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THEME

INVOLVEMENT OF BACTERIAL AND ORGANIC BIOSTIMULANTS IN OSMOPROTECTION AND PROMOTION OF GROWTH AND DEVELOPMENT OF TOMATO (*SOLANUM LYCOPERSICUM L*.) AGAINST SALT STRESS

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ABSTRACT

Salinity stress poses a significant threat to global food security by compromising crop quality and yield. To address this challenge, eco-friendly approaches were explored in this thesis, focusing particularly on mitigating salinity stress in tomato (*Solanum lycopersicum L.*) plants. The investigation centered on the efficacy of a selected PGPR strain, *Bacillus cereus* MR64, identified via 16S rRNA gene sequencing, alongside an aqueous extract from brown seaweed *Cystoseira compressa*, used as biostimulants. The assessment included the individual and combined effects of these biostimulants on plant growth, physiological parameters, biochemical markers, development and production responses.

FT-IR analysis of *C. compressa* confirmed the presence of various compounds, aligning with prior studies and showcasing the diverse organic components within the seaweed. LC-MS/MS analysis of the seaweed indicated a prevalence of essential amino acids such as L-alanine, L-glutamic acid, and L-aspartic acid. Furthermore, HPLC analysis revealed key phytohormones, particularly zeatin, and substantial quantities of essential sugars, including monosaccharides and disaccharides. Bacterial characterization demonstrated that *B. cereus* MR64 exhibited tolerance to elevated salt concentrations and displayed plant growth-promoting traits, including indole acetic acid (IAA) production.

The results indicated that the interactive treatments T7 (CLE at 10% + BT) and T8 (CLE at 15% + BT) significantly enhanced shoot and root lengths, biomass, and chlorophyll content, while also reducing electrolyte leakage. Additionally, biochemical analyses revealed a reduction in Na+ levels and an increase in K+ and proline concentrations, contributing to improved osmotic regulation and salt tolerance. FT-IR spectroscopy revealed significant spectral changes in treated plants, highlighting the presence of unique compounds characterized by functional groups such as O-H and C-H.

The seaweed extract treatments, particularly T5 (CLE at 15%) were more effective than the bacterial strain alone in enhancing shoot growth, photosynthetic pigments, membrane integrity, and proline content. When applied individually, the bacterial strain increased root length and biomass compared to the seaweed extract treatments and the control. The combined application of PGPR and algae extracts showed a synergistic effect, resulting in superior plant growth and enhanced physio-biochemical parameters. This synergy likely arose from the complementary actions of microbial and organic biostimulants.

The findings underscored the potential of integrating PGPR and algae extracts as a sustainable, eco-friendly and cost-effective strategy to enhance tomato resilience and growth in saline environments.

Key-words: Biostimulants, Tomato, Salinity stress, Seaweed, PGPR, Growth, Physiology, Proline, Phytohormones, Amino acids

LE RÉSUMÉ

Le stress salin constituait une menace pour la sécurité alimentaire mondiale en compromettant la qualité et le rendement des cultures. Pour relever ce défi, des approches respectueuses de l'environnement ont été explorées dans cette thèse, en se concentrant sur l'atténuation du stress salin chez les plants de tomate (*Solanum lycopersicum L.*). L'étude a porté sur l'efficacité d'une souche sélectionnée de PGPR, *Bacillus cereu*s MR64, identifiée par séquençage du gène 16S rRNA, ainsi que d'un extrait aqueux d'algue brune *Cystoseira compressa*, utilisés comme biostimulants. Les effets individuels et combinés de ces biostimulants sur la croissance, les paramètres physiologiques, les marqueurs biochimiques, les réponses de développement et de production des plants ont été évalués.

L'analyse FT-IR de *C. compressa* a confirmé la présence de divers composés, ce qui s'aligne avec les études antérieures. De plus, l'analyse LC-MS/MS de l'algue a indiqué une prévalence d'acides aminés essentiels tels que la L-alanine, l'acide L-glutamique et l'acide L-aspartique. Par ailleurs, l'analyse HP-LC a révélé des phytohormones clés, en particulier la zéatine, ainsi que des quantités substantielles de sucres essentiels, notamment des monosaccharides et des disaccharides. En revanche, la caractérisation bactérienne a démontré que *B. cereus* MR64 présentait une tolérance au sel, en complément de la production de l'acide indole acétique (IAA).

Les résultats ont indiqué que les traitements interactifs T7 (CLE à 10% + BT) et T8 (CLE à 15% + BT) amélioraient significativement les longueurs des pousses et des racines, la biomasse et la teneur en chlorophylle, tout en réduisant la fuite d'électrolytes. De plus, les analyses biochimiques ont révélé une réduction des niveaux de Na+ et une augmentation des concentrations de K+ et de proline, contribuant à une meilleure régulation osmotique et à une tolérance accrue au sel. La spectroscopie FT-IR a révélé des changements spectraux significatifs dans les plants traitées, mettant en évidence la présence de composés uniques caractérisés par des groupes fonctionnels tels que les groupes O-H et C-H.

Les traitements à base d'extraits d'algues, en particulier T5 (CLE à 15%), se sont révélés plus efficaces que la souche bactérienne seule pour améliorer la croissance des pousses, les pigments photosynthétiques, l'intégrité de la membrane et la teneur en proline. En revanche, l'application individuelle de la souche bactérienne a significativement augmenté la longueur et la biomasse des racines par rapport aux traitements à base d'extraits d'algues ainsi qu'au témoin. L'application combinée de PGPR et d'extraits d'algues a montré un effet

synergique, entraînant une croissance supérieure des plantes et des paramètres physio-biochimiques améliorés. Cette synergie est probablement due aux actions complémentaires des biostimulants microbiens et organiques.

Ces résultats soulignent le potentiel de l’intégration de ces biostimulants en tant que stratégie durable, respectueuse de l'environnement et économique pour améliorer la résilience et la croissance de la tomate dans des environnements salins.

Mots-clés: Biostimulants, Tomate, Stress salin, Algues, PGPR, Croissance, Physiologie, Proline, Phytohormones, Acides amines

الملخص:

يشكل الإجهاد الملحي تهديدًا كبيرًا للأمن الغذائي العالمي، حيث يؤثر سلبًا على جودة وإنتاجية المحاصيل. لمواجهة هذا التحدي، تم في هذه الأطروحة استكشاف أساليب مستدامة وصديقة للبيئة، مع التركيز على كيفية تخفيف الإجهاد الملحي في نباتات الطماطم (*Solanum lycopersicum L.*). ركزت الدراسة على فعالية سلالة مختارة من PGPR، *Bacillus cereus* MR64، التي تم تحديدها بواسطة التسلسل الجيني 16S rRNA، بالإضافة إلى المستخلص المائي للطحالب البنية *Cystoseira compressa*، المستخدمة كمنشطات حيوية. تم تقييم التأثيرات الفردية والجماعية لهذه المنشطات الحيوية على النمو، والقياسات الفسيولوجية، والعلامات البيوكيميائية، والاستجابات التنموية والإنتاجية للنباتات.

أكد تحليل FT-IR لـ*C.compressa* وجود مركبات مختلفة، وهو ما يتوافق مع الدراسات السابقة. بالإضافة إلى ذلك، أشار تحليل LC-MS/MS للطحالب إلى انتشار الأحماض الأمينية الأساسية مثل ل- ألانين، وحمض ل- الجلوتاميك، وحمض ل- الأسبارتيك. علاوة على ذلك، كشف تحليل HP-LC عن الهرمونات النباتية الرئيسية، وخاصة الزياتين، بالإضافة إلى كميات كبيرة من السكريات الأساسية، بما في ذلك السكريات الأحادية والسكريات الثنائية. من ناحية أخرى، أظهر التوصيف البكتيري أن *B. cereus* MR64 أظهرت تحمل ملحوظ للملح، بالإضافة إلى إنتاج حمض الإندول أسيتيك (IAA).

أشارت النتائج إلى أن المعالجات التفاعلية (10% CLE + BT) T7 و(15% CLE + BT) T8 حسنت بشكل كبير أطوال البراعم والجذور والكتلة الحيوية ومحتوى الكلوروفيل، مع تقليل تسرب الإلكتروليتات. بالإضافة إلى ذلك، كشفت التحليلات البيوكيميائية عن انخفاض مستويات Na+ وزيادة تركيزات K+ والبرولين، مما يساهم في تنظيم تناضحي أفضل وزيادة تحمل الملح. كشف التحليل الطيفي FT-IR عن تغيرات طيفية كبيرة في النباتات المعالجة، مما يسلط الضوء على وجود مركبات فريدة تتميز بمجموعات وظيفية مثل OH وCH.

تبين أن العلاجات المعتمدة على مستخلصات الطحالب، وخاصة (15٪ CLE) T5، أكثر فعالية من السلالة البكتيرية وحدها في تحسين نمو البراعم، وأصباغ التركيب الضوئي، وسلامة الغشاء ومحتوى البرولين. في المقابل، أدى التطبيق الفردي للسلالة البكتيرية إلى زيادة كبيرة في طول الجذر والكتلة الحيوية مقارنة بالمعالجات المعتمدة على مستخلصات الطحالب وكذلك مجموعة الشواهد. أظهر التطبيق المشترك لـ PGPR ومستخلصات الأعشاب البحرية تأثيرًا تآزريًا، مما أدى إلى نمو فائق للنبات وتحسين المعايير المرفولوجية والكيميائية الحيوية. ربما يرجع هذا التآزر إلى الإجراءات التكميلية للمنشطات الحيوية الميكروبية والعضوية.

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الكلمات المفتاحية: المنشطات الحيوية، الطماطم، الاجهاد الملحي، الطحالب،PGPR , النمو، علم وظائف الأعضاء، البرولين، الهرمونات النباتية، الأحماض الأمينية

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"The greatest glory in living lies not in never falling, but in rising every time we fall."

- Nelson Mandela

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LIST OF ABBREVIATIONS

IAA: Indole-3-acetic acid

ABA: Abscisic acid

CK: Cytokinins

GA: Gibberellins

Z: Zeatin

SA: Salicylic acid

BR: Brassinosteroids

C. compressa: Cystoseira compressa

B. cereus: Bacillus cereus

Ala: Alanine

Asp: Aspartic acid

Glu: Glutamic acid

Pro: Proline

Suc: Sucrose

l-Ara: Arabinose

Glu: Glucose

PGPR: Plant growth promoting rhizobacteria

ROs: Reactive oxygen species

NaCl: Sodium Chloride

LRWC: Leaf relative water content

EL: Electrolytes leakage

CLE: Cystoseira compressa liquid extract

BT: Bacterial treatment

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INTRODUCTION

INTRODUCTION

Modern agriculture faces significant challenges due to global factors such as population growth, climate change, and environmental pollution, which adversely affect food production worldwide (Peters et al., 2009). One of the most critical issues is salinity, which affects approximately 20% of irrigated land globally, particularly in Mediterranean regions (Tomaz et al., 2020). Salinity involves the accumulation of salts, such as sodium (Na+) and chloride (Cl-), in soil or groundwater, often exacerbated by irrigation practices. Without intervention, salinization could result in a 50% loss of arable land by 2050 (Sakadevan & Nguyen, 2010; Schofield et al., 2001).

Plants exposed to salt stress experience reduced water availability, which impairs essential physiological processes like germination, growth, photosynthesis, and nutrient uptake (H.A. et al., 2019). Addressing this challenge requires innovative, eco-friendly strategies to enhance crop productivity and resilience, moving away from excessive use of inorganic fertilizers and pesticides (Vafa et al., 2021).

One promising approach involves the use of biostimulants, substances, or microorganisms that enhance plant growth and stress tolerance by stimulating natural processes (W. Khan et al., 2009; Santini et al., 2021). Biostimulants include seaweed extracts, protein hydrolysates, chitosan, silicon, humic and fulvic acids, plant growth-promoting rhizobacteria (PGPR), and arbuscular mycorrhizal fungi (du Jardin, 2015). The global biostimulant market, valued at USD 2.53 billion in 2020, is projected to grow significantly, reaching USD 4.14 billion by 2025 (Hamid et al., 2021).

In particular, plant growth-promoting rhizobacteria (PGPR) and seaweed extracts have garnered significant attention due to their distinct yet potentially synergistic roles as microbial and organic biostimulants. (PGPR) are beneficial bacteria residing in the plant rhizosphere, have been recognized since 1978 for their ability to enhance plant growth and productivity (Pérez-Montaño et al., 2014). Microorganisms such as Bacillus, Pseudomonas, Azotobacter, and Azospirillum improve nutrient acquisition through nitrogen fixation, phytohormone synthesis, and mineral solubilization. They also promote root development and maintain osmotic balance, crucial for plant responses to abiotic stresses (Batool et al., 2020; Cordero et al., 2018; Kiran et al., 2022; Ruíz-Sánchez et al., 2011; Saravanakumar & Samiyappan, 2007).

On the other hand, seaweeds, particularly brown varieties like *Cystoseira compressa*, are rich in polysaccharides, phytohormones, amino acids, vitamins, and minerals (Leandro et al., 2020). Their extracts improve plant growth and resilience to salt stress by facilitating osmotic adjustment and nutrient uptake, generating antioxidants, and enhancing soil properties and microbial communities (Battacharyya et al., 2015; Carillo et al., 2020). While previous research has demonstrated the beneficial effects of biostimulants such as PGPR and seaweed extracts, studies exploring their characteristics and combined effects with other types of biostimulants against abiotic factors such as salinity stress remain scarce. Therefore, this thesis aims to investigate the potential of selected and characterized biostimulants of diverse origins to enhance plant resilience to salinity stress,

In this context, microbial-based biostimulants and their bioformulations, especially when used synergistically with other types of biostimulants such as organic ones, offer promising, natural solutions for sustainable agriculture (Song et al., 2023). This study aims to screen PGPR strains from the Constantine region of Algeria for plant growth-promoting traits, including indole-3-acetic acid (IAA) production, phosphate (P) solubilization, hydrogen cyanide (HCN) production, and halotolerance to NaCl. Additionally, it involves the phytochemical characterization of *Cystoseira compressa*, a brown seaweed from the coast of Tipaza, Algeria, quantifying its phytohormones, amino acids, and sugars using HP-LC and LC-MS/MS. The study further examines the effects of combining a selected PGPR strain, identified as *Bacillus cereus MR64* through 16S rDNA sequencing, with different concentrations of *Cystoseira compressa* extract on the growth, physiological, and biochemical responses of tomato plants (Solanum lycopersicum L.) under salinity stress (150 mM NaCl). In addition, utilizing FT-IR spectroscopy to evaluate the functional groups associated with the vibrational peaks in tomato plants under salinity stress subjected to different biostimulant treatments.

This thesis is structured into three primary research chapters, followed by a summary that discusses the conclusions and future work directions. The chapters are as follows:

Chapter 1: Theory. This chapter provides an extensive literature review on biostimulants, salinity stress, and tomato. It explores the existing research on biostimulants, including their types, mechanisms of action, and benefits in agricultural practices. The chapter also delves into the impact of salinity stress on plant growth and development, with a particular

focus on tomato plants. It synthesizes current knowledge to establish the foundation for the research conducted in this thesis.

Chapter 2: Methodology. This chapter details the methods employed throughout the research, encompassing both practical and theoretical aspects. It describes the experimental design, the selection and application of biostimulants. The chapter also outlines the analytical techniques used to measure tomato plant growth parameters, physiological responses, and biochemical markers, in addition to the screening and chromatographical methods used to characterize the biostimulants used in this research.

Chapter 3: This chapter presents the results obtained from the experiments and provides a comprehensive discussion of their implications. It includes detailed data on the effects of biostimulants on tomato plants under salinity stress, highlighting key findings related to plant growth, physiology, biochemical responses, yield, and stress tolerance. Additionally, it includes data on the characterization of the biostimulants used in the experiments. The discussion section interprets the results in the context of existing literature, identifying novel insights and potential mechanisms underlying the observed effects.

CHAPTER 1: LITERATURE REVIEW

1. Salinity

1.1. Generalities about salinity

Soil and water salinity is a global concern that impacts soil properties, crop yield. It's commonly described by researchers as an abundance indicating the excessive presence of salts and soluble minerals such as sodium (Na+), chloride (Cl-), calcium (Ca++), and magnesium (Mg++) in high concentrations (Allison, 1964; Doneen, 1954; Tanji, 2002). High soil salinity, primarily due to sodium chloride, affects approximately one-third of the world's irrigated land and poses a significant constraint on plant production in arid and semi-arid regions (Pitman & Läuchli, 2002). This phenomenon can arise from both natural processes, such as mineral weathering, and human activities like irrigation and industrial discharge (Singh et al., 2008). Elevated levels of salinity in soils can adversely affect plant growth and development by disrupting water uptake and nutrient absorption mechanisms. Moreover, it can lead to soil degradation, decreased crop yields, and consequent economic losses for farmers (Hasanuzzaman et al., 2013; Qadir et al., 2008).

1.2. Origins of salinity

According to Zhou et al. (2013), the origin of soil salinity can be delineated into two main categories. Firstly, primary salinity arises from natural sources, such as proximity to marine environments or geological deposits of saline minerals, with the latter sometimes still actively contributing to salinization. This phenomenon is referred to as primary salinization. Secondly, secondary salinization results from anthropogenic activities, notably poorly managed irrigation practices within specific agricultural regions.

1.2.1. Primary salinity or natural salinity

Primary salinization refers to the natural process whereby soils become saline due to geological or environmental factors without significant human involvement. It occurs when salts naturally exist in the soil parent material or are introduced by natural processes like rock weathering or marine deposition (Schofield et al., 2001). This type of salinization is often intrinsic to specific landscapes and can happen in regions with particular geological formations or climate conditions that encourage salt accumulation in the soil over time (Schofield & Kirkby, 2003).

1.2.2. Secondary or anthropogenic salinity

Secondary salinity or anthropogenic salinization refers to the phenomenon in which soils become saline as a result of human activities, specifically those associated with agriculture,

irrigation practices, or land management in contrast to primary salinity, which is driven by natural geological or environmental factors, secondary salinity arises from human interventions that disrupt the natural equilibrium of salt in the soil (Seydehmet et al., 2018). Common causes of secondary salinity encompass excessive or inefficient irrigation methods, inadequate drainage systems, deforestation, and inappropriate land use practices. These activities can culminate in the accumulation of salts in the soil, thereby adversely affecting soil fertility, crop productivity, and overall ecosystem health (Mustafa et al., 2019). The management of secondary salinity typically entails the implementation of strategies aimed at enhancing irrigation efficiency, improving drainage systems, and promoting sustainable land management practices (Cuevas et al., 2019).

1.3. Definition of salty soils and their classification

Depending on the intensity and physico-chemical characteristics of the processes involved, several types of saline soils are identified. However, their classification remains complex, and most classification systems recommend subdivision into three distinct categories (Rengasamy, 2010). These categories include saline soils, saline-alkali soils, and non-saline alkaline soils, primarily differentiated by their pH, electrical conductivity (EC), exchangeable sodium percentage (ESP), and sodium adsorption ratio (SAR) (Osman, 2018).

1.3.1. Salty soils

Saline soils can be described as soils with electrical conductivity (EC) greater than 4 dS/m at a temperature of 25°C, while simultaneously exhibiting an exchangeable sodium percentage (ESP) lower than 15% (Dagar et al., 2011). It should be noted that these soils typically have a pH lower than 8.5 and are characterized by excessive salt accumulation and relatively low levels of exchangeable sodium (Guo, 2009). From a physical structure standpoint, these soils generally display a flocculated arrangement, resulting in permeability equivalent to or greater than that of comparable non-saline soils (Rhoades & Miyamoto, 1990).

1.3.2. Saline to alkaline soils

Saline-alkaline soils exhibit distinctive characteristics in terms of electrical conductivity of the saturated paste extract at a temperature of 25°C, exceeding a value of 4 dS/m, and an exchangeable sodium percentage (ESP) greater than 15% and a pH lower than 8.5. These specific soils are the result of continuous processes of salinization and alkalinization. In

situations where there is an excess of salts, it is rare for the pH to exceed 8.5 and the soil particles remain flocculated (Dagar et al., 2011). Under these circumstances, the properties of these soils can undergo significant changes and become similar to those of non-saline alkaline soils. Their permeability is influenced by the ratio between EC and ESP, as well as the content and nature of the soil's clay fraction (Rhoades & Miyamoto, 1990).

1.3.3. Non-saline alkaline soils

Non-saline alkaline soils are characterized by an exchangeable sodium percentage (ESP) greater than 15%, electrical conductivity (EC) less than 4 dS/m at 25°C, and a pH typically ranging between 8.5 and 10 (Sakai et al., 2007). These soils are characterized by their alkalinity, which is attributed to the presence of basic minerals such as calcium carbonate (lime) or magnesium carbonate (Buehrer & Williams, 1936). Alkaline soils tend to have a light, chalky texture and may exhibit low nutrient availability due to high pH levels, which can affect plant growth (White, 1990). However, some alkaline soils can be fertile and suitable for certain crops, especially those adapted to such conditions. Alkaline soils are commonly found in arid and semi-arid regions but can also occur in other areas with specific geological formations (Khormali & Abtahi, 2003).

1.4. Salinity of irrigation waters

The salts present in irrigation water, including sodium chloride (NaCl), gypsum (CaSO4), Epsom salts (MgSO4), and sodium bicarbonate (NaHCO3), dissolve to produce ions, comprising both cations and anions (Longenecker & Lyerly, 1957). Major cations include calcium (Ca2+), magnesium (Mg2+), and sodium (Na+), while common anions consist of chloride (Cl-), sulfate (SO42-), and bicarbonate (HCO3-) (Bauder et al., 2008). However, the distribution of these ions varies depending on different water sources. Recognizing the significant potential for salinization arising from natural weathering and dissolution of soil parent materials is crucial, influencing the overall ionic composition of irrigation water (Ali, 2010). Two predominant methods are commonly used to assess irrigation water quality in terms of salinity. One approach involves reporting irrigation water salinity as total salt concentration or total dissolved solids (TDS), typically expressed in milligrams of salt per liter (mg/L) of water. Another commonly recorded measure in water quality assessments by commercial laboratories is specific conductivity, also known as electrical conductivity (EC), usually in millimhos per centimeter (mmhos/cm) or decisiemens per meter (dS/m) (Grattan, 2002).

