिनोसाइक्लोप्रोपेन-1-कार्बोक्सिलिक एसिड (ACC) डेमिनेज गतिविधि, साइडरोफोर उत्पादन, फॉस्फेट घुलनशीलता और इंडोल-3-एसिटिक एसिड (IAA) गतिविधि सहित नमक सहिष्णुता और पौधे की वृद्धि को बढ़ावा देने (PGP) लक्षणों के लिए जीवाणु उपभेदों की जांच की गई, इसके बाद नियंत्रित स्थितियों में लवणता तनाव (salt stress) के तहत उनके पौधे की वृद्धि को बढ़ावा देने वाली गतिविधि का परीक्षण किया गया। तीन नमक सहनशील जीवाणु अलगाव, अर्थात, *Pseudomonas* sp. 16.1, *Pseudomonas furukawaii* SP16.16, *Microbacterium resistens* SP16.19, सबसे पहले, तनाव अनुकूलन के आधारभूत आनुवंशिक तंत्रों को स्पष्ट करने के लिए तीन जीवाणु उपभेदों का संपूर्ण जीनोम अनुक्रमण किया गया। जीनोम एनोटेशन से कई जैवसंश्लेषी जीन समूहों (BGCs) का पता चला, जो गैर-राइबोसोमल पेप्टाइड सिंथेटेस (NRPS-like), बीटालैक्टोन (betalactone), टेरपीन (terpene) और रेडॉक्स (redox) सहकारकों को कूटबद्ध करते हैं, जो राइजोस्फीयर (rhizosphere) के भीतर एंटीऑक्सीडेंट (antioxidant) रक्षा, परासरण संरक्षण, और सूक्ष्मजीवी संचार से जुड़े हैं। इसके अलावा, इन तीन बैक्टीरियल स्ट्रेनों (bacterial strains) की अनटार्गेटेड मेटाबोलोमिक् (untargeted metabolomic) की गई ताकि लवण तनाव (salt stress) की उपस्थिति और अनुपस्थिति में मेsटाबोलाइट विशेषताओं (metabolite features) की उपस्थिति को समझा जा सके। पाया गया कि मेटाबोलाइट उत्पादन प्रजाति-विशिष्ट (species-specific) था, चाहे लवण तनाव हो या न हो। इसके बाद, प्राकृतिक परिस्थितियों में टमाटर पर लवणता तनाव (salt stress) न्यूनीकरण के लिए तीन-सदस्यीय एसएमसी (SMC) की प्रभावकारिता का मूल्यांकन किया गया। एसएमसी उपचार ने पौधे की

ऊँचाई, शुष्क भार, झिल्ली स्थिरता सूचकांक (MSI), क्लोरोफिल (chlorophyll) और कैरोटीनॉयड (carotenoid) के स्तर में उल्लेखनीय सुधार किया, जबकि प्रोलाइन (proline) और मैलोनडायल्डिहाइड (malondialdehyde) जैसे परासरणी और ऑक्सीडेटिव (oxidative) तनाव चिह्नकों को कम किया। देखे गए सहक्रियात्मक प्रभावों ने एसएमसी सदस्यों के बीच चयापचय सहयोग और संसाधन साझाकरण को प्रतिबिंबित किया, जिससे तनाव सहनशीलता प्रदान करने में सूक्ष्मजीवी अंतःक्रियाओं के महत्व को बल मिला। कुल मिलाकर, अध्ययन इस बात के ठोस सबूत प्रदान करता है कि लवण तनाव-अनुकूलित राइजोस्फीयर माइक्रोबायोम (salt stress-acclimatized rhizosphere microbiome) के एसएमसी (SMC) को टिकाऊ कृषि (sustainable agriculture) के लिए लवणता तनाव (salt stress) को कम करने के लिए जैविक रूप से मजबूत इनोक्युलेंट (inoculant) विकसित करने के लिए प्रभावी रूप से एकीकृत किया जा सकता है।