1.5. Definition of salt stress

Salinity stress occurs when plants are exposed to high levels of salts in their environment, whether in the soil or in the water used for irrigation. This condition encompasses a wide range of adverse effects on plant growth and development, resulting from the disruption of normal physiological processes (Dajic, 2006; Hasanuzzaman et al., 2013; Ondrasek et al., 2011). High salt concentrations can hinder water absorption by plants, leading to osmotic stress and dehydration of plant tissues. Additionally, excessive amounts of salts can impede the uptake of essential nutrients by plant roots, causing a nutritional imbalance and the manifestation of deficiency symptoms (Yadav et al., 2011). Furthermore, the presence of salts can trigger ion toxicity, with certain ions, such as sodium (Na+) and chloride (Cl-), accumulating to toxic levels in plant cells, thereby disrupting cellular functions and causing damage (Rasool et al., 2013). In agriculture, the presence of high salt levels poses a significant barrier to crop productivity, especially in areas where soil salinity or the use of saline irrigation water is widespread. This situation can result in a substantial decrease in crop yield and cases of poor harvests, negatively impacting food security and the livelihoods of the population (Yadav et al., 2011).

1.5.1. The effects of salt stress on plants

Salinity stress is recognized as one of the most detrimental environmental challenges for plants, inflicting ion toxicity, osmotic stress, and oxidative stress simultaneously (Khare et al., 2015). This hostile condition disrupts normal cellular functions, impedes water absorption, and creates nutrient imbalances, leading to the disturbance of various biochemical, physiological, and metabolic processes, ultimately hindering plant growth and development (Muchate et al., 2016).

1.5.1.1. Osmotic stress

According to Finan & Guilak (2010), osmotic stress results from an imbalance in solute concentrations separated by a selectively permeable barrier, leading to the movement of water molecules to equalize these concentrations through osmosis. This phenomenon occurs when a cell or organism encounters conditions of elevated concentrations of salts, substrates, or any solute (Yancey et al., 1982). Osmotic stress induced by salinity stress poses significant challenges for plants as soil salinity increases, reducing water availability due to higher salt concentrations surrounding plant roots. Consequently, plants undergo dehydration and struggle to maintain their water balance (Oliveira et al., 2013). Osmotic

stress disrupts crucial physiological processes such as photosynthesis and nutrient absorption, resulting in reduced growth, leaf wilting, and ultimately, decreased crop yields (Alam, 1999).

1.5.1.2. Ionic toxicity

Ionic toxicity induced by salinity stress in plants arises from the accumulation of high levels of ions, notably sodium (Na+) and chloride (Cl-), in the soil. This accumulation hampers the plant's normal physiological processes, resulting in a myriad of detrimental consequences (Evelin et al., 2009; Hagemeyer, 1997). An excess of sodium ions has the potential to replace vital nutrients such as potassium (K+) within plant cells, thereby disrupting enzymatic activities and metabolic pathways. Additionally, chloride ions have the ability to disrupt cellular functions and create an imbalance in ion distribution (Subbarao et al., 2003). This disruption of ion concentrations can lead to osmotic stress, desiccation of plant cells, and hindered nutrient absorption (Ma et al., 2020; Nawaz et al., 2010).

1.5.1.3. Oxidative stress

Salinity stress induces oxidative stress by initiating the release of free radicals that possess extremely high toxicity towards cellular metabolism, encompassing superoxides (O2-), hydroxyl radicals (OH·), and peroxides (H2O2) (Hasanuzzaman et al., 2012). As by-products of osmotic and ionic stress, these reactive oxygen species (ROS) can damage cellular components, including proteins, lipids, and DNA, disrupting cellular functions and compromising plant health. These damages may manifest as leaf chlorosis, cell death, and reduced growth (Carillo et al., 2011). To counteract the detrimental impact caused by ROS, plants activate specific defense mechanisms associated with antioxidants, involving the upregulation of crucial antioxidant enzymes such as catalase (CAT), peroxidase (POD), glutathione reductase (GR), and superoxide dismutase (SOD) (Gill & Tuteja, 2010). These enzymes play pivotal roles in capturing and neutralizing ROS, thus protecting cellular components against oxidative damage and enhancing plant resilience to salinity stress conditions (Hasanuzzaman et al., 2013).

1.5.1.4. Effect of salt stress on plant growth and development

Salinity stress exerts a multitude of detrimental effects on plant growth, including the inhibition of seed germination and seedling establishment, impaired growth, reduced biomass accumulation, leaf chlorosis, and necrosis due to nutrient deficiencies (Nawaz et

al., 2010). Furthermore, salinity diminishes shoot development by inhibiting leaf initiation and expansion, as well as internode growth, while accelerating leaf shedding, contributing to decreased flowering and fruit set, resulting in reduced yields (Bastam et al., 2013; Botía et al., 2005; Farooq et al., 2015). The growth and developmental alterations observed under salinity stress conditions result from a combination of factors, including inhibition of water absorption and transport due to osmotic stress, leading to reduced stomatal opening, decreased CO2 assimilation, and lowered photosynthesis rate, ultimately impairing overall plant performance and productivity (Farooq et al., 2015; Hasanuzzaman et al., 2013).

1.5.1.5. Effect of salt stress on plant physiology

Salinity stress disrupts plant physiology in various ways, primarily by altering the ionic balance within the protoplasm. Excessive salt concentrations lead to functional disturbances in key physiological processes, including photorespiration, resulting in decreased energy production (Djanaguiraman & Prasad, 2013; Koyro et al., 2011). Nitrogen assimilation and numerous metabolic pathways are also disrupted, further impacting plant metabolism (Silveira et al., 2001). When salt levels exceed the plant's tolerance threshold, photosynthesis is particularly affected due to salt-induced disruptions in the chloroplast stroma, hindering electron transport (Dajic, 2006). Additionally, glycolysis and the Krebs cycle undergo alterations (Saha et al., 2012). Salinity stress also affects water uptake by plants, disrupting water absorption and transport mechanisms in the roots (Aroca et al., 2012). The plant's ability to acquire essential mineral substances such as potassium or calcium is compromised under saline stress conditions (Cramer et al., 1991). Consequently, plants exhibit signs of stress, such as anthocyanin production or chlorophyll degradation (Eryılmaz, 2006).

1.5.1.6. Effect of salt stress on plant biochemical processes

When plants are subjected to salt stress, there is a notable reduction in carbon assimilation due to decreased photosynthesis and an increase in respiration maintenance (Schwarz & Gale, 1981). The impact of salinity on proteogenesis is evident as it leads to a decrease in protein synthesis and an increase in proteolysis rates. This, in turn, results in the accumulation of free amino acids and amides, such as proline (Omidbakhshfard et al., 2012). Additionally, salt stress induces alterations in carbohydrate metabolism, either by altering glycolysis pathways and suppressing the TCA cycle or by promoting starch accumulation, leading to an increase in total sugars (Chen & Hoehenwarter, 2015; Li et al., 2015). Salt stress causes alterations in the lipid composition of cell membranes, affecting

their stability (Mansour & Salama, 2004). Furthermore, salt stress stimulates the production of reactive oxygen species (ROS), thus disrupting cellular redox homeostasis. This disruption leads to protein and enzyme degradation, lipid peroxidation, as well as modifications of essential cellular structures, including the electron transport system and various membranes (Saha et al., 2015; Sudhir et al., 2005). Salt stress also disrupts the hormonal balance of plants and interferes with the biosynthesis of endogenous phytohormones such as gibberellins (GA), abscisic acid (ABA), and jasmonic acid (JA) (Kaleem et al., 2018).

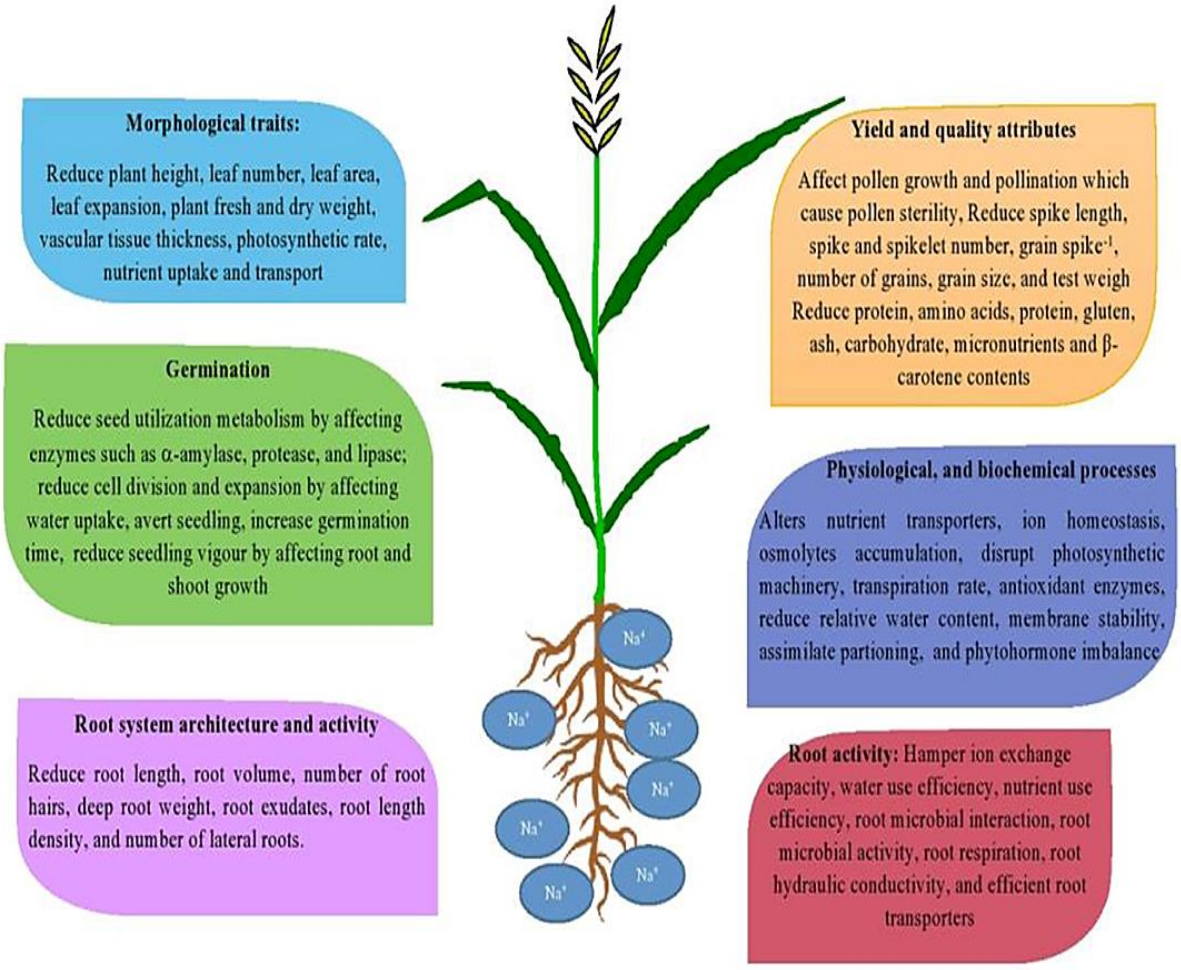

Figure 1: The impacts of salt stress on various growth phases and essential processes of plants (Sabagh et al., 2021).

1.5.2. Mechanisms and strategies of plant adaptation to salt stress

In response to salinity stress, plants employ a range of intricate mechanisms and strategies to ensure survival and sustained growth (Botella et al., 2005; Munns & Tester, 2008).

Glycophytes, which cannot tolerate high salt concentrations, and halophytes, which excel in saline environments, display distinct adaptations (Flowers & Colmer, 2008). Morphological and anatomical adaptations are adopted by plants to confront salinity (Hameed et al., 2010). In addition, ion homeostasis, compartmentalization and exclusion are crucial for effectively regulating internal ion concentrations. Transport mechanisms facilitate ion movement, while specialized uptake processes assist in managing external salt levels (Teakle et al., 2010). Furthermore, osmotic adjustments and accumulation of osmoprotectants play a vital role in maintaining cellular turgor pressure and protecting cells from damage under saline conditions (Singh et al., 2015). Additionally, plants activate antioxidant enzyme machinery to counteract oxidative damage and synthesize polyamines to mitigate stress-induced toxicity (Gill & Tuteja, 2010; Liu et al., 2015). Morever, hormonal regulation coordinates various physiological responses, optimizing plant resilience to salinity (Kaleem et al., 2018).

1.5.2.1. Exclusion

The exclusion process involves the restriction of salts such as sodium ion (Na+) intake in the root cortex, which assists in the expulsion of (Na+) from leaf regions and prevents its toxic accumulation within the leaf blades (Djanaguiraman & Prasad, 2013). The exclusion of (Na+) from the roots ensures that it does not reach harmful concentrations of salts within the plant, thus protecting against damage caused by salt (Farooq et al., 2015). This mechanism acts as a barrier against the entry of salt while allowing the passage of water, thereby enhancing the plant's ability to remove salt (Djanaguiraman & Prasad, 2013). Halophytes, which are specialized plants in saline environments, have developed strategies to exclude excessive accumulated Na+ and Cl– from their roots and lower stems (Glenn et al., 1999). Notably, the exchange of Na+ from xylem vessels for (K+) from surrounding parenchymal cells plays a crucial role in maintaining ion balance in stems and roots (Ahmad & Maathuis, 2014).

1.5.2.2. Ion homeostasis and compartmentalization

Plants uphold sodium Na+ homeostasis when subjected to salinity stress through the imposition of limitations on Na+ uptake, the compartmentalization of Na+, and the augmentation of Na+ efflux (Hertz et al., 2013). Ion homeostasis involves a dynamic process wherein plants establish energetically costly gradients to uptake necessary ions and eliminate toxic ones (Dajic, 2006). Whether glycophytes or halophytes, plants are susceptible to elevated concentrations of sodium ions Na+ in the cytoplasm. Sodium

uptake primarily occurs at the root-soil interface, facilitated by nonselective cation channels (Maathuis, 2014). Futhermore, according to Shabala & Pottosin (2014) plants sequester excess salts in the vacuole or different tissues to support metabolic functions. Potassium K+ ions, essential for enzyme activation, photosynthesis, and other functions, are predominant in the plant cytosol. Plants maintain a high K+/Na+ cytosolic ratio for normal functioning. In saline environments, NaCl ionizes into Na+ and Cl− ions, inhibiting K+ uptake by interfering with root cell plasma membrane K+ transporters. High-affinity K+ ion transporters may act as low-affinity Na+ ion transporters during salinity, potentially facilitating Na+ influx into the cells (Benito et al., 2014; Maathuis, 2014).

1.5.2.3. Osmotic adjustment and accumulation of osmoprotectants

Osmotic adaptation holds immense importance in the maintenance of cell turgor, a vital factor in augmenting plant growth, productivity, and yield. To achieve osmotic balance, plants synthesize and accumulate various molecules including amino acids, polyamines, quaternary ammonium compounds and sugars (Singh et al., 2015). These molecules, known as osmoprotectants or compatible solutes, are small organic compounds with a neutral charge and minimal toxicity even at elevated concentrations. They function as osmolytes and aid organisms in withstanding extreme osmotic stress (Altendorf et al., 2009; Csonka & Hanson, 1991). Proline, acting as both an amino acid and an osmoprotectant, accumulates in the plant cytosol in response to salinity stress. Its role is to stabilize membranes, enzymatic proteins, and other cellular constituents (Singh et al., 2015).

Moreover, proline regulates plant metabolism under stress conditions by upregulating the expression of membrane proteins, scavenging reactive oxygen species (ROS), and maintaining cellular solute balance (Hossain et al., 2014). Glycine betaine, along with other betaines, demonstrates robust osmoprotective properties by modulating the ratio of sodium (Na+) to potassium (K+) ions and accumulating within cells to counteract the effects of salinity (Tuteja et al., 2012). Sugars and sugar alcohols also contribute to cellular osmotic balance during high salinity as osmolytes. Increased production of reduced sugars, such as fructose, glucose, sucrose, and fructans, aids in maintaining membrane integrity and protecting proteins from damage (Nagabhyru et al., 2013). Additionally, sugar alcohols such as inositol, sorbitol, and mannitol assist in salinity tolerance by adjusting cellular osmotic equilibrium (Singh et al., 2015).

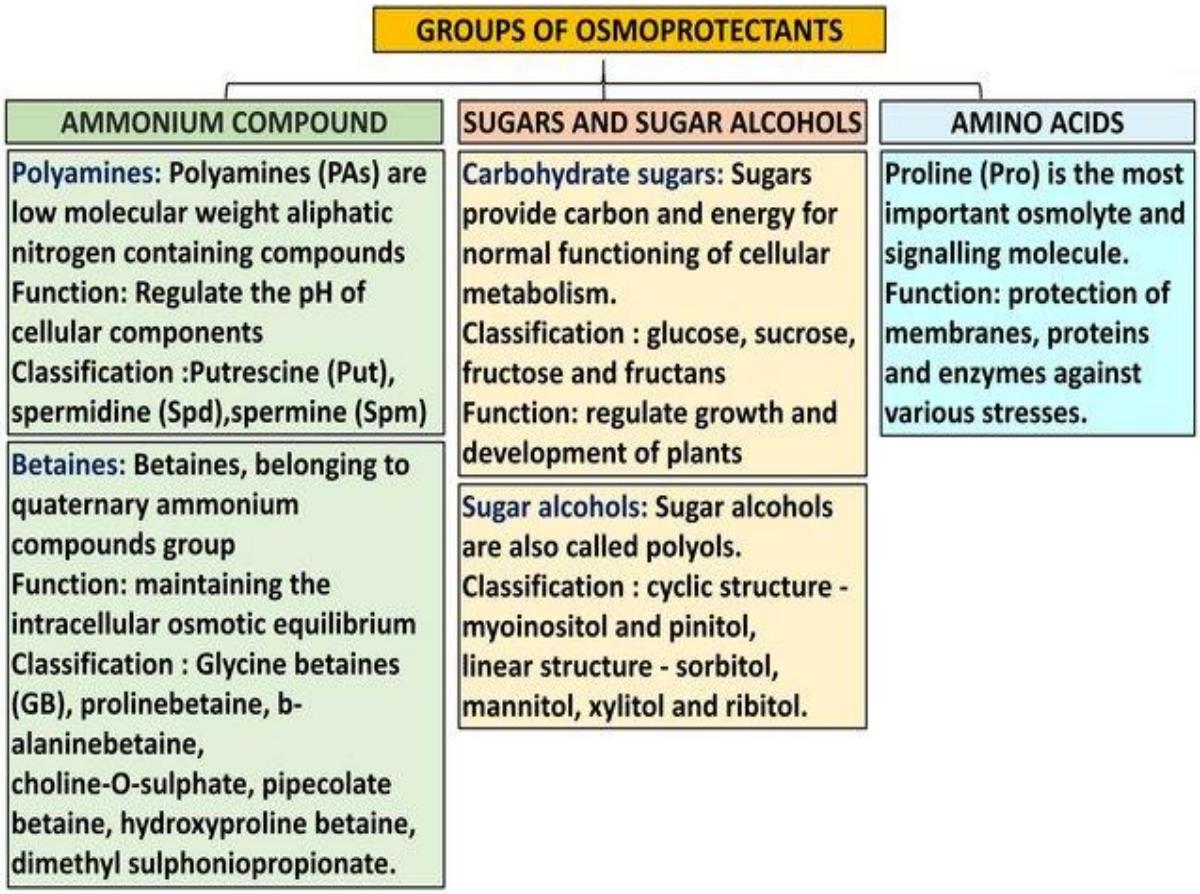

Figure 2: Classification of different osmoprotectants (Dubey et al., 2021).

1.5.2.4. Antioxidant defense

Reactive oxygen species (ROS), including superoxide (O2−), hydrogen peroxide (H2O2), and singlet oxygen (1O2), are produced in response to high salinity stress and can cause significant damage to membrane lipids, proteins, and nucleic acids (Gill & Tuteja, 2010). Detoxifying ROS is essential for plant defense against abiotic stresses like salinity (Hasanuzzaman et al., 2012). These defense mechanisms involve activating antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and ascorbate peroxidase (APX), which eliminate ROS and protect cellular components from oxidative damage (Gill & Tuteja, 2010). Additionally, plants may increase the production of non-enzymatic antioxidants such as glutathione, ascorbic acid, and tocopherols, which directly neutralize ROS and maintain cellular redox balance (Waśkiewicz et al., 2014).

1.5.2.5. Endogenous phytohormonal adaptations

Phytohormonal responses play a crucial role in mediating plant adaptations to salinity stress. Gibberellins (GAs), ethylene (ET), cytokinins (CKs), salicylic acid (SA),

jasmonates, abscisic acid (ABA), and brassinosteroids (BRs) are essential hormones involved in the signaling pathways activated by salinity stress, modulating different organs and regulating specific genes to facilitate plant adaptation (Fahad et al., 2015; Javid et al., 2011). For instance, ABA, known as the stress hormone, accumulates in tomato leaves and roots under saline conditions, prompting stomatal closure to manage low soil water potential, thus affecting photosynthesis and promoting root growth (Fahad et al., 2015). Another hormone, indole acetic acid (IAA), is synthesized at higher levels during salinity stress, alleviating osmotic and oxidative stress effects across various plant developmental stages (Kaya et al., 2010). Salinity stress is known to downregulate endogenous levels of bioactive gibberellic acid (GA) in plants. However, research has shown that exogenous application of GA3 can mitigate the detrimental effects of salt stress and promote plant growth (Hamayun et al., 2010).

Additionally. Salicylic acid (SA) concentration increases during salinity stress, promoting growth, yield, and development, while also upregulating genes involved in antioxidant enzyme expression and secondary metabolite synthesis (Singh & Gautam, 2013). Similarly, Brassinosteroids (BRs) emerge as crucial players in enhancing plant tolerance to abiotic stresses like salinity. They promote germination, pollen tube growth, vascular development, and even reproduction under stress conditions. This stress-mitigating effect of BRs is attributed to their ability to elevate the levels of osmoprotectants and antioxidants (Ashraf et al., 2010). Moreover, plant growth regulators, cytokinins (CKs) and auxin (AUX), contribute in diverse plant processes like cell division, photomorphogenetic differentiation, and promoting photosynthesis (Boivin et al., 2016). However, the response of these hormones under salt stress is complex. While some studies suggest increased levels of certain (CKs) might contribute to salt stress tolerance, endogenous (CKs) levels generally decrease under salinity (Javid et al., 2011).

1.5.2.6. Morphological and anatomical adaptations

The roots modify their growth patterns to enhance their water and nutrient uptake capabilities. Consequently, this often leads to the development of a denser root system with increased diameter and lateral roots (Bernstein & Kafkafi, 2002; Mohammad et al., 1998). Additionally, the thickening of root cell walls serves as a protective barrier against excessive salt intake (Lux et al., 2004). To minimize water loss through transpiration, plants may also regulate their leaf area, potentially through the reduction of specific leaf area or leaf area ratio, or even shedding leaves altogether (Zia, 1990). Furthermore, the

control of water loss may involve the regulation of stomatal conductance, whereby sunken stomata can reduce the efflux of water vapor while still allowing for the uptake of CO2 for photosynthesis (Chaves et al., 2016). In terms of anatomical adaptations, modifications specialized structures, such as aerenchyma tissue, assist in the transport of oxygen in waterlogged soils (Shiono et al., 2008). Changes in leaf anatomy may include the prominence of the palisade mesophyll and a reduction in the spongy parenchyma, along with the development of thicker cuticles in aerial parts to minimize transpiration and maintain cell turgor (Yadav et al., 2011).

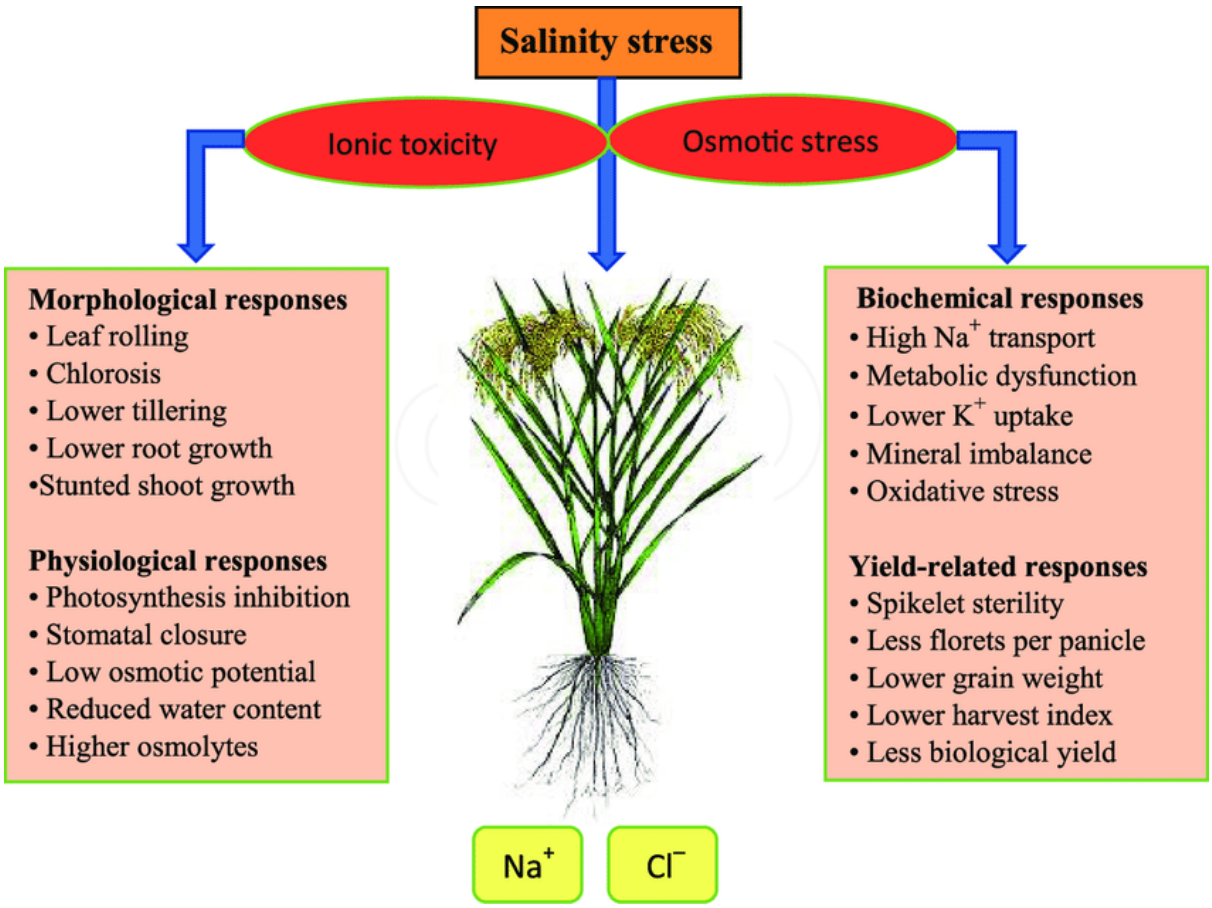

Figure 3: Responses and adaptations of plants to salinity stress (Hasanuzzaman, 2022).

2. Biostimulants

2.1. Definition and introduction to Biostimulants

Biostimulants are becoming increasingly recognized in modern agriculture as effective means to enhance plant growth and development, fortify resilience to stress, and maximize crop productivity (Nephali et al., 2020). According to (Calvo et al., 2014). These innovative tools are substances or microorganisms when applied to plants, seeds, or growing medium they facilitate nutrient absorption and assimilation, influence plant growth processes by improving tolerance to abiotic stresses and increase yield and quality. Biostimulants, are different from fertilizers, they do not directly supply nutrients to plants. Instead, they may enhance nutrient uptake by promoting metabolic activities within soil and plants. For instance, they may aid in the establishment of arbuscular mycorrhizal fungi, which facilitate nutrient transport to the host plant (Tavarini et al., 2018). Biostimulants can include a wide variety of categories, such as: seaweed extracts, seaweed extracts, protein hydrolysates, chitosan, silicon, humic and fulvic acids, and microorganisms (Bulgari et al., 2019; Rouphael & Colla, 2020). In the legislation passed by the European Parliament and Council on June 5, 2019, known as Regulation (EU) 2019/1009 defines biostimulants are defined as follows: “A product that stimulates plant nutrition processes independently of the product’s nutrient content, with the sole aim of improving one or more of the following characteristics of the plant or the plant rhizosphere: nutrient use efficiency; tolerance to abiotic stress; quality traits; or availability of confined nutrients in the soil or rhizosphere”. Over time, various classification systems have been proposed to categorize biostimulant compounds (Yakhin et al., 2017). Overall, biostimulants have the potential to enhance global food security and address challenges related to population growth and climate change (Bashir et al., 2022; Buono, 2021).

2.2. Types of Biostimulants

du Jardin (2015) relegated them into seven different categories: Humic/Fulvic acids, Seaweed/Botanical extracts, Protein hydrolysates, Biopolymers, Salutary minerals, Propitious bacteria. Later on, this system was revised by Bulgari et al. (2019), who integrated another category including extracts from industrial or victuals wastes and grouped nanomaterials and nanoparticles into the category of biopolymers. Over the years, several authors have proposed different classifications of biostimulants based on their origin, main component, or mode of action (du Jardin, 2015; Yakhin et al., 2017). A

simpler categorization based on the source of raw material in which Biostimulants can be relegated into five major groups was suggested by (Franzoni et al., 2022) as summarized below:

- Seaweeds and plant extracts
- Microorganisms
- Humic substances
- Hydrolyzed proteins and nitrogen-containing compounds
- Inorganic compounds with biostimulant action

Biostimulants may also be categorized according to their application method (either soil or foliar), their source (plant-derived or animal-derived), and the production technique employed (such as hydrolysis, fermentation, or extraction) (Drobek et al., 2019).

2.2.1. Biostimulants of plant and algal origin

Biostimulants can be obtained from plants opulent in secondary metabolites, which are withal one of the main kinds of bioactive compounds proposed as responsible for activating the physiological replications of plants (Bulgari et al., 2017; Moreno-Hernández et al., 2020). For example, the extract obtained from the maceration of borage leaves or flowers showed biostimulant effects on the magnification and quality of lettuce (Moreno-Hernández et al., 2020).

Seaweed extracts are currently exploited in agriculture as soil conditioners or as plant biostimulants (Battacharyya et al., 2015). Seaweeds are a sizably voluminous group and include macroscopic marine algae and multicellular algae belonging to different taxonomic groups, such as brown, red, and green algae (Khan et al., 2009; Leliaert et al., 2012). They are a consequential source of nutrients, bioactive compounds, organic matter, and fertilizers. Algae have been utilized in agriculture since archaic times as fertilizers, due to the positive effects on crops (Battacharyya et al., 2015). When employed as biostimulants, their biological impact is demonstrated through enhancements in plant growth, crop yield, and product quality, as well as increased tolerance to abiotic stress such as salinity (O. Ali et al., 2021). The algae utilized in the engenderment of biostimulants contain plant hormones such as cytokinins and auxins or other hormone-like substances (Mukherjee & Patel, 2020). Algae-predicated biostimulants additionally contain many mineral and bioactive compounds, including involute polysaccharides such as laminarine, fucoidan, and alginates (Bulgari et al., 2019; Rouphael & Colla, 2020).

2.2.1.1. Seaweed-based extracts

2.2.1.1.1. Overview of marine macroalgae

Seaweeds, also referred to as marine macroalgae, represent a diverse array of multicellular mostly photosynthetic algae found in marine environments. The term includes some types of Rhodophyta (red), Phaeophyta (brown) and Chlorophyta (green) macroalgae. These organisms are classified within the kingdom Protista or Plantae, depending on their taxonomic categorization (Douglas et al., 2003; Larkum et al., 2003; Medlin et al., 2007). Cardol & Franck (2010) defined marine macroalgae as a subset of eukaryotic algae, referring to algae with a minimum linear size of at least 1 mm. This classification includes certain phytoplankton organisms. Therefore, we append 'commonly benthic' to align with the conventional understanding of macroalgae among most scientists. Seaweeds exhibit various forms, ranging from large kelps capable of forming underwater forests to smaller filamentous algae (Van Patten & Yarish, 2009). They fulfill vital ecological functions in marine ecosystems by offering habitats for a wide range of marine organisms, contributing to the cycling of nutrients, and serving as a food source for numerous species, including humans (Peterson & Lubchenco, 1997). In addition, seaweed farming, also known as kelp farming, involves the cultivation and harvesting of seaweed. This practice ranges from simple gathering from natural beds to complete control over the crop's life cycle by farmers (Khan & Satam, 2003). Seaweeds possess significant values because of their derived bioactive substances, with applications in food, agriculture, cosmetics, and pharmaceuticals, attributed to their abundant nutritional content and bioactive compounds (Kumar et al., 2008). Moreover, over the last 45 years, numerous bioactive secondary metabolites had been isolated and characterized from various macroalgae species (Elsayed et al., 2012). These natural compounds provide novel systems and mechanisms of applications and for bioformulation (Ioannou & Roussis, 2009).

2.2.1.1.2. Classification of marine macroalgae

2.2.1.1.2.1. Chlorophyta (green macroalgae)

According to several studies (Bremer et al., 1987; Kenrick & Crane, 1997; Sluiman, 1985; Stewart, 1984) green algae are photosynthetic eukaryotes that have double membrane-bound plastids containing chlorophyll a, b, accessory pigments found in embryophytes (beta caroteine and xanthophylls), and a special stellate structure connecting nine pairs of microtubules in the flagellar base. The plastid stores starch, and when cell walls are present, they are often made of cellulose (Graham et al., 1991). The prokaryotic origin of

green algae's plastids is shared by several other eukaryotic lineages, whose descendants live endosymbiotically in their host cells (Delwiche, 1999; Delwiche & Palmer, 1997). These plastids are known as primary because they were directly descended from a prokaryotic ancestor that was free-living (Delwiche, 1999; Delwiche & Palmer, 1997). Green algae thrive in both freshwater and saltwater environments, ranging in size from singular cells to complex, visible form. Their characteristic green appearance is attributed to the presence of chlorophyll. In order to survive, these organisms require copious amounts of sunlight, which is most abundant in shallow waters. As a result, green algae can often be found near the shore or along the periphery of the ocean (Dhargalkar & Kavlekar, 2004).

2.2.1.1.2.2. Rhodophytes (red macroalgae)

Rhodophytes are characterized by their red or pink coloration, which is due to the presence of pigments such as phycoerythrin and phycocyanin. Red algae exist as epiphytes, appearing as large, fleshy, branching, or blade-like structures forming crusts on rocks or shells (Morrissey et al., 2001). Species of seaweed containing red algae tend to be more delicate, smaller, and branch-like in appearance. Molecular studies of nuclear, plastid, and mitochondrial genes have united members of the red algae (Rhodophyta), establishing them as a distinct eukaryotic lineage (Freshwater et al., 1994; Ragan et al., 1994; Van de Peer & De Wachter, 1997). Rhodophytes lack chlorophyll b and c but possess phycobilisomes with phycocyanin, phycoerythrin, and allophycocyanin on unstacked thylakoids (Lin, 1991). Their plastids are enclosed by two membranes and produce floridean starch deposited in the cytoplasm (Bouzon et al., 2014). Throughout their life cycles, all members of this group lack centrioles and flagella (Gabrielson et al., 1990).

2.2.1.1.2.3. Phaeophytes (brown macroalgae)

Brown algae represent some of the fastest-growing seaweed species they exhibit a diverse array of shapes, ranging from simple filaments with free branches to highly distinctive morphologies (Lobban & Harrison, 1994). Many species possess buoyancy due to their large thalli, which feature specialized air bladders, vesicles, or floats. The hues of brown algae span from olive-yellow to deep brown, attributed to the photosynthetic pigment fucoxanthin and accessory carotenoid pigment. Xanthophylls, chlorophylls a and c, along with other photosynthetic pigments, are also found in brown algae (Milchakova, 2011). These algae encompass both simpler, mainly microscopic, filamentous forms and complex, macroscopic thalli containing parenchyma and meristematic sections (Hoek et al., 1995;

Wehr et al., 2015). In some species, specific phaeophycean tannins, which accumulate in cytoplasmic inclusions known as physodes. These tannins potentially serve as UV protection or as inducible defense against herbivory (Lüder & Clayton, 2004; Schoenwaelder, 2002). Chloroplasts, containing chlorophylls a, c1, and c2, as well as other xanthophylls, can be discoid or ribbon-like and may or may not contain pyrenoids, located in one to several cells (Pueschel & Stein, 1983; Silberfeld et al., 2011).

Figure 3: Types of macroalgues: (A): green seaweed (*Cladophora rupestric L.*), (B): red seaweed (*Mastocarpus stellatus Kutz.*), (C): brown seaweed (*Fucus serratus L.*) (GBIF.org (2023), GBIF data base, https://www.gbif.org).

2.2.1.1.3. Overview on the seaweed used in the study *Cystoseira compressa*

Cystoseira compressa is a multicellular, flexible brown alga with an upright, tree-like growth form, ranging in color from yellow-green to dark brown (Bruno et al., 2019). Its height varies from a few centimeters in turbulent environments to over 50 centimeters in calm waters such as small harbors. This alga attaches to rocks via a small discoid base from which several short, upright axes emerge, measuring 2 to 3 centimeters (Project M.A.R.E, 2019). These axes, virtually absent in juveniles, bear long primary branches flattened at the base and arranged in a distichous manner, further branching up to the third or fourth order (Marletta & Lombardo, 15 C.E.).

Figure 4: Brown macroalgae *Cystoseira compressa* (original picture).

The thallus is smooth, lacking spiny branchlets, with primary branches being flattened, while secondary and tertiary branches may be flattened or cylindrical. These algae form characteristic rosettes, with short, flat branches arranged more or less horizontally on the substrate. In spring and early summer, the thalli become erect and highly branched, particularly in the apical region (Farghaly, 2019). *Cystoseira compressa* belongs to the genus *Cystoseira* which belongs to the *Phaeophyceae* class of brown algae and is part of the family *Sargassaceae* according to Gerloff & Nizamuddin (1975) the following taxonomy:

- Domain: *Eukaryota*
- Reign: *Chromista*
- Junction: *Heterokonta*
- Class: *Phaeophyceae*
- Order: *Fucales*
- Family: *Sargassaceae*
- Genus: *Cystoseira*

Among the approximately 40 species of algae in the *Cystoseira* genus (Phaeophyta), *C. compressa* is prevalent along the Eastern Atlantic and Mediterranean coasts, with notable distribution in the Adriatic Sea (Robvieux, 2013). According to Bahbah et al. (2022) the genus *Cystoseira* is represented in Algeria by 19 taxa, including species such as *Cystoseira algeriensis*, *Cystoseira amentacea*, *Cystoseira barbata*, and *Cystoseira compressa*.

Cystoseira species have a monogenetic diplobiontic life cycle, with a predominant diploid sporophyte phase and a haploid phase limited to gametes. Male and female gametes are produced in small fertile crypts on the terminal branches. Fertilization occurs in water after the release of sperm and oospheres from conceptacle openings. Fertilized eggs sink and adhere to the substrate, limiting species dispersion. However, currents can transport detached fertile thalli, aiding species propagation (Falace et al., 2005).

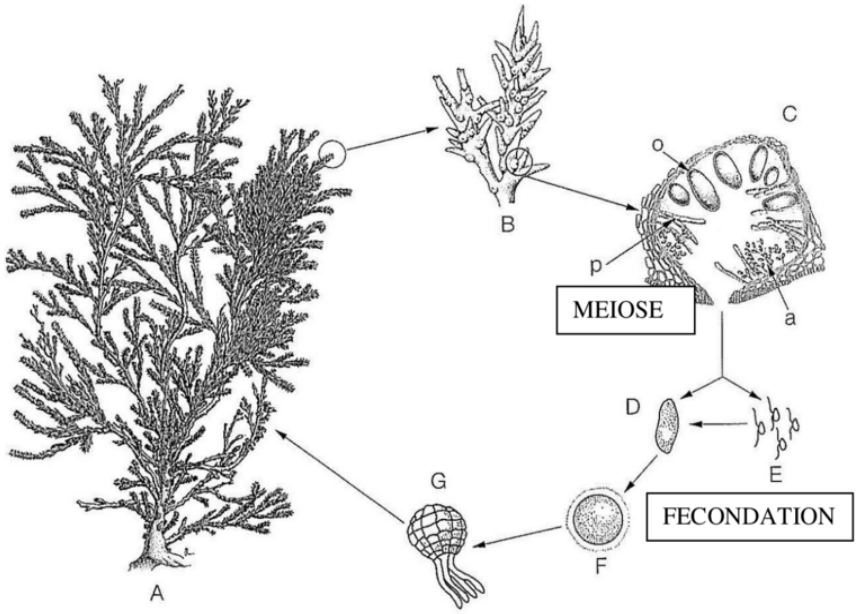

Figure 5: The schematic representation illustrates the life stages of a species belonging to the genus *Cystoseira*. Key elements include: A) mature organism, B) terminus of a branching structure featuring conceptacles, C) cross-sectional view of a conceptacle, D) female gamete, E) male gamete, F) zygote, and G) zygote accompanied by rhizoids (Garreta & Ribera, 2002).

2.2.1.1.4. Chemical constitution of marine macroalgae

The phytochemicals of seaweeds can be divided into two major groups: primary metabolites and secondary metabolites. Primary metabolites, namely carbohydrates, amino acids, lipids, and nucleic acids, are responsible for the development and growth of organisms. Secondary metabolites, on the other hand, are a group of compounds that, while not essential, give plants the ability to survive and overcome many obstacles, and allow them to interact and adapt to their surroundings; thus, the same plant species growing in different locations may have different concentrations of compounds, or even different compounds in their constitution (Azmir et al., 2013; Lobo & Lourenço, 2007; Santos et al., 2016).

2.2.1.1.4.1. Phytohormones

Phytohormones, also known as plant hormones, are essential signaling molecules synthesized in plants to regulate various physiological processes (Fahad et al., 2015; Nadeem et al., 2016). They influence plant growth, development, and responses to stress, playing a fundamental role in plant biology. Phytohormones encompass structurally diverse compounds including auxin, abscisic acid (ABA), gibberellins (GA), cytokinins, and ethylene, while newer classes include jasmonates (JAs), salicylic acid (SA), brassinosteroids, and strigolactones (Santner & Estelle, 2009). Seaweeds contain natural plant growth-promoting hormones such as auxin, cytokinin, and abscisic acid-like substances, which enhance growth and yield (Crouch & Van Staden, 1993; Reitz & Trumble, 1996). Many researchers located Indole -three- acetic acid (IAA) and any other hormone from marine algae that stimulate plant boom and improvement traits (Zhang et al., 1993). Cytokinins affected flora for the duration of the whole cell cycle and influence numerous developmental applications (Werner et al., 2001). It's determined in lots of marine macroalgae consisting of *Porphyra perfroata, Sargassum muticum* as well as in algae *Chara globularis* (Zhang et al., 1989, 1991). In addition, according to Yalçın et al. (2019) The *Cystoseira barbata* seaweed from the brown algae group was observed to be the only species containing zeatin, GA, BAP, IAA, ABA hormones together. Seaweeds exhibit a remarkable diversity and variety of phytohormones, contributing to their adaptability and resilience in marine environments (Stirk & van Staden, 2020).