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Abbreviations

Formula/Abbreviation	Media, molecules and chemicals
MeOH	Methanol
$(NH_4)_2SO_4$	Ammonium sulfate
$Ca_3(PO_4)_2$	Calcium phosphate
CO_2	Carbon dioxide
CTAB	Cetyltrimethylammonium bromide
$CuSO_4.5H_2O$	Copper (II) sulfate pentahydrate
$FeCl_3$	Ferric chloride
$FeCl_3 \cdot 6H_2O$	Ferric chloride hexahydrate
$FeSO_4.7H_2O$	Ferrous sulfate heptahydrate
H_3BO_3	Boric acid
HCl	Hydrochloric acid
KCl	Potassium chloride
KH_2PO_4	Potassium dihydrogen phosphate
$MgCl_2.6H_2O$	Magnesium chloride hexahydrate
$MgSO_4.7H_2O$	Magnesium sulfate heptahydrate
$MnSO_4.H_2O$	Manganese (II) sulfate monohydrate
MoO_3	Molybdenum trioxide
Na_2HPO_4	Disodium hydrogen phosphate
NaCl	Sodium chloride
NaOCl	Sodium hypochlorite
NaOH	Sodium hydroxide
NH_4Cl	Ammonium chloride
tris-HCl	Tris(hydroxymethyl)aminomethane hydrochloride
$ZnSO_4.7H_2O$	Zinc sulfate heptahydrate

Terminology used in the study	Terminology description
1C	Composite soil
ACC	1-aminocyclopropane-1-carboxylic acid
ANOVA	One-way analysis of variance
ASV	Amplicon sequencing variant
BGCs	Biosynthetic gene clusters
BP	Bell pepper
Br	Brinjal
C	Control
CAS	Chrome azurol sulphonate
CDSs	Coding sequences
CFU	Colony forming units
Ch	Chilli
CTAB	Cetyltrimethylammonium bromide
DADA	Divisive amplicon denoising algorithm
DDA	Data-dependent acquisition
df	Dilution factor
DF	Dworkin and Foster
DNP	2,4-Dinitrophenol
FBMN	Feature based molecular networking

FDR	False discovery rate
GNPS	Global natural products social molecular networking
HCN	Hydrogen cyanide
IAA	Indole-3-acetic acid
IARI	Indian Agricultural Research Institute
IC_{50}	Half-maximal inhibitory concentration
IIT	Indian Institute of Technology
IIVR	Indian Institute of Vegetable Research
KO	KEGG ortholog
LB	Luria bertani
LC-MS	Liquid chromatography mass spectrometry
M	Microbiome
MCT	Microcentrifuge tube
MS	Microbiome+Salt
m/z	Mass/charge ratio (ion mass)
NAGGN	N-acetylglutaminnylglutamine amide
NBRIP	National Botanical Research Institute's phosphate medium
NCBI	National Center for Biotechnology Information
NRPS	Nonribosomal peptide synthetase
O	Okra
OD	Optical density
ONT	Oxford nanopore technology
PCA	Principal component analysis
PCoA	Principle coordinate analysis
PCR	Polymerase chain reaction
PERMANOVA	Permutational multivariate analysis of variance
PGAP	Prokaryotic genome annotation pipeline
PGC	Plant growth cycle
PGP	Plant growth promoting
PIPES	Piperazine-N,N'-bis(2-ethanesulfonic acid)
QIIME	Quantitative insights into microbial ecology
qRT-PCR	Quantitative reverse transcriptase polymerase chain reaction
RIPP	Ribosomally synthesized and post-translationally modified peptides
RMT	Rhizosphere microbiome transplantation
RO	Reverse osmosis
ROS	Reactive oxygen species
RSA	Root system architecture
S	Salt
SDS	Sodium dodecyl sulphate
SMC	Synthetic microbial community
sORFs	Small open reading frames
SPSS	Statistical Package for Social Sciences
T3PKS	Type III polyketide synthase
TCA	Trichloroacetic acid

Tris-EDTA	Tris(hydroxymethyl)aminomethane and ethylenediaminetetraacetic acid
TSB	Tryptone soy broth
UHPLC	Ultra-high-performance liquid chromatography

Elements/ions formula	**Elements/ions name**
H_2O_2	Hydrogen peroxide
O_2^-	Superoxide
O^{2-}	Oxide
OH^-	Hydroxide
Ca^{2+}	Calcium
Cl^-	Chloride
HCO_3^-	Bicarbonate ion
K^+	Potassium
Mg^{2+}	Magnesium
Na^+	Sodium
NO_3^-	Nitrite
SO_4^{2-}	Sulfate

Units	**Description of units**
%	Percent
°C	Degree Celsius
µg	Micro gram
µl	Micro litre
CFU	Colony forming units
cm	Centi meter
df	Dilution factor
dS/m	deciSiemens per meter
EC	Electrical conductivity
ESP	Exchangeable sodium percentage
g	Gram
h	Hour
IAA	Indole-3-acetic acid
IBA	Indole-3-butyric acid
min	Minutes
ml	Milli litre
mM	Milli molar
ng	Nano gram
nm	Nano meter
ppm	Parts per million
psu	Percentage siderophore unit
rpm	Revolution per minute
µg	Micro gram