2.2.1.1.4.2. Polysaccharides

Seaweeds synthesize polysaccharides primarily for storage and as constituents of their cellular structures. These macromolecules are present in both the fibrous cell walls and the intercellular matrix, often alongside other biopolymers (Mišurcováa et al., 2014; Stiger-Pouvreau et al., 2016). Notably, commercially and biomedically relevant polysaccharides have been extracted from various seaweed groups: red seaweeds (*Rhodophyta*), such as carrageenans and agarans; brown seaweeds (*Phaeophyta*), including alginates and fucoidans; and certain green seaweeds (*Chlorophyta*), such as ulvans (Cosenza et al., 2017; Khalid et al., 2018). Each of these polysaccharides exhibits a specific chemical composition, which can vary depending on factors such as species, life stages, seasonal variation, habitat, and extraction methods, Polysaccharides can make up to 76% of their total dry weight of seaweeds (Kraan, 2012; Pomin, 2012; Synytsya et al., 2015). Furthermore, they are abundant in renewable sources, non-toxic, and possess rheological

and/or biological properties, making them valuable for diverse applications (Ciancia et al., 2020). Polysaccharides found in the cell walls of *Ulvophyceae* (green seaweeds) encompass both neutral and sulfated varieties. The former typically comprise fibrillar polysaccharides like cellulose, β-mannans, and β-xylans, the presence of which is species-dependent and sometimes influenced by the life cycle (Cosenza et al., 2017).

2.2.1.1.4.3. Proteins and amino acids

Seaweeds exhibit a protein content up to 47% of their dry mass, manifesting in various forms and cellular locations such as peptides, enzymes, glycoproteins, lectins, and amino acids (Thiviya et al., 2022). However, detailed information regarding their distribution across taxa remains limited, with few exceptions like the well-documented cases of light-harvesting proteins in eukaryotic algae and glycoproteins present in the cell walls of green algae (Stengel et al., 2011). The composition of seaweed amino acids is diverse, characterized by notable concentrations of glycine, alanine, arginine, proline, glutamic acid, and aspartic acid (Černá, 2011). Different seaweed species exhibit varying protein content and amino acid profiles; for instance, red species such as *Porphyra* and *Gracilaria* are known for their high levels of free alanine, glutamic acid, and aspartic acid (Vieira et al., 2018). In *Fucus sp*. (brown seaweeds), the specific amino acids mentioned may represent anywhere from 22% to 44% of the total amino acid composition, while in green seaweeds like *Ulva rigida* and *Ulva rotundata*, their proportion within the total amino acid pool can range from 26% to 32%, respectively (Fleurence et al., 1995; Munda, 1977). The protein, peptide, and amino acid content exhibit fluctuations influenced by factors such as species, seasonal variations, maturity, and environmental conditions (Stengel et al., 2011; Thiviya et al., 2022).

2.2.1.1.4.4. Polyphenols

Marine macroalgae are a rich source of polyphenolic compounds inclusive of catechins, flavonols, and phlorotannins specially (Apostolidis & Lee, 2011; Freile-Pelegrín & Robledo, 2013). The largest share of phenolic compounds contained in green and red algae are bromophenols, phenolic acids, and flavonoids. On the other hand, phlorotannins, a group of complex polymers of phloroglucinol (1,3, five-trihydroxybenzene), are the dominant polyphenolic secondary metabolites observed only in marine brown algae (Corona et al., 2017; Heo et al., 2005; Wells et al., 2017). Those phytochemicals have attracted a great deal attention because, much like different polyphenolic compounds, they may be bioactive compounds with potential biological activities and abilities that can be

explored in health advantages in human diseases due to their enzyme inhibitory impact like antiviral, anticancer, antidiabetic, antiallergic and anti-inflammatory activities (Li et al., 2011; Lopes et al., 2016).

2.2.1.1.4.5. minerals and vitamins

Vitamins are crucial organic micronutrients that organisms cannot synthesize in adequate amounts and therefore must be acquired through the diet. Serving as precursors for essential enzyme cofactors, they play pivotal roles in metabolic functions (Arnold & Barbul, 2006; Fitzpatrick et al., 2012). Various algal species including *T. Suecica, I. Galbana, D. Tertiolecta, and C. Stigmatophora* are notably rich in lipid-soluble vitamins A and E as well as B-group vitamins including vitamins B1, B2 (riboflavin), B6 (pyridoxal), and B12 (Ramos-Romero et al., 2021). Seaweed species, being abundant sources of beneficial nutrients such as vitamin C, vitamin B-complex (e.g., folic acid and B12), and precursors of vitamin A like β-carotene (Kumar et al., 2008). Consequently, seaweed can potentially be a significant reserve for portions of important vitamins (Škrovánková, 2011). Additionally, the mineral composition of seaweeds varies widely depending on factors such as seaweed genus, seasonal variations, geographical location, light intensity, and seaweed type (Teas et al., 2004; Villares et al., 2002).

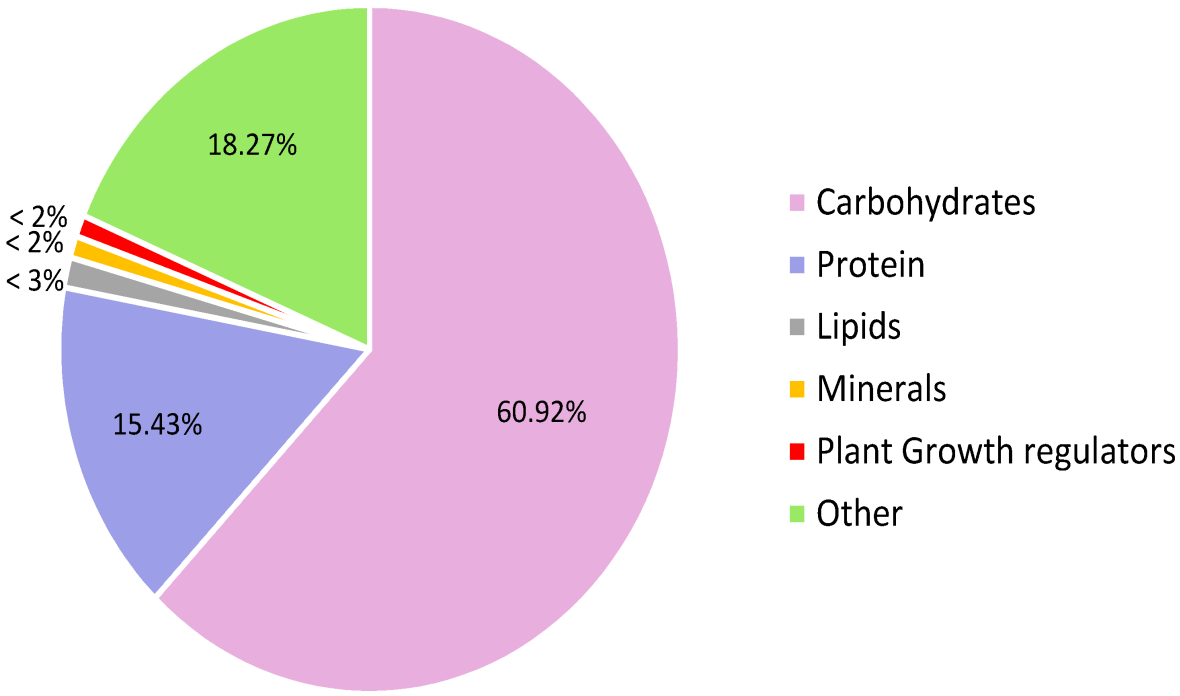

Figure 6: The estimated composition of seaweed extracts belonging to the three mega classes of seaweeds (Ali et al., 2021).

2.2.1.1.5. Mechanisms of the beneficial actions of seaweed extracts

Seaweed extracts contain a diverse array of bioactive compounds, encompassing polysaccharides, phlorotannins, proteins, peptides, amino acids, lipids, terpenoids, vitamins, phytohormones, and minerals (du Jardin, 2015). These extracts exhibit positive effects on various stages of plant growth, from seed germination to post-harvest, by promoting increased germination rates, enhancing seedling vigor (Ali et al., 2021; Carrasco-Gil et al., 2021; Khan et al., 2009).

Furthermore, applications of extracts from species like *A. nodosum and K. alvarezii* have been associated with improved water uptake and nutrient absorption, and increasing chlorophyll pigments content resulting in enhanced overall plant vigor and growth (Crouch et al., 1990; Senthuran et al., 2019). Studies have also revealed the influence of seaweed extracts on phytohormonal activity, such as increasing the levels of endogenous cytokinins in spinach and promoting early flowering and increased fruit set in various crop plants like tomato, pepper, and bean (Blunden et al., 1996; Werner et al., 2001; Whapham et al., 1993). These effects are attributed to the presence of phytohormones and the modulation of gene expression responsible for growth hormone biosynthesis induced by seaweed extracts (Werner et al., 2001). Moreover, betaine compounds contained in seaweed extracts prevent chlorophyll degradation, preserving photosynthetic activity (Ali et al., 2021). Additionally, extracts from diverse seaweeds confer plant resistance to various biotic and abiotic stresses, for instance treatments with seaweed extracts, such as those from *A. nodosum* and *Sargassum spp*., have demonstrated reduced leaf osmotic potential and electrolyte leakage in plants exposed to salinity stress by promoting the accumulation of osmoprotectants like proline, amino acids, and total protein, which help maintain cellular osmotic balance and protect against oxidative damage (Di Stasio et al., 2018; Jayaraman & Ali, 2015; Khan et al., 2009; Parađiković et al., 2019).

2.2.1.1.6. Extraction methods for preparation of seaweed extracts

Various extraction techniques have been utilized to extract compounds from seaweed, employing both conventional methods like maceration, infusion, percolation, and decoction, as well as modern techniques such as microwave-assisted extraction (MAE), ultrasound-assisted extraction (UAE), and enzyme-assisted extraction (EAE) (Chemat et al., 2017). Conventional methods like maceration involve submerging seaweed biomass in solvents like water or alcohol for extended periods, characterized by their cost-effectiveness, simplicity, and adaptability to different conditions (Perez-Vazquez et al.,

2023). In contrast, microwave-assisted extraction utilizes microwave radiation to hasten intracellular content release, resulting in shorter extraction times. ultrasound-assisted extraction employs ultrasonic waves to disrupt cell walls, reducing solvent usage and equipment needs. enzyme-assisted extraction employs enzymes to gently break down cell walls, preserving compound integrity (Quitério et al., 2022; Wu, 2017). These methods offer various options for extracting bioactive compounds from seaweed biomass, each with its own advantages and considerations related to efficiency, yield, and compound preservation (Perez-Vazquez et al., 2023).

2.2.2. Microbial biostimulants

This category primarily comprises bacteria, yeasts, and filamentous fungi (Bell et al., 2022; Fadiji et al., 2022). They are commonly found in soil, plants, and various organic substrates. These microorganisms are utilized in agricultural practices by application to soil or seeds, where they can exert direct or indirect effects to enhance crop productivity (Castiglione et al., 2021).

2.2.2.1. Plant growth promoting rhizobacteria

PGPR stands for Plant Growth-Promoting Rhizobacteria. These are a group of beneficial bacteria that colonize the rhizosphere the region of soil surrounding plant roots and promote plant growth through various mechanisms (Glick, 2012). These unique bacterial genera serve as vital components of soil ecosystems, engaging in various biotic activities that promote soil dynamism and sustainability for crop production (Chandler et al., 2008; Zaidi et al., 2009). They contribute to plant growth by mobilizing nutrients, synthesizing plant growth regulators, and protecting plants from phytopathogens through control or inhibition mechanisms. Additionally, they enhance soil structure and remediate polluted soils by sequestering toxic heavy metal species and degrading xenobiotic compounds such as pesticides (Ahemad & Malik, 2011; Hayat et al., 2010; Rajkumar et al., 2010). Notably, rhizobacteria inhabiting the vicinity of plant roots exhibit greater adaptability in transforming, mobilizing, and solubilizing nutrients compared to those found in bulk soils (Hayat et al., 2010). Plant growth-promoting rhizobacteria (PGPR), as outlined by Kloepper and Okon (1994), possess several inherent characteristics:

- They must be capable of colonizing the root surface.
- They must survive, proliferate, and compete with other microbiota, at least long enough to exert their plant growth promotion or protection activities.

- They must promote plant growth.

Approximately 2–5% of rhizobacteria can have a beneficial impact on plant growth and are designated as plant growth-promoting rhizobacteria (Kloepper, 1978).

2.2.2.2. Types of PGPRs

Gray and Smith (2005) have demonstrated that PGPR associations vary in terms of bacterial proximity to the root and the intimacy of association. Generally, these associations can be classified as:

- Extracellular PGPR (ePGPR): These bacteria reside within the rhizosphere, at the rhizoplane, or in the intercellular spaces of the root cortex. Examples include *Agrobacterium, Arthrobacter, Azotobacter, Azospirillum, Bacillus, Burkholderia, Caulobacter, Chromobacterium, Erwinia, Flavobacterium, Micrococcous,* and *Pseudomonas*(Bhattacharyya & Jha, 2012).
- Intracellular PGPR (iPGPR): These bacteria exist inside root cells, typically within specialized nodular structures. Examples include *Allorhizobium, Azorhizobium, Bradyrhizobium, Mesorhizobium,* and *Rhizobium* of the *Rhizobiaceae* family. The majority of rhizobacteria belonging to this group are Gram-negative rods, with a smaller proportion being Gram-positive rods, cocci, or pleomorphic (Bhattacharyya & Jha, 2012).

2.2.2.2.1. Overview on Bacillus species group

Bacillus belong to the family *Bacillaceae*, order *Bacillales*, and class *Bacilli*. Bacteria of the genus *Bacillus spp*. are widely distributed in nature, proliferate easily, and have a long lifespan when in sporulated form (Wang & Sun, 2009; Yakoubou et al., 2010). The genus *Bacillus* comprises heterogeneous Gram-positive rods capable of forming endospores, enabling them to survive for extended periods under unfavorable environmental conditions (Priest, 1993). These bacteria, including species such as *Bacillus subtilis, Bacillus cereus, Bacillus amyloliquefaciens, and Bacillus megaterium*, inhabit the rhizosphere, the soil region surrounding plant roots, where they establish symbiotic relationships with plants (Beattie, 2006). These microorganisms are known for their ability to synthesize a wide variety of beneficial substances according to Chanway (2002), including the production of IAA, phosphate solubilization, nitrogen fixation, as well as characteristics of biological control such as the production of HCN, siderophores, hydrolytic enzymes, and antibiotics (Ahmad et al., 2008; Mehta et al., 2010).

2.2.2.3. Beneficial mechanisms of Plant growth-promoting rhizobacteria

PGPR (Plant Growth-Promoting Rhizobacteria) promote plant growth through two primary mechanisms: first, by facilitating resource acquisition, including nitrogen, phosphorus, and essential minerals; and second, by modulating plant hormone levels. Additionally, they can indirectly enhance plant growth by reducing the inhibitory effects of various pathogens through biocontrol mechanisms (Glick, 2012). For instance, certain strains of *Bacillus* and *Pseudomonas spp.* can directly solubilize phosphorus and fix atmospheric nitrogen, while also producing plant growth-promoting hormones (Mehmood et al., 2023; A. K. Saxena et al., 2020). Furthermore, these bacteria can suppress the growth of pathogenic fungi such as *Fusarium* through the production of antifungal compounds, thereby promoting overall plant health and growth (Quan et al., 2011).

2.2.2.3.1. Direct mechanisms

2.2.2.3.1.1. Nitrogen fixation

Nitrogen (N) is the most essential nutrient for plant growth and productivity. However, despite the fact that there is approximately 78% N2 in the atmosphere, it is unavailable to growing plants (Smil, 1999). Atmospheric N2 is converted into plant-utilizable forms by organic N2 fixation (NFB), which changes nitrogen to ammonia through nitrogen-fixing microorganisms using a complex enzyme system called nitrogenase (Kim & Rees, 1994). Organic nitrogen fixation occurs generally at mild temperatures by nitrogen-fixing microorganisms, which are widely distributed in nature (Raymond et al., 2004). Furthermore, NFB represents an economically beneficial and environmentally sound alternative to chemical fertilizers (Ladha et al., 1997). Nitrogen-fixing organisms are commonly classified as (a) symbiotic N2-fixing bacteria, including members of the family *Rhizobiaceae*, which form symbiosis with leguminous plants (e.g., *Rhizobia*) (Ahemad & Khan, 2012; Sawada et al., 2003). In addition to non-leguminous trees (e.g., *Frankia*); and (b) non-symbiotic (free-living, associative, and endophytes) nitrogen-fixing forms such as cyanobacteria (*Anabaena*, *Nostoc*), *Azospirillum*, *Azotobacter*, *Gluconoacetobacter diazotrophicus*, and *Azocarus*, among others (Bhattacharyya & Jha, 2012). However, non-symbiotic nitrogen-fixing bacteria provide only a small amount of the fixed nitrogen that the bacterially-associated host plant requires (Glick, 2012). Symbiotic nitrogen-fixing rhizobia in the *Rhizobiaceae* family (α-proteobacteria) infect and establish a symbiotic relationship with the roots of leguminous plants. The process of N2 fixation is carried out by a complex enzyme, the nitrogenase complex (Kim & Rees, 1994).

2.2.2.3.1.2. Phosphate solubilization

Phosphorus (P), the second most crucial nutrient for plant growth after nitrogen, is widely present in soils in both natural and inorganic forms (Ahemad & Khan, 2011). Despite its abundance, the availability of phosphorus to plants is often limited because the majority of soil phosphorus exists in insoluble forms, while plants can only absorb it in two soluble forms: monobasic (H2PO4-) and dibasic (HPO42-) ions (Bhattacharyya & Jha, 2012). Insoluble phosphorus can be found as inorganic minerals or in various organic forms such as inositol phosphate (soil phytate), phosphomonesters, and phosphotriesters (Glick, 2012). Organisms with phosphate solubilizing activity, commonly referred to as phosphate-solubilizing microorganisms (PSM), offer potential alternatives to chemical phosphatic fertilizers by making phosphorus available to plants (M. S. Khan et al., 2009). Typically, inorganic phosphorus solubilization is facilitated by the secretion of low molecular weight organic acids synthesized by various soil bacteria (Zaidi et al., 2009). Conversely, organic phosphorus mineralization occurs through the synthesis of various phosphatases, enzymes catalyzing the hydrolysis of phosphoric esters (Glick, 2012). Notably, phosphate solubilization and mineralization can coexist within the same bacterial strain (Tao et al., 2008).

2.2.2.3.1.3. Siderophore production

Iron is indispensable for the viability of nearly all forms of life. With the exception of certain lactobacilli, virtually all known microorganisms rely on iron for their essential functions (Neilands, 1995). In aerobic environments, iron predominantly exists as Fe3+ and tends to form insoluble hydroxides and oxyhydroxides, rendering it largely inaccessible to both plants and microorganisms (Rajkumar et al., 2010). Bacteria acquire iron by secreting low-molecular-weight iron-binding compounds known as siderophores, which exhibit high affinity for iron binding. Most siderophores are water-soluble and can be categorized as either extracellular or intracellular siderophores (Sah & Singh, 2015). Rhizobacteria exhibit variability in their ability to utilize siderophores; some are proficient in utilizing siderophores produced by organisms of the same genus (homologous siderophores), while others can utilize those produced by different rhizobacteria from various genera (heterologous siderophores) (Walia et al., 2013).

The binding of siderophores to iron increases the concentration of soluble metal (Rajkumar et al., 2010). Thereby alleviating the stresses imposed on plants by elevated levels of heavy metals in the soil. Plants employ various mechanisms to assimilate iron from bacterial

siderophores, including chelation and release of iron, direct uptake of siderophore-iron complexes, or via a ligand exchange reaction (Schmidt, 1999).

2.2.2.3.1.4. Phytohormone production

It has been understood that Plant Growth-Promoting Rhizobacteria (PGPR) are capable of synthesizing phytohormones such as auxin, specifically indole-3-acetic acid, gibberellic acid, cytokinin, and others (Cassán et al., 2011; Jha & Saraf, 2012). Studies suggest that approximately 80% of microorganisms isolated from the rhizosphere of various crops have the ability to produce and release auxins as secondary metabolites (Patten et al., 2013). The secretion of phytohormones by rhizobacteria can interfere with various plant developmental processes by modifying the endogenous pool of plant hormones through the acquisition of externally secreted phytohmornes from soil bacteria (Glick, 2012; Spaepen et al., 2007). Moreover, phytohormones serves as a signaling molecule affecting gene expression in numerous microorganisms, thus playing a pivotal role in rhizobacteria-plant interactions (Spaepen & Vanderleyden, 2011). Among the phytohormones synthesized by PGPR, the auxins, particularly indolyl-3-acetic acid (IAA), have gained significant attention in research (Ignatova et al., 2015). The production of these hormones has been documented in PGPR strains belonging to genera such as *Enterobacter, Pseudomonas*, *Azospirillum*, and *Bacillus* (Swarnalakshmi et al., 2020). These phytohormones can exerts diverse effects on plant physiology, including influencing cellular division, elongation, and differentiation; regulating vegetative growth processes; initiating lateral and adventitious root formation; mediating responses to light, gravity, and flowering; impacting photosynthesis, pigment formation, biosynthesis of various metabolites, and resistance to stressful conditions (Javid et al., 2011; Santner & Estelle, 2009).

2.2.2.3.1.5. Production of osmoprotectants

According to Panwar et al. (2014) Halotolerant PGPR (Plant Growth-Promoting Rhizobacteria) which can survive in saline environments have been observed to synthesize exopolysaccharides, promoting biofilm formation, and produce osmoprotectants and antioxidant enzymes, which collectively contribute to stimulating plant growth in saline ecosystems. Additionally, halotolerant PGPR possess the capacity to generate osmoprotectants such as ectoine, and hydroxyectoine that assist plants in maintaining their osmotic balance amidst saline conditions (Hamedi et al., 2015). In a study, the PGPR *Virgibacillus halodenitrificans* was reported to synthesize compatible solutes, ectoine and hydroxyectoine to cope with salt stress (Das et al., 2015). This suite of mechanisms enables

PGPR to enhance plant growth and resilience in saline environments, offering potential solutions for sustainable agriculture in challenging conditions (Nadeem et al., 2013).

2.2.2.3.2. Indirect mechanisms

The utilization of microorganisms for disease management, a form of biological control, represents an environmentally friendly approach (Lugtenberg & Kamilova, 2009). A primary indirect mechanism through which rhizobacteria promote plant growth is by serving as biocontrol agents (Glick, 2012). Generally, niche exclusion, induced systemic resistance, and production of antifungal metabolites are the main modes of biocontrol activity in Plant Growth-Promoting Rhizobacteria (PGPR) (Lugtenberg & Kamilova, 2009). Numerous rhizobacteria have been reported to produce antifungal metabolites such as hydrogen cyanide (HCN), phenazines, pyrrolnitrin, 2,4-diacetylphloroglucinol, pyoluteorin, viscosinamide, and tensin (Bhattacharyya & Jha, 2012). The interaction of certain rhizobacteria with plant roots can induce plant resistance against various pathogenic bacteria, fungi, and viruses, a phenomenon known as induced systemic resistance (ISR) (Lugtenberg & Kamilova, 2009). Furthermore, ISR involves signaling pathways mediated by jasmonate and ethylene within the plant, which stimulate the host plant's defense responses against a range of plant pathogens (Glick, 2012). Several individual bacterial components can induce ISR, including lipopolysaccharides (LPS), flagella, siderophores, cyclic lipopeptides, 2,4-diacetylphloroglucinol, homoserine lactones, and volatile compounds such as acetoin and 2,3-butanediol (Lugtenberg & Kamilova, 2009).

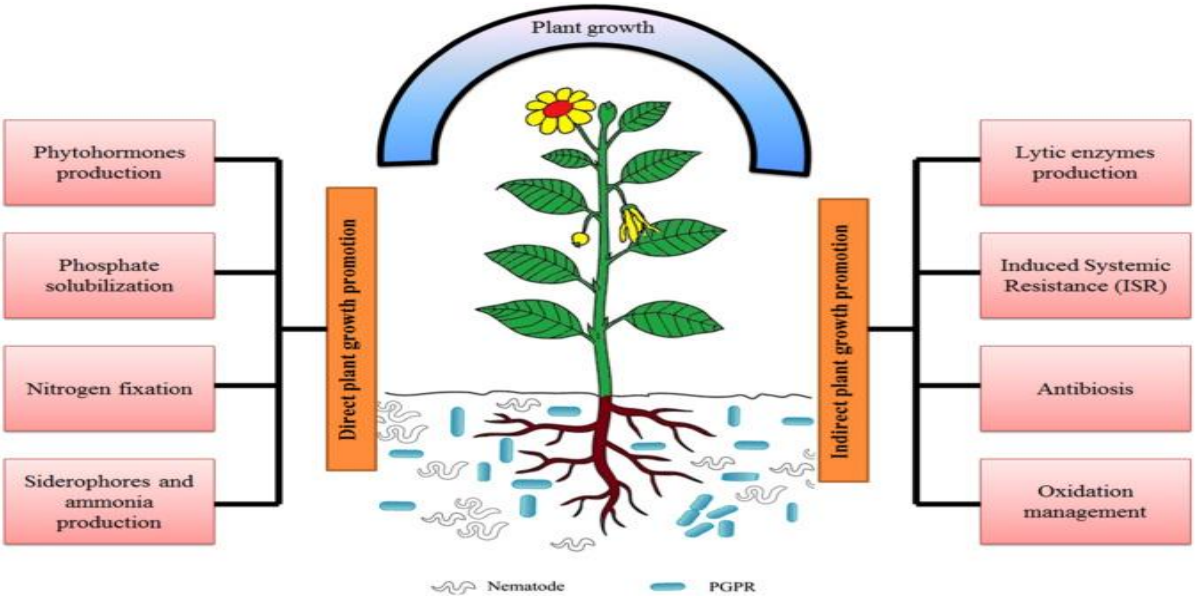

Figure 7: Direct and indirect plant growth promotion mechanisms exerted by PGPR (Mekonnen & Kibret, 2021).

2.2.3. Arbuscular mycorrhizal fungi (AMF)

Arbuscular mycorrhizal fungi (AMF), which are obligate symbiotic soil fungi, establish symbiotic relationships with the roots of most plants, forming unique structures known as arbuscules within the cortical cells of plant roots (Harrison, 2005). Additionally, certain genera such as *Glomus, Entrophospora, Acaulospora*, and *Sclerocystis* produce vesicles, resulting in their classification as vesicular-arbuscular mycorrhizal (VAM) fungi, which contain lipid-rich structures within the root cortex. In contrast, the genera *Gigaspora* and *Scutellospora* produce arbuscules as well as inter- and intracellular hyphae (Strullu et al., 1983). The AM symbiosis is typically mutualistic, with AMF believed to rely on host plants for fixed carbon. In return, plants receive various benefits leading to increased growth, including improved water relations, pest and disease resistance, enhanced nutrient uptake, and modification of root morphology (Berta et al., 1990; Davies Jr et al., 1993; George et al., 1995; Hooker et al., 1994). The most significant benefit is increased nutrient uptake, particularly of immobile nutrients like phosphorus and zinc (Bolan, 1991; Bürkert & Robson, 1994). Extra-radical hyphae of AMF can extend up to 8 cm from the root, effectively increasing nutrient absorption from the soil (Rhodes & Gerdemann, 1975).

AMF also play a crucial role in soil ecology by enhancing soil aggregate stability and influencing nutrient cycling through their impact on root exudation and carbon transport (Gianinazzi & Schüepp, 1994; Miller & Jastrow, 1990; Tisdall & Oades, 1979). AMF primarily enhance phosphate uptake by the host plant due to the ability of their mycelium to reach beyond the phosphate depletion zone around the root (George et al., 1995; Koide, 1991; Sanders et al., 1977). In return, the fungi receive carbon from the host plant. Other benefits to the host include increased resistance to foliar feeding insects, improved drought resistance, enhanced resistance to soil pathogens, and increased tolerance to salinity and heavy metals. Additionally, AMF enhance uptake of macronutrients such as nitrogen, potassium, and magnesium, as well as certain micronutrients. Moreover, mycorrhizas play a crucial role in maintaining soil aggregate stability (Degens et al., 1996; Tisdall & Oades, 1979).

2.2.4. Biostimulant based on humic and fulvic acid

Humic substances (HSs), which are made up of fulvic acid (FA), ulmic acid (UA), and humic acid (HA), are a significant class of biostimulants that have been shown to increase plant growth, yield, and nutritional quality, as well as improving plant tolerance to biotic

and abiotic stresses (Canellas et al., 2015; Canellas & Olivares, 2014; Cha et al., 2020; Guo et al., 2019; Jannin et al., 2012). Because of their intricate structure and naturally sluggish rate of mineralization, HSs are not currently regarded as a dependable source of direct nutrients for plant growth. Changes in physiological and molecular reactions brought about by HSs' contact with plant cell receptors appear to be related to improved plant growth (Canellas et al., 2015). The structure, chemical composition (such as aliphatic and aromatic functional groups), hydrophobicity, molecular size, and interactions with other chemical components present in rhizosphere soil are the main factors influencing the role of HSs in enhancing crop performance (Bento et al., 2020; Canellas & Olivares, 2017; Spaccini et al., 2019). Numerous humic-based compounds are utilized globally in horticulture and agriculture as plant biostimulants that have been produced.

One humic material found in the organic matter of the soil that has been utilized as a plant biostimulant is fulvic acid. Its low molecular weight, high concentration of carboxylic groups and phenolic compounds, and low concentration of aromatic structures contribute to its increased cation exchange capacity and improved water solubility (Canellas & Olivares, 2014). Fulvic acid boosts the creation of 2 ATP and ions, increases respiration, photosynthesis, and chlorophyll levels, and encourages the growth of roots, leaves, and shoots (Calvo et al., 2014; Canellas & Olivares, 2014).

2.2.5. Hydrolyzed proteins and nitrogen-containing compounds

Biostimulants originating from hydrolyzed proteins and nitrogen-containing substances are progressively utilized in the agricultural sector due to their ability to enhance the growth and productivity of plants (Caruso et al., 2020). These biostimulants are comprised of amino acids, peptides, and other nitrogen-based compounds, which effectively stimulate a variety of physiological processes in plants, such as nutrient absorption, root growth, and tolerance to stress (Bhavsar et al., 2016; Caruso et al., 2020). By supplying accessible nitrogen forms, these biostimulants stimulate vegetative growth and improve overall plant health by enhancing iron and nitrogen metabolism, as well as increasing the efficiency of nutrient uptake and utilization, including both macro and micronutrients (Colla et al., 2015; Leghari et al., 2016). Additionally, the existence of bioactive peptides and signaling molecules in hydrolyzed proteins can initiate specific responses in plants, strengthening their ability to withstand various stress factors (Pan et al., 2019). According to Colla, Nardi, et al. (2015) over 90% of the horticultural biostimulant market relies on products derived from chemically hydrolyzed proteins sourced from animal origins. For instance,

collagen extracted from leather by-products is widely used in Europe, India, and China, while fish by-products are prevalent in the United States. In contrast, enzymatically produced protein hydrolysates sourced from plant biomass are less prevalent in the biostimulant market, as they have only recently been introduced. Numerous investigations conducted on horticultural crops like tomatoes, wheat and capsicum have demonstrated that the utilization of protein hydrolysates can enhance crop growth and bolster their resilience against environmental stresses confirming that hydrolyzed proteins and nitrogen-containing compounds offer a natural and efficient means of maximizing plant productivity and yield (Agliassa et al., 2021; Francesca et al., 2021; Mironenko et al., 2022).

2.2.6. Inorganic biostimulant

Inorganic biostimulants are minerals or elements that can improve plant growth, nutrient uptake, and stress tolerance when applied to the plant or soil. Among the primary beneficial elements are Silicon (Si), Selenium (Se), Cobalt (Co), and Aluminum (Al) (Ayub et al., 2023). These elements exist in soils and plants primarily as inorganic salts, including insoluble forms like amorphous silica found in grasses. The beneficial effects they induce can be either constitutive, such as the reinforcement of cell walls through silica deposition, or transient, particularly in response to specific abiotic stresses (Franzoni et al., 2022). Various previous studies reported the beneficial effects of inorganic compounds in enhancing growth and resilience of crops to abiotic stresses such as rice, wheat, and maize (Khan et al., 2015; Maghsoudi et al., 2016; Singh et al., 2006). Trejo-Téllez & Gómez-Merino (2023) stated that Silicon (Si) has the ability to mitigate the harmful impacts of pollutants, drought, and saline conditions, trigger defense mechanisms against pests and diseases, enable the creation of nanostructures, enhance the durability and rigidity of plant tissues, activate antioxidant pathways, diminish ethylene production, and prolong the shelf life of plants.

2.3. Methods of application of biostimulants

Biostimulant application encompasses a variety of techniques including foliar application, soil application, seed priming, and irrigation with fertigation designed for specific situations to enhance plant growth and development (Bashir et al., 2021). Foliar application consists of the direct application of liquid biostimulants onto the leaves, facilitating rapid absorption through stomata and the leaf epidermis. This strategy is particularly effective for biostimulants such as protein hydrolysates and seaweed extracts

(Soppelsa et al., 2019). Conversely, soil application involves the integration of biostimulants into the soil directly to improve soil fertility, chemical composition, physical structure and soil microbiome, supporting the plant growth by supplying necessary macronutrients and micronutrients (El Boukhari et al., 2020). Seed priming is an additional method in which seeds are treated with biostimulants prior to planting, augmenting germination, vitality, and early growth phases. This technique promotes consistent seedling emergence, efficient water utilization, and resilience to various stresses and diseases (Baby, 2020). Lastly, irrigation with biostimulants entails the direct delivery of biostimulants to plants through irrigation water, optimizing nutrient absorption and water resource management, especially in arid conditions (Naorem et al., 2023). Each approach confers distinct benefits and can be tailored to meet specific crop demands and environmental variables (du Jardin, 2015).

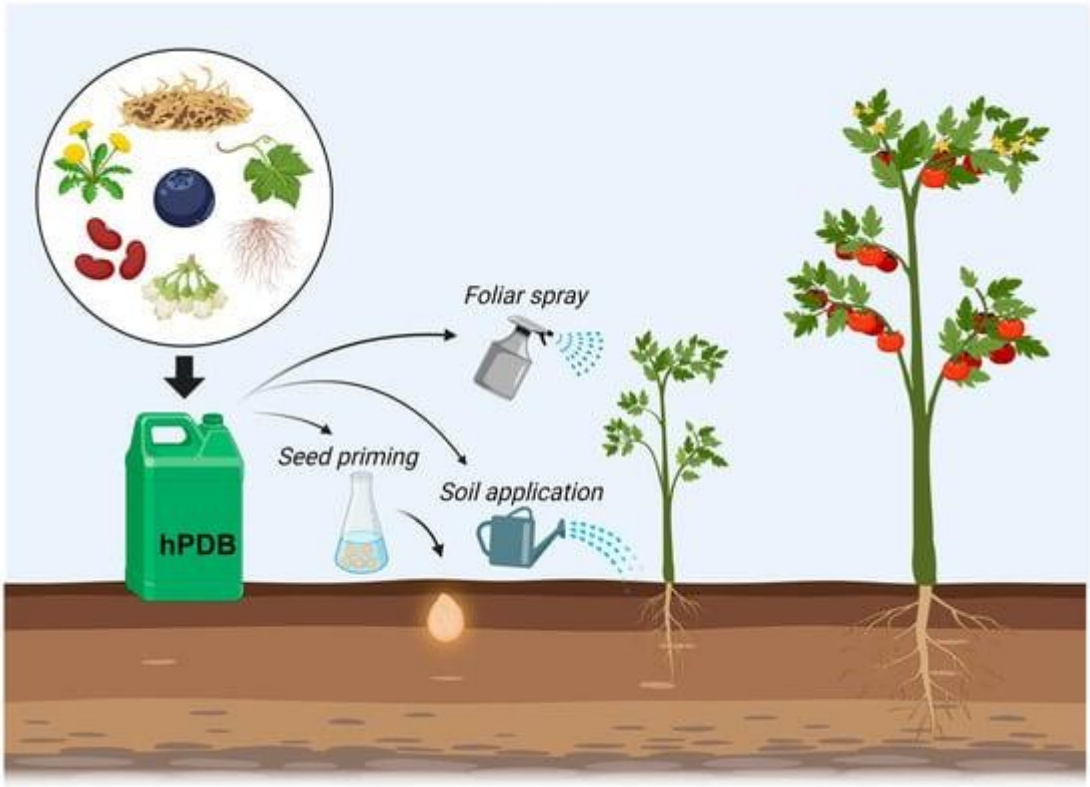

Figure 8: Methods of application of biostimulants (Martínez-Lorente et al., 2024).

2.4. Formulation of biostimulants

Biostimulant formulation, as described by Rouphael and Colla (2018), involves formulating biologically natural materials and their derived metabolites into practical

products to be used in various agricultural practices such as plant growth promotion, nutrient acquisition, and disease control in an eco-friendly manner. These formulations utilize various raw ingredients, often sourced from plant components like seeds, leaves, and roots, seaweed extracts and aqueous or organic solvent-based plant extracts commonly employed to improve crops and yields. However, their limited water solubility poses challenges for field application, as bioactive chemicals can degrade and volatilize outdoors without proper preparation (Bhargava et al., 2015; Borges et al., 2018). Another type recently recognized is microbial based bioformulation that utilizes microbes or microbial products as the active ingredients. These formulations are designed to harness the beneficial properties of specific microorganisms for various agricultural applications, such as plant growth promotion, disease suppression, and soil fertility enhancement (Jones & Burges, 1998). Microbial-based bioformulations can include beneficial microbes like plant growth-promoting rhizobacteria (PGPR) such as *Pseudomonas, Bacillus, Azotobacter,* and *Azospirillum spp* that contribute to sustainable agriculture practices (Aamir et al., 2020; Rani & Kumar, 2019). The success of microbial-based bioformulations depends on the potency of the microbial strains used, their mode of formulation, and the delivery system employed. Formulated products offer improved handling, transportation, and storage compared to raw materials, making them more effective in practical use (Aamir et al., 2020).

2.5. Importance of Biostimulants in agriculture

In today's context, modern agriculture plays a pivotal role in tackling urgent global issues. With projections indicating a population surge to approximately 9 billion by 2050, the agricultural sector confronts the significant challenge of meeting rising food needs while minimizing reliance on synthetic fertilizers and pesticides due to their detrimental effects on human health and the environment (Krid et al., 2023; Rana et al., 2022). Consequently, the adoption of sustainable farming practices, supported by innovative methods, has become imperative in contemporary agriculture (Adnan et al., 2019). Biostimulants offer sustainable alternatives to chemical fertilizers, aiding in reducing environmental impact by enhancing crop growth, yield, and quality (Hamid et al., 2021; Malik et al., 2020). Previous studies have highlighted the effectiveness of biostimulants in improving the performance of key crops like tomatoes, rice, and wheat under various environmental stresses like drought stress and salinity stress (Azeem et al., 2015; Khan et al., 2021; Paul et al., 2019). Their potential lies in stimulating growth, mitigating stress-related limitations,

and ultimately enhancing yield. However, the precise mechanisms by which biostimulants operate remain somewhat unclear (Basile et al., 2020). They may directly impact plant productivity through immediate responses to application or indirectly influence the soil and plant microbiome, thereby affecting plant productivity (Trivedi et al., 2022). This dual pathway underscores the complexity of biostimulant action, emphasizing the necessity for further research to unlock their full potential in agricultural contexts (du Jardin et al., 2020).

3. Tomato (*Solanum lycopersicum L.*)

3.1. General information about tomato (*Solanum lycopersicum L.*)

Tomato, scientifically known as *Solanum lycopersicum L.*, holds the distinction of being the most widely consumed vegetable globally (Kimura & Sinha, 2008; Kinkade, 2010). Belonging to the Solanaceae family, alongside several other economically significant species such as potato and eggplant, the tomato is cultivated extensively worldwide, both for domestic consumption and as a major export commodity (Dam et al., 2005). In the year 2022, global tomato production amounted to approximately 186.82 million tons, cultivated across a total area of 5 million hectares with an average productivity achieved of 36.97 tons per hectare (Bebeli & Mazzucato, 2008; Tiwari et al., 2022). China, with a production of 64.86 million metric tons, holds the position of the leading tomato producer globally, contributing nearly 34.72% to the total world production. Following China is India, with a production of 20.57 million tons, and Turkey, with a production of 13.20 million tons (FAOSTAT, 2022). The size of the tomatoes market has experienced robust growth in recent years, fueled by increasing consumer demand for tomato-based products across various industries such as food and beverage, pharmaceuticals, and cosmetics. This growth trend is projected to continue, with the market size expected to increase from 174.7 billion dollars in 2023 to 186.46 billion dollars in 2024 (Tomatoes Global Market Report, 2024). Despite being commonly considered vegetables, tomatoes are botanically are classified as fruits, specifically as berries because they develop from the ovary of the flower and contain seeds (Kimura & Sinha, 2008). Tomatoes come in a wide range of shapes, sizes, and colors, from small cherry tomatoes to large beefsteak varieties, appearing in red, yellow, orange, and even purple hues (Morganelli, 2007). Additionally, they are considered a rich source of minerals and essential vitamins such as potassium, vitamin C and vitamin K, as well as important minerals like potassium. Additionally, they contain antioxidants like

lycopene, which have been associated with several health benefits, including reduced risks of certain cancers and cardiovascular diseases (Dorais et al., 2008; Rajoria et al., 2010).

3.2. Botanical classification of tomato

Tomatoes have had various scientific names including *Solanum lycopersicum* and *Lycopersicon esculentum* due to evolving botanical understandings. Carl Linnaeus assigned tomatoes to *Solanum* genus in the 1753, but Philip Miller later disagreed and placed them in *Lycopersicon* instead. Recently, taxonomists reconsidered and moved tomatoes back to the *Solanum* genus based on genetic research insights (Bailey, 1963; Darwin et al., 2003). According to Kimura and Sinha (2008) Tomatoes are part of the *Solanaceae* family, which comprises economically significant plants like potatoes, eggplants, and peppers. Specifically, within the *Solanum* genus, tomatoes are specifically classified under the species *Solanum lycopersicum* as follows:

Table 1: Tomato taxonomy (Kimura & Sinha, 2008).

Rank	**Scientific name**
Kingdom	Plantae
Subkingdom	Tracheophyta
Super division	Spermatophyta
Division	Angiosperms
Class	Magnoliopsida
Subclass	Asteridae
Order	Solanales
Family	Solanaceae
Genus	Solanum
Species	Solanum lycopersicum

3.3. Genetic classification and origins

Wild tomatoes originated in the Andean region of South America (Peralta & Spooner, 2000). It is hypothesized that the cherry tomato (*Solanum lycopersicum var. cerasiforme*) served as the potential precursor to larger-fruited tomato varieties and is presumed to have undergone domestication from the wild species *Solanum pimpinellifolium*, which produces red fruits (Ranc et al., 2008). The cultivated tomato is classified as a diploid organism possessing 24 chromosomes (2n=24). Therefore, each individual cell of the tomato plant generally contains two complete sets of chromosomes (Peterson, 1998; Tanksley & Rick, 1980). Tomatoes exhibit a dual reproductive mechanism involving both self-pollination (autogamous) and some degree of cross-pollination (allogamous). Despite their predominant self-fertilizing nature, in which fertilization can occur without external intervention, cases of cross-fertilization can occur under the influence of insects, wind, or other vectors (Nettancourt & de Nettancourt, 2001). This propensity for occasional crossbreeding serves to increase genetic diversity within tomato populations, thus playing a central role in the process of selection and improvement of traits (Gressel, 2008). Furthermore, the presence of monogenic variants paves the way for targeted selection strategies aimed at cultivating tomato cultivars with specific and desirable characteristics such as resilience to diseases and enhanced yields (Foolad, 2007; FAO, 2008).

3.4. Definition and types of varieties

The Convention of the International Union for the Protection of New Varieties of Plants (UPOV, 2012) offers the following explanation of the term "variety": "A group of plants within a botanical taxon of the lowest established rank, which may or may not meet all the criteria for acquiring breeder's rights, yet can be delineated by specific characteristics resulting from a particular genotype or a precise combination of genotypes, distinguished from other plant assemblages by possessing at least one of these characteristics, and recognized as a separate entity due to its ability for uniform reproduction". A variety needs to be recognizable based on its attributes, display notable differentiation from other varieties, and maintain uniformity during the reproduction or multiplication processes (Geves, 2017). Based on the breeding approach employed, we classify varieties into inbred lines and hybrid varieties (Hallauer et al., 1988). In Addition, according to the growth habits of tomato, varieties can be determinate and indeterminate (Pittenger, 2005).

3.4.1. Inbred tomato varieties

An inbred tomato variety represents a pure lineage, indicating that its progeny or subsequent generations will inherit identical genetic traits (Allard, 1999; Hartman & St. Clair, 1998). It emerges from a crossbreeding process involving two or more distinct varieties, followed by rigorous selection over multiple cycles of self-pollination or inbreeding. Each cycle of self-pollination or inbreeding serves to reinforce desired genetic traits while eliminating unwanted variations (Carena et al., 2010). Inbred varieties are valued for their stability and uniformity, making them particularly suitable for agricultural production and breeding programs aimed at developing cultivars with specific traits or characteristics (Allard & Hansche, 1964; Gunjaca et al., 2008).

3.4.2. Hybrid tomato varieties

According to Cheema and Dhaliwal (2004) Hybrid tomato cultivars emerge from the hybridization process involving two genetically diverse parental lines or varieties. In contrast to inbred cultivars, hybrids lack genetic uniformity and do not give rise to progeny with stable traits. Rather, they manifest the phenomenon termed heterosis or hybrid vigor, wherein the descendants frequently exhibit improved attributes like heightened yield, resistance to diseases, or overall vigor in comparison to the parental lines (Allard & Hansche, 1964). Hybrid varieties are widely utilized in agriculture due to their potential for improved performance and productivity (Saxena & Nadarajan, 2010).

3.4.3. Determinate tomato varieties

Determinate tomatoes, also called bush tomatoes, demonstrate a growth pattern wherein plants achieve a predetermined height before ceasing further growth and produce their fruit within a relatively short period (Peet & Welles, 2005). They grow up to 0.9-1.5 m tall only, making them easy to cultivate with minimal pruning, especially suitable for compact spaces like patio gardens (Pittenger, 2005). Examples of determinate tomato varieties are: Roma, San Marzano, and Celebrity (Master Gardener Association of San Diego, 2022).

3.4.4. Indeterminate tomato varieties

According to (Pittenger, 2005) Indeterminate tomato varieties are those that continue to grow and produce fruit throughout the growing season. Indeterminate tomato plants can grow up to 3.65 meters in height and require staking and pruning. Some examples of

indeterminate tomatoes are Black Cherry, Juliet, and Cherokee (Master Gardener Association of San Diego, 2022).

3.5. Morphological characteristics of the tomato

The morphology of tomatoes consists of various distinct parts of the plant, each contributing to its overall appearance and function. These morphological parts can be divided into the vegetative system which include the roots, stems, leaves, and the reproductive system which include the flowers, fruits, and the seed (Chime et al., 2017; Gelmesa et al., 2013).

3.5.1. The vegetative system

According to Kraus and Kraybill (1918) the vegetative system of tomato includes roots, stems, and leaves, these organs are responsible of nutrition, growth and maintenance of plant body and they are not directly involved in sexual reproduction. Vegetative parts often are used in asexual forms of reproduction (Rick, 1974).

3.5.1.1. The stem

The stem of the tomato plant presents an angular form and a notable thickness between nodes covered with fine hairs. During the early stages of growth, the stem has a herbaceous consistency but gradually becomes lignified as the plant matures (Brewer et al., 2007). Initially, the plant follows a monopodial growth pattern, characterized by uninterrupted elongation with a single main stem. However, after the emergence of 4 or 5 leaves, it transitions to a sympodial growth pattern (Grbić, 2002). In this phase, the axillary buds at the leaf axils give rise to successive branches. Conversely, the terminal buds may either develop into flowers or cease growth (Chaux & Foury, 1994). The branches originating from axillary buds are adorned with leaves at each node and terminate in an inflorescence (Chaux & Foury, 1994; Nairne, 1993).

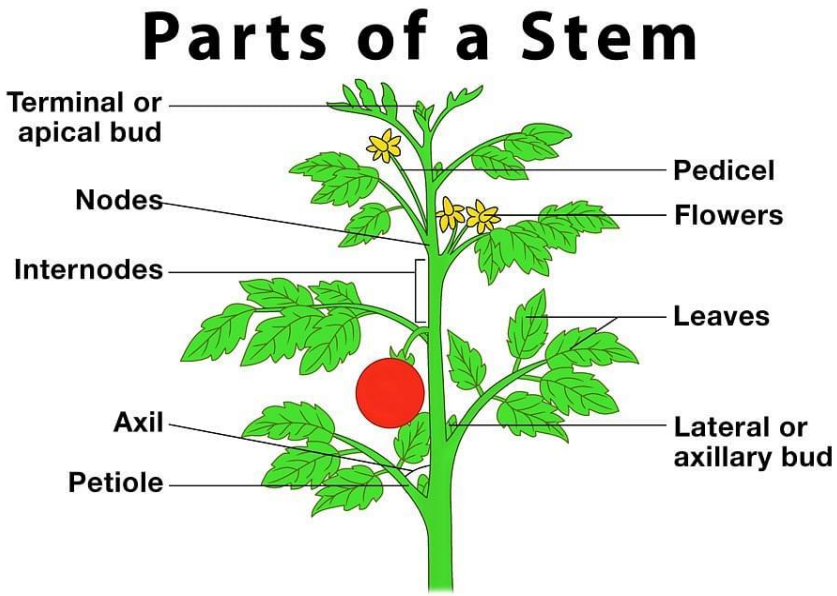

Figure 9: Morphology of tomato stem (Srivastava, 2023).

3.5.1.2. The leaves

Tomato leaves function as the primary sites for essential biological processes such as photosynthesis and transpiration (Karlberg et al., 2006). Typically, the leaves of a tomato plant comprise 5 to 7 main leaflets organized along the leaf rachis. Each leaf is attached to the stem through a petiole, while the leaflets are connected to the leaf rachis by petioles (Hareven et al., 1996). The arrangement and characteristics of tomato leaves vary across different varieties and can be influenced by environmental factors such as light intensity, temperature, humidity, and nutrient availability (Chitwood et al., 2012).

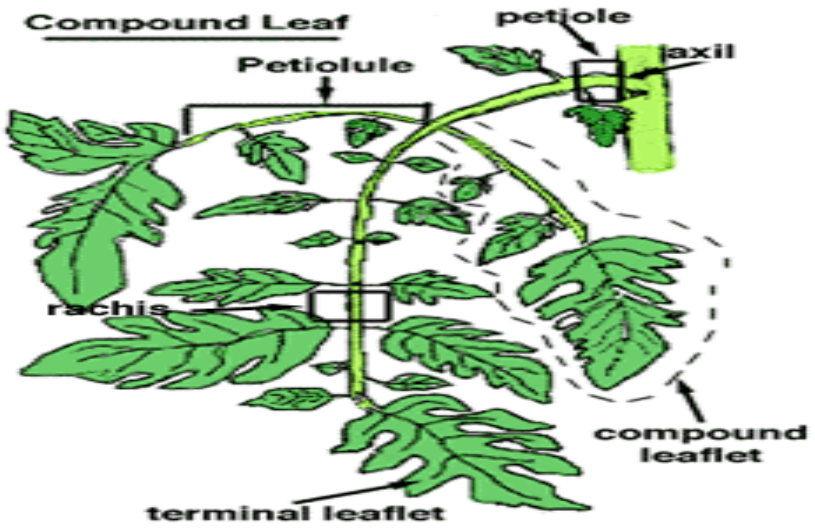

Figure 10: Tomato leaves anatomy (Rost, 1996).

3.5.1.3. The root system

The root system of the tomato is fibrous and branched usually between 40 to 60 centimeters in depth. Nevertheless, in favorable soil conditions with adequate moisture and nutrients, tomato roots can penetrate deeper into the soil, reaching depths of up to 1 meter (Portas & Dordio, 1979; Weaver & Bruner, 1927). Its primary function of nutrient and water absorption, tomato roots also play a role in anchoring the plant in the soil, providing stability against wind and other environmental stresses (Fournier et al., 2006).

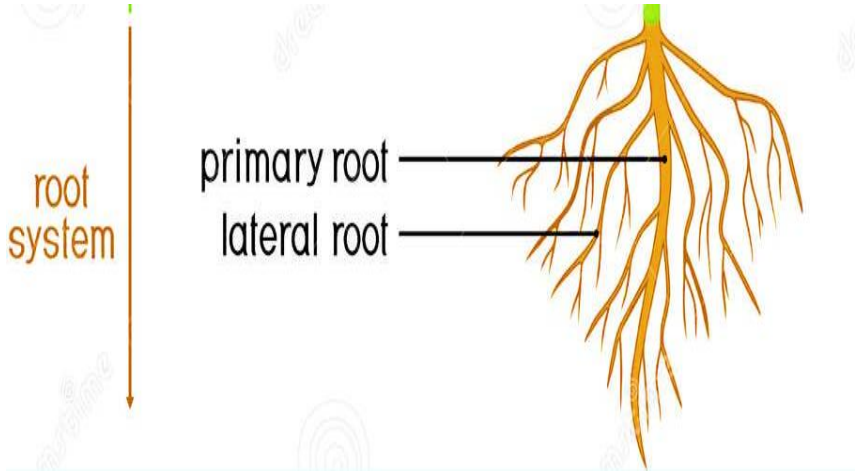

Figure 11: Root system of tomato plant (Dreamstime, 2022).

3.5.2. The reproductive system

The reproductive components of a tomato plant include the flower, fruit, and seeds. The flower has male (stamens) and female (pistil) parts producing pollen and comprising stigma, style, and ovary (Gasser & Robinson-Beers, 1993; Rick, 1980). After pollination and fertilization, the ovary becomes the fruit protecting the mature seeds (Osei et al., 2017). The seeds, a result of fertilization, are within the fruit aiding in plant sexual reproduction (Ariizumi et al., 2013).

3.5.2.1. The flower

Tomato plants produce small yellow flowers that are typically less than one inch in diameter when fully open, they can appear individually or in clusters known as inflorescences, which can be simple or complex in structure (Dam et al., 2005). The number of flowers in each inflorescence varies, ranging from 5 to 12. Each flower typically consists of 5 to 8 sepals, 5 to 8 petals, and 5 to 8 stamens surrounding an ovary composed

of 2 to 10 carpels (Brukhin et al., 2003; Swanson et al., 2008). After fertilization, the sepals persist at the top of the developing fruit. The corolla consists of five bright yellow petals that are fused at the base, often bending backward to form a star shape with five points (Wang et al., 2009). The stamens, which contain the pollen-producing anthers, with the elongated anthers cluster around the central pistil, forming a tight cone. The pistil is composed of two fused carpels, resulting in a superior ovary divided into two compartments, with the ovules attached to a central placenta. In some tomato varieties, the ovary may have multiple compartments (Munos et al., 2011; Tiwari, 2012).

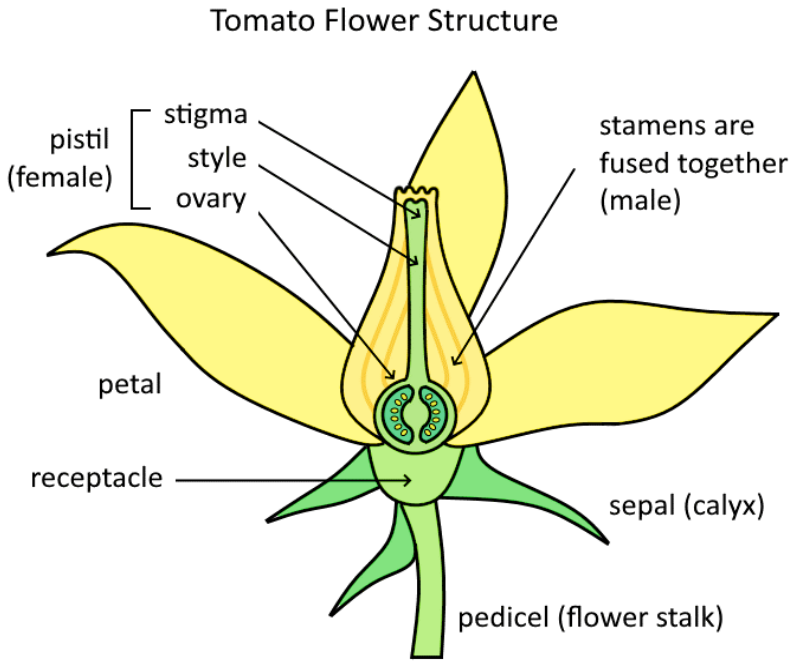

Figure 12: Tomato flower structure (Angelo, 2022).

3.5.2.2. The fruit

The characteristics of tomato fruits can vary depending on the variety (Davies et al., 1981). Each fruit consists of a pericarp, which is divided into compartments that may vary in number. These compartments contain a gelatinous fluid where the seeds are located (Davies et al., 1981; Gierson & Kader, 1986; Madhavi & Salunkhe, 1998). Tomatoes can have either two or more compartments (bilocular or multilocular), with most cultivated types having four or five compartments, except for cherry tomatoes (Falcone, 2010). The pericarp is divided into three layers: the exocarp, mesocarp, and endocarp. The outermost layer of cells in the exocarp is the epidermis, followed by two to three layers of hypodermal cells with thick cell walls (Mintz-Oron et al., 2008). The epidermis lacks

stomata and has a relatively thin cuticle, which thickens as the fruit grows. The mesocarp is made up of large cells with thin walls and vascular tissue (Barclay, 2007; Rančić et al., 2010). According to Xiao et al. (2009) the growth and development of tomato fruit can be segmented into four distinct phases. The initial phase involves the development of the ovary and fertilization. Following fertilization, the second phase commences, characterized by cell divisions within the ovary spanning 7-10 days, succeeded by tissue differentiation, seed development, and the initial growth of the embryo.

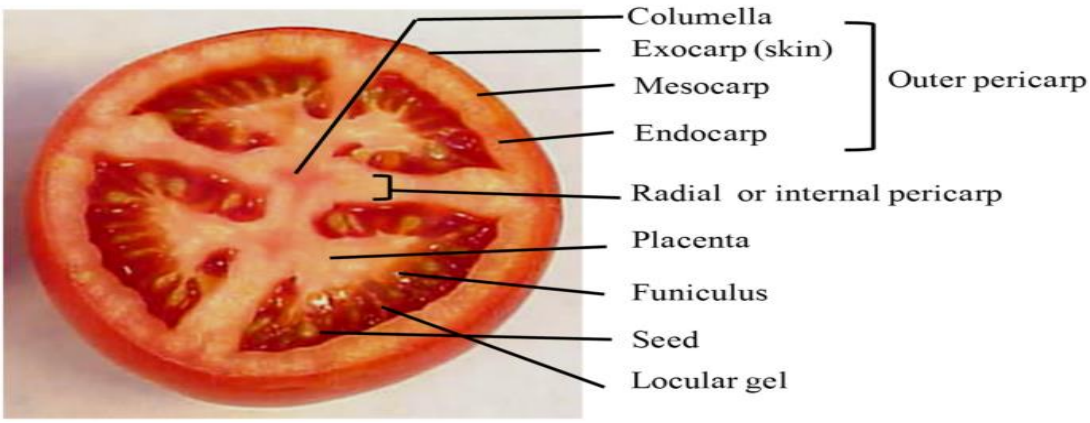

Figure 13: tomato fruit structure (Ramesh et al., 2021).

3.5.2.3. The seed

Tomato seed is typically small, round, and yellow to brown in color, with small hairs on the surface enclosed within a protective seed coat protecting the embryo (Liu, 1996; Madhavi & Salunkhe, 1998). This embryo, consisting of the radicle, and cotyledons, the seed remains dormant until triggered by suitable environmental conditions, such as humidity, temperature, and oxygen, initiating the germination process, with the radicle emerging first followed by the cotyledons developing into the initial true leaves, while the cotyledons, initially serving as nutrient storage organs, provide essential resources for seedling establishment (Bewley et al., 2013; Bradford, 2017; Roldan et al., 2014).

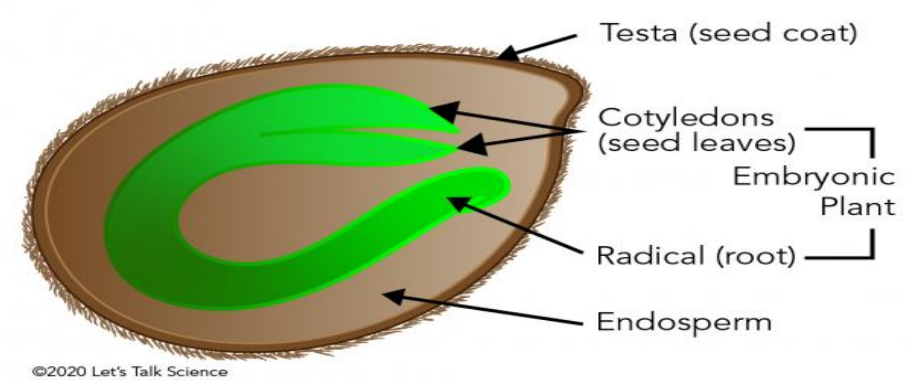

Figure 14: Tomato seed anatomy (Let's talk science, 2020).

3.6. Tomato life cycle

The tomato life cycle starts with a seed that sprouts into a seedling, which develops into a mature plant that bears fruit and flowers later on. Once the fruit is taken, the plant will eventually die off, ending the cycle and maybe producing seeds for new development. Tomatoes grow via five distinct phases, which include germination, vegetative phase, flowering phase, fruiting phase, and mature fruiting according to Short et al. (1997) and Jones Jr (2007). The specific duration of each stage varies depending on factors such as the tomato variety and environmental conditions, including air temperature, light exposure, soil quality, and nutrient availability (Shamshiri et al., 2018).

3.6.1. Germination and early growth phase

Germination phase is the transformation of a dormant tomato seed into a growing seedling, triggered by imbibition of water that initiates metabolic processes, followed by increased respiration, mobilization of stored food reserves for the embryo, radicle emergence for water uptake, shoot emergence with cotyledons, and finally, seedling establishment through photosynthesis as the primary source of nutrition (Martinez et al., 2009; Shamshiri et al., 2018). During this phase, proper soil moisture, temperature, and sunlight are essential for successful germination. Germination occurs within a duration of approximately 25 to 35 days following sowing, under temperatures ranging between 18 and 24°C (Bussell & Gray, 1976; Shamshiri et al., 2018).

3.6.2. Vegetative phase

The vegetative phase is characterized by the growth of leaves, stems, and roots to support the development of flowers and fruit during the fruiting phase (Kerstetter & Hake, 1997).

According to Jones Jr (2007) the vegetative phase of the tomato begins right after germination and typically lasts around 20-25 days. During this time, the main root system grows deeper into the soil, while secondary roots spread out to absorb water, minerals and nutrients. At the same time, the stem grows taller, and new leaves and branches continue to appear, which helps the plant to capture more sunlight for photosynthesis (Dam et al., 2005; Peet & Welles, 2005).

3.6.3. Flowering phase

The flowering phase, comes after the vegetative stage, signifies the transition of tomato plant to reproduction stage. This phase is characterized by the development of flower buds at stem nodes in which they mature into hermaphroditic yellow flowers requiring pollination for fruit set wherein pollen grains are transferred from the anther to the stigma of flowers, either naturally or through intervention such as wind, humans or water (Auxcilia & Shabha, 2017; Lozano et al., 2009). According to Jones Jr (2007) and Dam et al. (2005) the flowering phase can last between 20 to 30 days, and depends on many factors such as varieties, for instance, determinate varieties producing a single flush of flowers rapidly and indeterminate varieties flowering continuously.

3.6.4. Fruiting phase

During this phase the fertilized ovaries after a successful pollination at the base of flowers develop rapidly into initial green fruit tomato fruits, while the other floral parts wither and fall away (Dam et al., 2005; Karapanos et al., 2008). This phase typically takes about 20 to 30 days (Jones Jr, 2007).

3.6.5. Mature fruiting phase

Fruit ripening is characterized by the enlargement of the fruit, and the change of color from green to red due to the chlorophyll pigments breaking down and lycopene accumulation (Bhatla et al., 2018; Gierson & Kader, 1986; Motilva & Romero, 2010). The duration of this phase varies depending on the variety, with some varieties reaching maturity between 15 to 20 days, and environmental factors like temperature and light influence the fruit ripening (Brandt et al., 2006; Jones Jr, 2007).

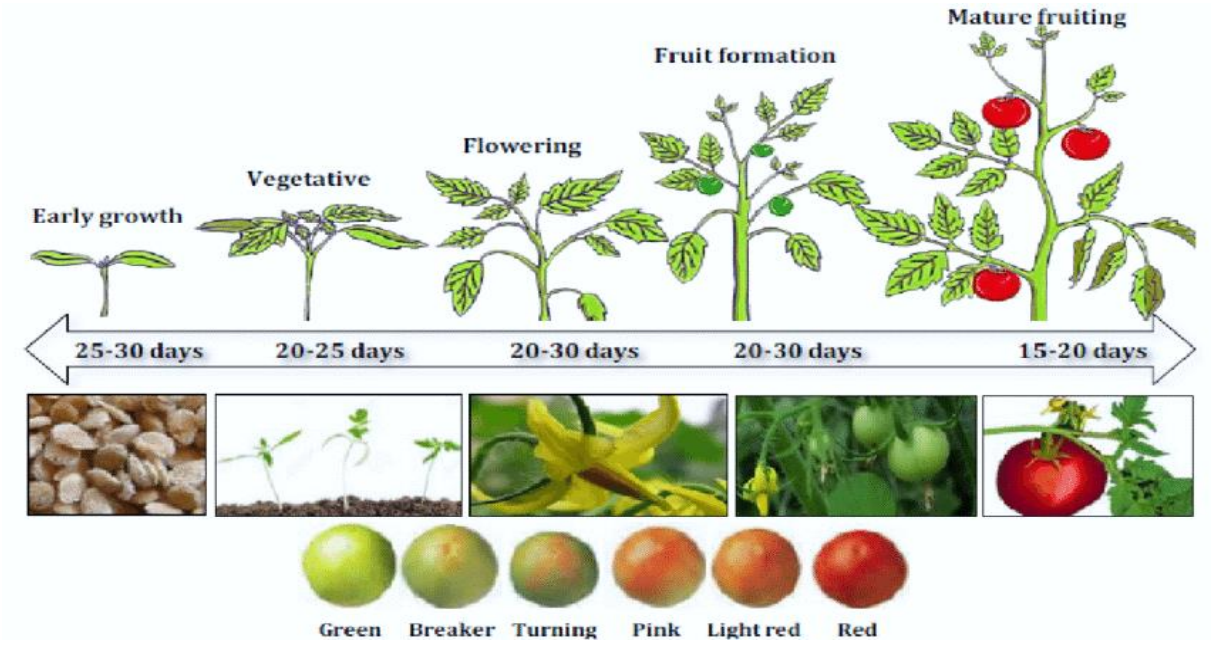

Figure 15: Tomato life cycle (Shamshiri et al., 2018).

3.7. Tomato growth requirements

Tomato plants have particular needs crucial for their best growth and development, including climatic factors like temperature, humidity, sunlight, and watering. Additionally, they rely on soil conditions such as type, drainage, pH level, and organic content (Dam et al., 2005; Schwarz et al., 2014; Shamshiri et al., 2018). Furthermore, nutrient supply is essential, including both macronutrients like nitrogen, phosphorus, and potassium, and micronutrients such as iron, manganese, and zinc (Sainju et al., 2003).

3.7.1. Climatic requirements

Tomatoes, being a warm-season crop, have specific climatic requirements for optimal growth and fruit quality. Ideal average daily temperatures range from 20°C to 27°C, with extremes below 10°C or exceeding 38°C causing significant plant and fruit damage (Dam et al., 2005; Nicola et al., 2009). Light intensity also plays a crucial role, with 400 µmol m^{-1} s^{-1} considered optimal (Balkaya & Özkaplan, 2019). Water needs vary depending on cultivation methods, with greenhouse tomatoes requiring approximately 75% of crop evapotranspiration for ideal growth (Salokhe et al., 2005). Relative humidity is another key factor, with a range of 65-75% fostering optimal development. Higher humidity levels can hinder plant growth, while hot, dry winds may cause excessive flower drop (Bakker, 1991; Schwarz et al., 2014). Conversely, overly moist and rainy conditions promote leaf diseases, making control more challenging (Huber & Gillespie, 1992). It's important to note that these requirements for temperature, humidity, and irrigation can fluctuate based on the

growth stage, light exposure, and whether cultivation occurs in open fields or greenhouses (Shamshiri et al., 2018).

3.7.2. Edaphic requirements

Edaphic parameters are soil characteristics that affect plant growth and development, including soil type, drainage, pH, and, texture, determined by the proportions of sand, silt, and clay, plays a crucial role in plant growth (Li et al., 2017). According to Shamshiri et al. (2018) tomatoes thrive in various growing media, such as soil, organic substrates, soilless mixes, perlite, sand, or hydroponic systems. Adequate aeration and drainage are essential for healthy plant roots, as root asphyxiation, even temporarily, can harm the crop. To achieve good yields, the soil should have a high organic matter content (Pignata et al., 2017). Moreover, as reported by Sainju et al. (2003) the optimal pH range for tomato growth is typically between 5.5 and 7.0.

3.7.3. Water and mineral requirements

Tomato plants require a balanced supply of macronutrients such as nitrogen, phosphorus, potassium, calcium, and magnesium, in addition to micronutrients like iron, manganese, zinc for optimal growth and development (Roosta & Hamidpour, 2013; Sainju et al., 2003). Adequate nutrient management, through soil testing and appropriate fertilization practices is essential to promote healthy growth, maximize yield, and enhance resistance to biotic and abiotic factors (Shamshiri et al., 2018).

3.8. Production of tomatoes in the world

The tomato (*Solanum lycopersicum L.*) stands as a globally significant vegetable crop, valued for both fresh consumption and its versatility in processed products. the Food and Agriculture Organization (FAO) reveals that in 2023, world production reached nearly 190 million metric tonnes of tomatoes per year, cultivated across 5 million hectares with an average yield of 36.97 tonnes per hectare. China reigns supreme as the top producer, contributing nearly 34.72% of the global total with a production of 67.5 million tonnes, followed by India with a production of 21.18 million tonnes and Turkey reaching a production of 13.09 million tonnes. The processing of tomatoes holds immense economic importance on a global scale. In 2023, the global tomato market is valued at 174.7 billion dollars and it’s estimated to reach 207.17 billion dollars in 2024 (Mordor, 2024). The increasing global demand for tomatoes is due to the rise in population size, increased awareness of health-related issues, and the extensive use of tomatoes in cooking. This

phenomenon is amplified by the development of the processed food industry and the rising desirability of dishes centered around tomatoes globally. As a result, it is predicted that the demand for tomatoes will continue to rise in the future (Collins et al., 2022; Motamedzadegan & Tabarestani, 2018; Ouattara & Konate, 2024).

3.9. The importance and nutritional value of tomato

3.9.1. Nutritional value of tomato

Tomatoes are widely recognized for their exceptional nutritional profile, rendering them an integral component of various cuisines worldwide (Madhavi & Salunkhe, 1998). They are comprised mostly of water (95%) but contain a significant amount of vitamin C, potassium, and folate alongside smaller quantities of vitamins A and K, minerals like magnesium, phosphorus, calcium, and iron, and the antioxidant lycopene, responsible for their red color (Butnariu & Butu, 2015; Ghorbani et al., 2012; K. P. S. Kumar et al., 2012).

Table 2: Nutritional value of tomato per 100g (Butnariu & Butu, 2015).

Element	Value /100g	Element	Value /100g
Vitamin C	14 mg	Lycopene	2.753 µg
Vitamin E	0.54 mg	Thiamine	0.037 mg
Vitamin K	7.9 µg	B-carotene	449 µg
Vitamin B6	0.08 mg	Water	94.5 g
Vitamin A	42 µg	Proteins	0.9 g
Potassium	237 mg	Carbohydrates	3.9 g
Magnesium	11 mg	Fat	0.2g
Manganese	0.114 mg	Phosphorous	24 mg

3.9.2. Health benefits of tomato

Tomatoes offer a multitude of health benefits, positioning them as a fundamental part of a nutritious diet. They are packed with essential nutrients such as vitamins, minerals and phytochemicals that have the potential to alleviate the onset of chronic diseases (K. P. S. Kumar et al., 2012). One of the main benefits of tomatoes is their abundant content of

lycopene, a powerful antioxidant associated with reduced susceptibility to cardiovascular disease and some forms of cancer (Borguini & Ferraz Da Silva Torres, 2009; Mordente et al., 2011). Research indicates that lycopene may also help decrease levels of atherogenic LDL cholesterol and protect against oxidative stress-induced cellular damage facilitated by harmful free radicals (Kiokias et al., 2018). Additionally, tomatoes are a notable storehouse of vitamin C, strengthening the immune system and promoting accelerated wound healing. They also contain vitamin K, essential for skeletal health and hemostasis (K. P. S. Kumar et al., 2012). Furthermore, according to Perveen et al. (2015) the potassium in tomatoes confers benefits related to managing blood pressure and maintaining optimal fluid balance in the body. Additionally, the dietary fiber in tomatoes facilitates gastrointestinal processes and satiety, potentially contributing to weight regulation (Palafox-Carlos et al., 2011).

CHAPTER 2: MATERIALS AND METHODS

1. Objective of the work

The aim of this research was to evaluate various plant growth-promoting traits exhibited by PGPR strains obtained from the Constantine region of Algeria, including indole-3-acetic acid production (IAA), phosphate (P) solubilization, hydrogen cyanide (HCN) production, and tolerance to NaCl-induced salinity stress. Additionally, the phytochemical composition of *Cystoseira compressa*, a brown seaweed collected from the Coast of Bouharoun in Tipaza, Algeria, was analyzed using analytical techniques such as FT-IR to identify functional groups, LC-MS/MS to characterize the profile of amino acids (AAs) and HP-LC analysis to characterize the profiles of phytohormones and sugars of this algae. Furthermore, the study investigated the impact of both individual and combined applications of a selected growth-promoting rhizobacterium *Bacillus cereus* MR64 which its identification was confirmed through the 16S rRNA gene sequencing and varying concentrations (5%, 10%, and 15%) of the aqueous extract derived from *Cystoseira compressa* on the growth, physiological, biochemical, development and production responses of tomato (*Solanum lycopersicum L.*) under salinity stress induced by 150 mM NaCl. Additionally, the characterization of tomato plants under salinity stress was performed using FT-IR analysis.

2. Collection area and identification of brown algae *C. compressa*

Fresh samples of *Cystoseira compressa* were manually collected at depths of 20 and 30 cm in April, 2022 from the coastal area of Tipaza, Algeria (Saîdia rocks 36°37'03.8"N 2°38'21.2"E). The site and the species selection were based on the following criteria:

- The abundance of *Cystoseira* algae species along Tipaza's coast with significant quantities.
- The ease of collection of *Cystoseira compressa* without the need for deep diving or specialized equipment.
- *Cystoseira compressa*, classified within the category of brown seaweeds, have historically been recognized for their application as biostimulants in various agricultural contexts, exhibiting compatibility with a broad range of crops such as fruits, vegetables, and grains.

The collected algae samples were harvested by hand with thalli and carefully rinsed with seawater to remove all impurities. Subsequently, the samples were transported to the laboratory and washed with tap water to eliminate epiphytes and adherent sand particles.

Algae identification was conducted at the Laboratory of Plant Production Biotechnology Research, Department of Biotechnology, Faculty of Natural and Life Sciences, in Blida, Algeria, under the expertise of Dr. Hafidha Metidji.

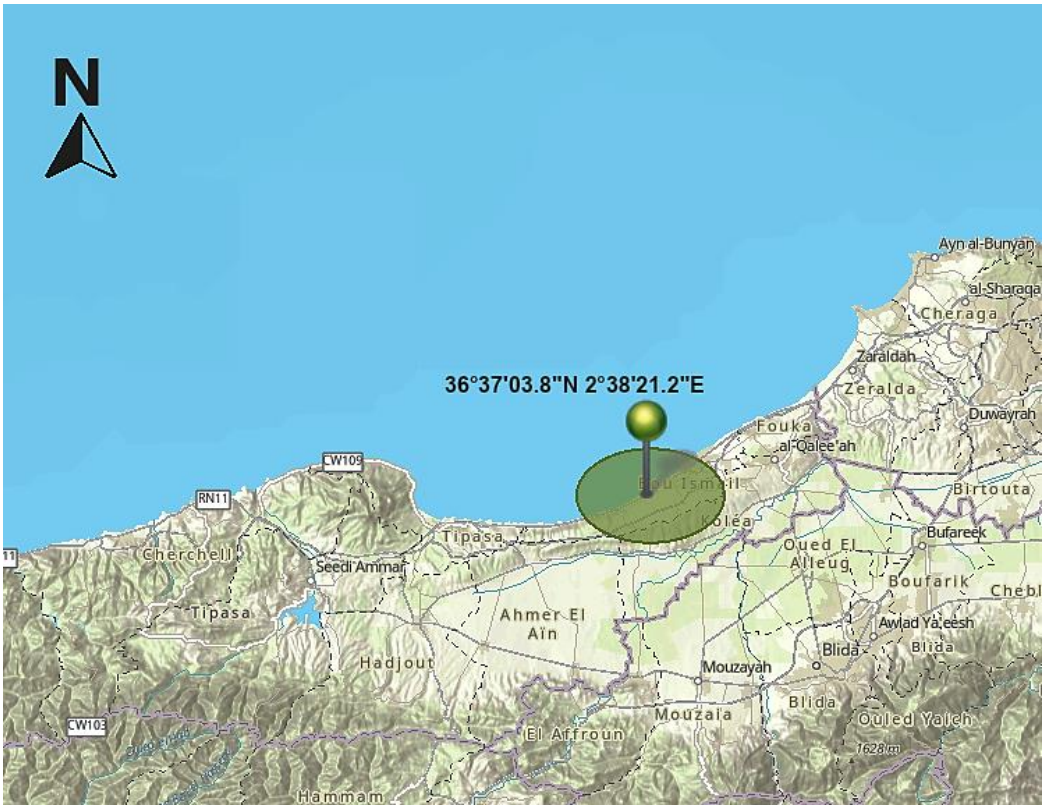

Figure 16: The geographical location of the *Cystoseira compressa* algae sampling site.

3. Preparation of aqueous extracts

The samples were air-dried, then grinded using an electric blender, and stored in sterilized glass jars at an ambient temperature. Subsequently, 100 g of algae powder underwent a heating process for 45 minutes at 60°C in 1 liter of sterile distilled water. The obtained extracts were filtered and stored. Different concentrations of 5%, 10%, and 15% of the liquid algae extract were prepared by diluting the filtrate with distilled water, then kept at 4°C for further applications, with the original filtrate serving as 100% concentration, as detailed by Hamouda et al. (2022).

4. Phytochemical characterization of brown algae C. compressa

The phytochemical characterization of the brown seaweed *C. compressa* was conducted using multiple analytical techniques. Analysis by Fourier-transform infrared spectroscopy

(FT-IR) of the algae powder, as well as analysis of the amino acid profile by liquid chromatography coupled with tandem mass spectrometry (LC/ESI-MS/MS), and the phytohormone and sugar profiles by high-performance liquid chromatography (HP-LC), were respectively carried out at the Research Laboratory Practice and Research Center of Igdir University, Turkey.

4.1. FT-IR analysis

Fourier-transform infrared spectroscopy (FT-IR) analysis was conducted using a Shimadzu FTIR-8900 spectrophotometer. In this process, the powdered sample was carefully mixed with potassium bromide (KBr) to meticulously prepare a solid pellet. This solid pellet was then subjected to spectral analysis in the frequency range of 500 to 4000 cm-1, following the established procedure described by Abdul Khalil et al. (2017).

4.2. Analysis of the amino acid profile by LC/ESI-MS/MS

4.2.1. Extraction

The extraction of amino acids was conducted according to the method of Konieczna et al. (2018) involved dissolving 2 g of algae powder in 15 ml of 0.1 N HCl, followed by vigorous agitation and filtration using a No. 1 filter paper. Subsequently, 200 µL of the filtrate were combined with 800 µL of acetonitrile, centrifuged, and then 100 µL of the supernatant were injected into the instrument after adding 450 µL of ultrapure water and 450 µL of methanol. Prior to injection, the solution was pre-filtered through a 0.22 µm filter.

4.2.2. LC/ESI-MS/MS settings

The LC-MS/MS analysis was performed using an Agilent Technologies 1260 Infinity II, 6460 Triple Quad mass spectrometer equipped with a Poroshell® 120 SB-C18 column (3.0 × 100 mm, ID, 2.7 µm). The injection volume was set to 5.18 µL, and the flow rate was adjusted to 0.40 ml/min. The mobile phase consisted of formic acid (0.1%) and ammonium formate (5.0 mM) in ultrapure water (solution A) and formic acid (0.1%) and ammonium formate (5.0 mM) in methanol (solution B). The gradient program was configured with an increase to 25% for 1 to 3 minutes, 50% for 4 to 12 minutes, 90% for 13 to 21 minutes, and a decrease to 3% for 22 to 25 minutes for mobile phase B. The column temperature was maintained at 40°C. The capillary voltage was set to 4000 V, and the nebulizing gas flow (N2) rate was 11 L/min at a pressure of 15 Psi. The gas temperature was maintained at

300°C. The LC-MS/MS system was controlled, and the data were analyzed using Agilent MassHunter Workstation software. Amino acid quantification was performed using the external standards method Konieczna et al. (2018).

4.3. Analysis of the phytohormone composition of the algae by HP-LC/DAD

4.3.1. Extraction

Phytohormone extraction was conducted by dissolving 5 g of algae powder in a mixture of 100 ml (70 ml methanol and 30 ml ultrapure water, v/v). After 24 hours of incubation in a water bath at 40°C, the solution was filtered through Whatman No. 1 filter paper, and the solvent was removed using a rotary evaporator. Subsequently, 1 ml of methanol was added to 50 mg of the dried extract, followed by mixing and centrifugation at 10,000 rpm for 15 minutes. Then, 100 µL were sampled, diluted with 450 µL of ultrapure water and 450 µL of methanol, filtered through a 0.22 µm filter, and injected into the instrument (Kosakivska et al., 2020).

4.3.2. HP-LC/DAD settings

High-performance liquid chromatography (HP-LC) analysis was conducted using an AGILENT 1260 series instrument. The method employed included the use of a Zorbax® C18 column (4.6 x 250 mm) packed with 5 µm particles. The mobile phase (A) consisted of 1% phosphoric acid and 99% ultrapure water (V/V), with pH adjusted to 2.92. The mobile phase (B) was composed of 26% acetonitrile (100%). The column temperature was maintained at 30°C with a flow rate of 0.8 ml/min, and the system was isocratic (74% water + 26% acetonitrile). Detection was performed using a diode array detector (DAD) at 208/4 nm, with a reference wavelength of 360/4 nm. The injection volume was set at 10 µl according to Kosakivska et al. (2020) method. The quantities of different compounds were calculated using the Gauss method, based on the calibration curve.

4.4. Analysis of the sugar composition of the algae by HP-LC/RID

4.4.1. Extraction

Sugar extraction was performed by dissolving precisely 1 g of algae powder in 10 ml of a mixture composed of 75% ultrapure water and 25% methanol. The mixture was thoroughly mixed, with sonication for 2 minutes. After sonication, the resulting solution was filtered using a 0.45 µm filter with a syringe prior to injection into the instrument.

4.4.2. HP-LC/RID settings

The HP-LC procedure was carried out using an AGILENT 1260 series instrument, equipped with a Hi-Plex H column (300x7.7 mm) with a particle size of 8 µm. The mobile phase (A) consisted of 100% ultrapure water. The column was maintained at a temperature of 65°C, with a flow rate of 0.6 ml/min. Compound detection was performed by refractive index detection (RID), and the detector temperature was maintained at 35°C. The injection volume was set at 20 µl. Quantities of different compounds were calculated using the Gauss method, based on the calibration curve (Bokov DO et al., 2020).

5. Bacterial material and culture of strains

Pure cultures of rhizobacterial strains coded as MR62, MR63, and MR64 were acquired from the Laboratory of Genetics, Biochemistry, and Plant Biotechnology at the University of Constantine, Algeria. The bacteria were cultured on nutrient agar medium, maintained at a temperature of 30 ± 2°C for 48 hours, and then suspended in sterile flasks containing 250 ml of liquid Lauria Bertani medium. These flasks were subjected to continuous agitation at a speed of 80 rpm for 48 hours at a temperature of 30°C.

5.1. Determination of the tolerance of bacterial strains to NaCl

The halotolerance of rhizobacterial strains was screened by observing their growth on Luria-Bertani medium (Bertani, 1951) at 37°C supplemented with various concentrations of NaCl ranging from 2% to 8%. Bacterial growth was determined by measuring the OD600 nm after 3 days.

5.2. Screening for growth-promoting traits

The ability of rhizobacterial strains to promote plant growth was assessed through qualitative tests for the synthesis of indole-3-acetic acid (IAA), inorganic phosphate solubilization, and hydrogen cyanide (HCN) production. Each test was conducted in triplicate.

5.2.1. The synthesis of indole-3-acetic acid (IAA)

The production of indole-3-acetic acid (IAA) was qualitatively evaluated using the method described by Bric et al. (1991). Bacterial cultures were grown in LB medium supplemented with tryptophan (1 mg/ml) at 37°C for 48 hours. After centrifugation (3000 rpm, 30 minutes) of fully developed cultures, 2 ml of supernatant were mixed with orthophosphoric

acid and 4 ml of Salkowski reagent (containing 35% perchloric acid and 0.5 M FeCl3). The development of a pink color indicates the production of indole-3-acetic acid (IAA).

5.2.2. Solubilization of phosphate (P)

Phosphate solubilization was qualitatively assessed following the method described by Katznelson and Bose (1959). Bacterial cultures were grown on modified Pikovskaya agar (Pikovskaya, 1948) with insoluble tricalcium phosphate (TCP), incubated at 30°C, and observed daily for 7 days until the formation of a clear halo around each colony.

5.2.3. Hydrogen cyanide (HCN) production

Hydrogen cyanide (HCN) production was tested through a qualitative screening using the method described by Lorck (1948). Bacteria were streaked onto modified nutrient agar supplemented with glycine. Whatman filter paper No. 1 soaked in 2% sodium carbonate and 0.5% picric acid was placed on the plate, which was then sealed and incubated at 37°C for 4 days. The development of an orange-red color indicates the production of hydrogen cyanide (HCN).

5.3. Molecular identification of the selected strain with 16S rRNA sequencing

The rhizobacterial strain MR64 was selected due to its ability to tolerate NaCl and its favorable plant growth characteristics. For the identification of this bacterial strain, a method based on the analysis of the 16S rRNA gene sequence was employed. The DNA from each bacterial sample was extracted through a heat shock procedure, where an isolated colony from a young bacterial culture grown on a nutrient agar plate was mixed with sterile water. This mixture underwent freezing at -20°C for 30 minutes followed by heating at 95°C for 3 minutes. This cycle of freezing and heating was repeated two to three times. Universal primers as described by Weisburg et al. (1991), were used for amplifying the 16S rRNA gene. The amplification protocol included an initial denaturation at 94°C for 5 minutes, followed by 35 cycles of denaturation at 94°C for 30 seconds, annealing at 55°C for 45 seconds, extension at 72°C for 90 seconds, and a final extension at 72°C for 10 minutes. The amplified PCR products were analyzed by 1% agarose gel electrophoresis and visualized with ethidium bromide under short-wavelength UV light. The sequences of each strain were checked and extracted using Mega X (version 10.0.5). A Blastn analysis was employed to identify the corresponding sequences in the NCBI GenBank database. Alignment with close neighbors was performed using Mega X (version 10.0.5) with

MUSCLE, followed by neighbor-joining (NJ) algorithms. A phylogenetic tree was constructed with MEGA-X (version 10.0.4) using the NCBI GenBank accession numbers.

5.4. Preparation of bacterial inoculum

A bacterial suspension was prepared using distilled water, and adjustments to the concentration of this suspension to 10^8 colony-forming units per milliliter (CFU/ml) (OD600nm = 0.8) were made through spectrophotometric measurements, following the methodology of Barra et al. (2016).

6. Preparation and germination of tomato seeds

The tomato variety selected for this study was the Saint Pierre variety, which is genetically stable, approved, and certified. The seeds were obtained from the Technical Institute of Horticultural and Industrial Crops, located in Stouali, Algiers, Algeria. Surface sterilization of tomato seeds was performed according to the method described by Götz et al. (2006), Initially, the seeds were treated with 70% ethanol for 1 minute, followed by acidified 12% hypochlorite for 15 minutes. Subsequently, the sterilized seeds were thoroughly rinsed with sterile water and germinated in Petri dishes at a temperature of 25°C.

7. Soil preparation and analysis

The soil used underwent sterilization in an oven for one hour at a temperature of 120°C. The soil characteristics are presented in Table 1, including particle size distribution, calcium carbonate content, cation exchange capacity (CEC), pH, electrical conductivity, total nitrogen content, assimilable phosphorus content (P2O5), assimilable potassium content (K2O), carbon content, organic matter content, exchangeable bases (K+, Na+, Ca++, Mg++), as well as the ionic balance (Ca++, Na+, Cl-, CO3-), were analyzed at the Soil and Water Analysis Laboratory of the National Bureau of Rural Development Studies (B.N.E.D.E.R) located in Bouchaoui, Chéraga, Algiers.

Table 3: The characteristics of the soil used in the experiment

Characteristic		**Measure**
Total Caco3 (in %)		13,13
CEC (in meq /100 g)		15,93
pH (1/5)		6.43
Conductivity in Emmhos/cm. (1/5)		0,29
Total nitrogen N%		2,24
Assimilable phosphorus P2O5 ppm		65,65
Assimilable potassium K2O ppm		21,46
Carbon C %		0,72
Organic matter OM%		1,24
Granulometry (In %)	A (Clay)	35,18
	LF (fine silts)	26,00
	LG (coarse silts)	12,67
	SF (fine sand)	10,05
	SG (coarse sand)	16,10
Exchangeable bases (In meq/100g)	K+	0,25
	Na+	0,73
	Ca++	10,14
	Mg++	3,99
Ion levels (In meq/100g)	Ca++	0,73
	Na+	0,44
	Cl-	0,50
	Co3-	0,75

The soil is a clay loam with low salinity (EC 0.29 dS/m) and slightly acidic pH (6.43), ideal for most crops. The soil has a high content of nitrogen (2.24%) and phosphorus (65.65 ppm) while low potassium (21.46 ppm) and organic matter (1.24%). Calcium carbonate (13.13%) content are moderate (e.g., iron, zinc, manganese). Sodium (0.44 meq/100g) and chloride (0.50 meq/100g) levels are low.

8. Experimental design and setup of the bioassay

The pot experiment was conducted in a semi-controlled greenhouse at the Department of Biotechnology, Faculty of Natural and Life Sciences, University of Blida 1, from January to April 2023. After tomato seeds germinated, the young plants were transferred to germination trays to ensure uniform initial growth. Subsequently, they were transplanted into pots measuring 11 cm in height and 12 cm in diameter, containing 6 kg of soil. These pots were placed on a metal stand, subjected to environmental conditions with daily maximum and minimum temperatures of 25 ± 3°C and 18 ± 2°C, respectively, along with a relative humidity of 60%. The experiment followed a randomized complete block design with six replicates, totaling 48 pots, initiated at the 3-leaf stage, 15 days after transplanting. Tomato plants were regularly irrigated with a 150 mM NaCl saline solution twice a week and subjected to eight distinct treatments:

Experiment 1: Control, consisting of irrigation solely with a 150 mM NaCl saline solution.

Experiment 2: 10 ml of the bacterial suspension of strain MR64 + irrigation with a 150 mM NaCl saline solution.

Experiments 3, 4, 5: 10 ml of 5%, 10%, and 15% aqueous extract of *Cystoseira compressa* seaweed, respectively + irrigation with a 150 mM NaCl saline solution.

Experiments 6, 7, 8: 10 ml of the bacterial suspension of strain MR64 + 10 ml of aqueous extract of *Cystoseira compressa* seaweed at 5%, 10%, and 15%, respectively + irrigation with a 150 mM NaCl saline solution.

Three applications of these treatments were carried out at 10-day intervals. The choice of a 150 mM sodium chloride NaCl salinity stress level was selected because it is recognized to induce significant detrimental effects on tomato plants. This concentration provides a clear contrast with the control group, allowing for precise observation of the effects of the experimental treatments on salinity-induced stress according to prior studies (El-Mogy et al., 2018; He et al., 2009; Rofekuggaman et al., 2020). Growth, physiological, and biochemical parameters were measured 10 days after the third application, while development and production parameters were evaluated 20 days after the third application of the treatments.

Figure 17: Germination of tomato seeds and implementation of the trial in the greenhouse using a randomized block design.

9. Parameters studied

Measurements of growth, physiological, and biochemical parameters were conducted on randomly selected plants from different blocks, 10 days after the third application of the treatments. Similarly, the assessment of production parameters was conducted 20 days after the third application of the treatments.

9.1. Growth parameters

Morphological responses, such as shoot length, root length, fresh and dry weight of the aerial part, fresh and dry weight of roots, total fresh weight, total dry weight, and leaves number, were measured. The length of the aerial part was measured using a scale from the root-shoot junction to the tip. Root length was measured from the root-shoot junction to the tip of the longest root. Leaves number of each plant was accurately recorded. To determine the fresh weight and dry weight of aboveground and root parts, plant parts were cut at the junction, and the fresh weights of roots and shoots were immediately measured. For dry weight, samples were placed in an oven at 80°C until a stable weight was obtained using a precision balance. Total fresh weight and total dry weight were estimated from the fresh and dry weights of shoots and roots.

9.2. Physiological parameters

9.2.1. Photosynthetic pigments

The chlorophyll content was estimated using the method described by Arnon (1949). Fresh leaves (100 mg) were ground in a mortar and pestle with 10 ml of chilled 80% acetone. The extract was filtered through Whatman filter paper, and 1 ml of the filtered extract was used for spectrophotometric determination at 645 and 663 nm using a spectrophotometer. Chlorophyll a, b, and total chlorophyll were calculated using the following formula:

$$\textbf{Chlorophyll a} = \mathbf{11.23A663 - 2.04A645}$$

$$\textbf{Chlorophyll b} = \mathbf{20.13A645 - 4.19A663}$$

$$\textbf{Total chlorophyll} = \mathbf{7.05A663 + 18.09A645}$$

Where A is the absorbance at a specific wavelength (nm).

9.2.2. Leaf Relative water content (LRWC%)

The relative water content of leaves (LRWC %) was determined following the method described by Turner (1981). The fresh weight of the leaves was measured immediately after harvesting. Samples were then immersed in distilled water for 24 hours to achieve full turgor. After removing excess water by blotting the samples, their turgid weight was recorded. Subsequently, the samples were placed in an oven at 80°C until a constant weight was obtained, indicating complete dryness and allowing determination of the dry weight. The RWC % was calculated using the following formula:

$$\textbf{RWC}\ (\%) = [(\mathbf{FW - DW}) / (\mathbf{TW - DW})]\ \mathbf{x\ 100}$$

Where FW is the fresh weight (g), DW is the dry weight (g), and TW is the turgid weight (g).

9.2.3. Leaf electrolyte leakage (EL%)

The membrane integrity was assessed following the method described by Sun et al. (2006) by evaluating electrolyte leakage. Tomato leaves (200 mg) were washed with distilled water, cut into small pieces, and placed in test tubes containing 20 ml of distilled water. The electrical conductivity (C1) of the solution was measured using an electrical conductivity meter after incubating it at 25°C for 30 minutes. The samples were then incubated at 100°C for 30 minutes and cooled to room temperature. The second

conductivity (C2) was measured after stabilization at 25°C. Electrolyte leakage was determined using the following equation:

$$\mathbf{EL}\% = [\mathbf{C1/C2}] \times \mathbf{100}$$

Where C1 is the electrical conductivity of the solution before incubation at 100°C, and C2 is the electrical conductivity of the solution after incubation at 100°C.

9.3. Biochemical parameters

The measurements of biochemical parameters, including sodium (Na+) and potassium (K+) concentrations, proline content, quantification of total soluble sugars, as well as FT-IR analysis, were conducted 10 days after the third application of treatments on the plants.

9.3.1. Sodium (Na+) and potassium (K+) content

The concentrations of sodium (Na+) and potassium (K+) were measured using a flame photometer. Approximately 100 mg of leaf samples were collected and subjected to oven drying. The dried samples were then digested in 0.5 ml of 0.5N HNO3 for a period of 2 hours at 80°C, following the method established by Munns et al. (2010). After digestion, the samples were centrifuged, and a 100 µl aliquot of the supernatant obtained was diluted at a ratio of 1:100 with distilled water. The concentration in mg/g of dry matter of sodium (Na+) was determined based on a previously established standard curve, using NaCl standards, according to the following equation:

$$\mathbf{OD} = \mathbf{10926} * \mathbf{C} + \mathbf{24.788}\ \mathbf{with}\ (\mathbf{R^2} = \mathbf{0.9907})$$

The concentration of potassium (K+) in mg/g of dry matter was determined by reference to a previously established standard curve using KCl as the standard, according to the following equation:

$$\mathbf{OD} = \mathbf{65351} * \mathbf{C} + \mathbf{551.25}\ \mathbf{with}\ (\mathbf{R^2} = \mathbf{0.9892})$$

9.3.2. Proline content

To quantify the proline content, the method described by Bates et al. (1973) was used. Fresh leaves (200 mg) were combined with 2 ml of distilled water and subjected to boiling for 30 minutes in a water bath. After centrifugation, 1 ml of the supernatant was combined with 2 ml of freshly prepared ninhydrin reagent (1%; 0.5 g ninhydrin in 50 ml 60% acetic acid). After incubating the samples for 20 minutes in a boiling water bath, 3 ml of toluene was added, and the supernatant was collected. The optical density (OD) was measured at a

wavelength of 520 nm using a spectrophotometer, and the proline concentration, expressed in µg/g of fresh plant material, was determined by reference to a previously established standard curve according to the following equation:

$$\mathbf{OD} = \mathbf{0,091} * \mathbf{C} + \mathbf{0.0381\ with}\ (\mathbf{R2} = \mathbf{0,987})$$

9.3.3. Total soluble sugars content

The quantification of total soluble sugars was performed following the method described by McCready et al. (1950). Extraction was carried out by combining 100 mg of fresh material with 2 ml of 80% ethanol. The mixture was shaken and centrifuged for 20 minutes at 5000 rpm. The supernatant was collected and mixed with 2 ml of anthrone reagent (0.2 g anthrone in 100 ml sulfuric acid + 1 ml extract). The tubes were shaken, incubated in a water bath at 95°C for 10 minutes, then placed in a water bath at 30°C for 10 minutes. Absorbance was measured at a wavelength of 490 nm using a spectrophotometer, and the concentration of total soluble sugars in mg/g of fresh plant material was estimated by reference to a standard curve established with glucose as the standard, according to the following equation:

$$\mathbf{DO} = \mathbf{0.1418} * \mathbf{C} + \mathbf{0.0699\ with}\ (\mathbf{R}^2 = \mathbf{0.9925})$$

9.4. Development and production parameters

During the development and production phase of tomato plants, we implemented the practice of pruning, which involves removing all buds emerging at the leaf axils. This procedure also includes the removal of the oldest leaves from the base of the plant to reduce the risk of disease establishment. Additionally, topping was performed, involving the removal of the terminal bud from the main stem (2nd floral cluster). This specific operation was carried out towards the end of the tomato plant's vegetative cycle. Parameters, including the number of flowers per plant, the number of fruits per plant, and the average distance between cluster 1 and cluster 2 on each plant were evaluated 20 days after the third application of the treatment.

9.4.1. Number of flowers

We conducted an accurate count of the number of flowers present in each floral cluster. Additionally, we performed a count of the total number of flowers on each plant.

9.4.2. Number of fruits

We counted the fruits for each floral cluster as well as for each plant.

9.4.3. Distance between floral clusters

We measured the distance between the first floral cluster and the second floral cluster for each plant.

10. FT-IR analysis of different treatments

The plants were dried in an oven at 40°C for one week, then pulverized using an electric blender, and finally stored in sterilized glass jars. Subsequently, they underwent analysis using Fourier-transform infrared spectroscopy (FT-IR) with the Agilent Cary 630 FTIR spectrometer. The analysis data are processed using Spectragryph software (Ver 1.2) and OriginLab software (Ver 2023B).

11. Data treatment and statistical analysis

Significant differences between the means of plant samples subjected to treatments and control plants were evaluated using a two-factor ANOVA and Tukey's test, using the 18th edition of the Genstat software. Tukey's test was employed to detect significant variations between the means of different treatments, with a significance level set at ($P < 0.05$). The results are presented as mean ± standard deviation.

CHAPTER 3: RESULTS AND DISCUSSION

1. Phytochemical characterization of the brown alga *Cystoseira Compressa*

1.1. Characterization of the algae by FT-IR

The FT-IR spectrum in the range of 4000 to 400 cm^{-1} was obtained for the *Cystoseira compressa* powder as shown in Figure 18, the FT-IR spectrum of the sample shows significant vibrational peaks at wavenumbers of 679, 818, 1045, 1258, 1447, 1531, 1639, 2353, 2928, 3437, and 3734 cm^{-1}.

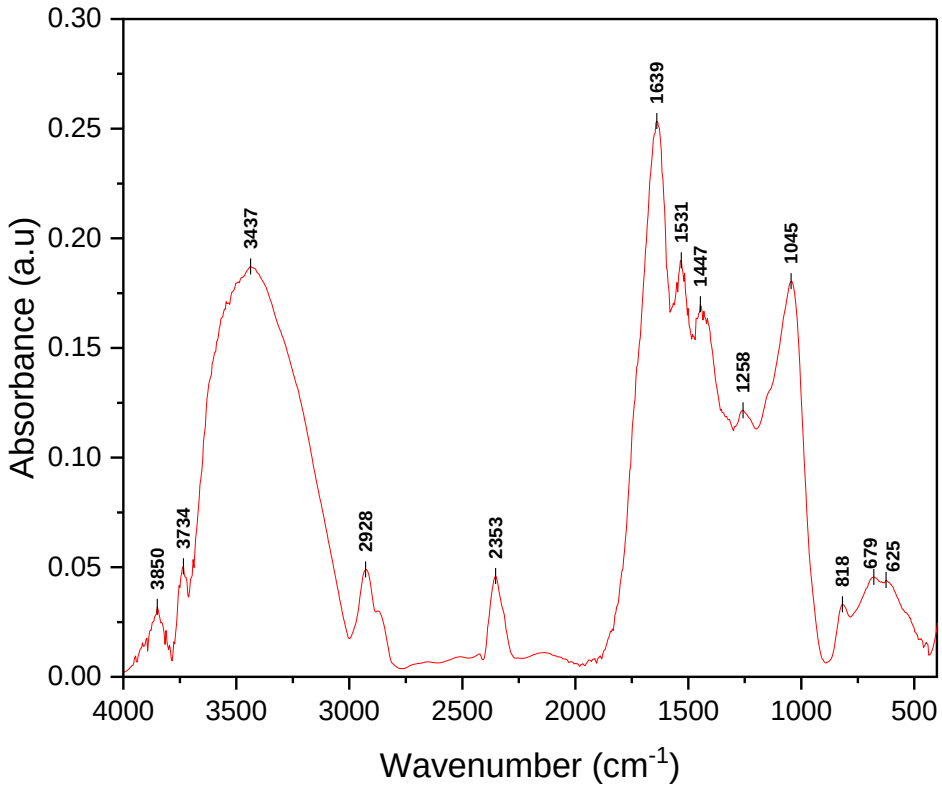

Figure 18: FT-IR analysis spectra result of *Cystoseira compressa*.

1.2. Characterization of the amino acid profile of *C. compressa* by LC-MS/MS

The quantitative evaluation of amino acid compounds in the seaweed *Cystoseira compressa* was performed using liquid chromatography-tandem mass spectrometry (LC-MS/MS), the results are summarized in Table 4. The analysis revealed the presence of a wide diversity of amino acids in the seaweed extract. In total, eight major amino acids

were successfully identified and quantified in the seaweed extract. The quantification data are expressed in mg/100 g of extract. Specifically, the results highlight the predominance of L-alanine, L-glutamic acid, and L-aspartic acid, which exhibited relatively higher concentrations in the seaweed extract. Conversely, L-valine, L-leucine, L-proline, L-threonine, and L-lysine were detected in smaller amounts.

Table 4: LC-MS/MS analysis for amino acids profile of *C. compressa*.

Compounds	Retention time	Mass Fragments		Frag	Collision energy	Resp.	Final concentration
	[min]	Precursor Ion (m/z)	Product Ion (m/z)	[V]	[V]		[mg/100g extract]
L-Lysine	3.980	147	84.1	75	12	676	2.4511
L-Histidine	3.514	156.1	110.1	80	12	92	ND
L-Arginine	3.513	175.1	70.3	90	24	16	ND
L-Cystine	3.620	240.9	152.1	75	6	2	ND
L-Glycine	3.536	76.1	30.1	35	8	3	ND
L-Serine	3.544	106.1	60.2	60	8	28	ND
L-Aspartic acid	4.263	134.1	74.2	60	10	664	14.5324
L-Alanine	3.843	90.2	44.3	42	10	5210	23.1010
L-Threonine	4.007	120.1	74.2	60	10	497	5.5599
L-Glutamic acid	4.163	148.1	84.1	70	14	1858	19.7570
L-Proline	4.639	116.1	702	75	16	5176	7.3421
L-Valine	5.353	118.1	72.2	65	8	9072	9.5855
L-Tyrosine	7.971	182.1	165.1	75	6	18	ND
L-Isoleucine	7.593	132.2	86.3	65	8	5284	ND
L-Leucine	7.577	132.1	86.2	70	6	6608	9.5251
L-Phenylalanine	8.503	166	120.2	75	10	23	ND

Frag - Fragmentor voltage, Resp – Response factor, ND – not detected

1.3. Analysis of the phytohormone composition of *C. compressa* by HP-LC/DAD

The results of the analysis of phytohormones in the *Cystoseira compressa* algae by high-performance liquid chromatography (HP-LC) are summarized in Table 5. The study revealed the presence of a variety of phytohormones and sugars in the algal extract. Overall, five phytohormones were successfully identified and quantified, with the results expressed in milligrams per 100 grams of extract. Zeatin (Z) emerged as the predominant phytohormone, displaying a substantial concentration, followed by gibberellic acid (GA), salicylic acid (SA), abscisic acid (ABA), and indole-3-acetic acid (IAA), each showing a relatively lower concentration.

Table 5 : HP-LC analysis for phytohormones profile of *C. compressa.*

Compounds	Retention time	Amt/Area	Amount	Final concentration
	[Min]		[ng/µl]	[mg/100g extract]
Zeatin	2.996	6.75410e-3	63.43126	243.966
Gibberellic acid	6.046	8.43423e-3	4.47847	17.225
Salicylic acid	12.155	7.72126e-3	1.99731	7.682
İndole-3-acetic acid	14.172	9.73978e-3	4.86604e-1	1.872
Abscisic acid	17.426	4.52079e-3	9.25584e-1	3.560

ND – not detected

1.4. Analysis of the sugar composition of the *C. compressa* by HP-LC/RID

The results of the analysis of sugars in the *Cystoseira compressa* algae by high-performance liquid chromatography (HP-LC) are summarized in Table 6. The analysis revealed the presence of four distinct sugars. Specifically, arabinose and sucrose were identified as major carbohydrates, displaying significant concentrations. Additionally, lower concentrations of glucose and maltose were observed, contributing to the overall carbohydrate composition of the algal extract.

Table 6: HP-LC analysis for sugars profile of *C. compressa*.

Compounds	Retention time	Amt/Area	Amount	Final concentration
	[Min]		[ng/µl]	[mg/100g extract]
Turanose	8.483	/	ND	ND
Sucrose	9.261	2.41235e-2	550.13585	3,667
Fructose	10.454	/	ND	ND
Arabinose	10.970	1.49997e-2	1441.4671	4002
Maltose	9.194	4.02462e-3	85.87159	572
Xylose	10.397	/	ND	ND
Glucose	9.256	6.46814e-3	172.52178	1146

ND – non detected

2. Characterization and selection of the bacterial strain

2.1. Halotolerance and screening of PGP character of isolates

The plant growth promoting (PGP) traits and halotolerance of the three rhizobacterial isolates are presented in Table 7, Figure 19, and Figure 20, respectively. Specifically, isolate MR62 showed the ability to tolerate up to 4% NaCl, as indicated by an OD600 of 1.122. However, growth was inhibited in the presence of higher concentrations of NaCl. In contrast, isolates MR63 and MR64 demonstrated better tolerance when exposed to 8% NaCl, as indicated by their OD600 values (0.616 and 0.583, respectively). Notably, isolates MR64 and MR62 exhibited the ability to produce indole-3-acetic acid (IAA), indicated by the development of a pink color in LB + tryptophan tubes. Isolate MR64 also tested positive for hydrogen cyanide (HCN) production. Conversely, MR63 showed no PGP traits, and all three isolates yielded negative results in phosphate solubilization screening tests. Isolate MR64 was selected based on its NaCl tolerance and PGP characteristics.

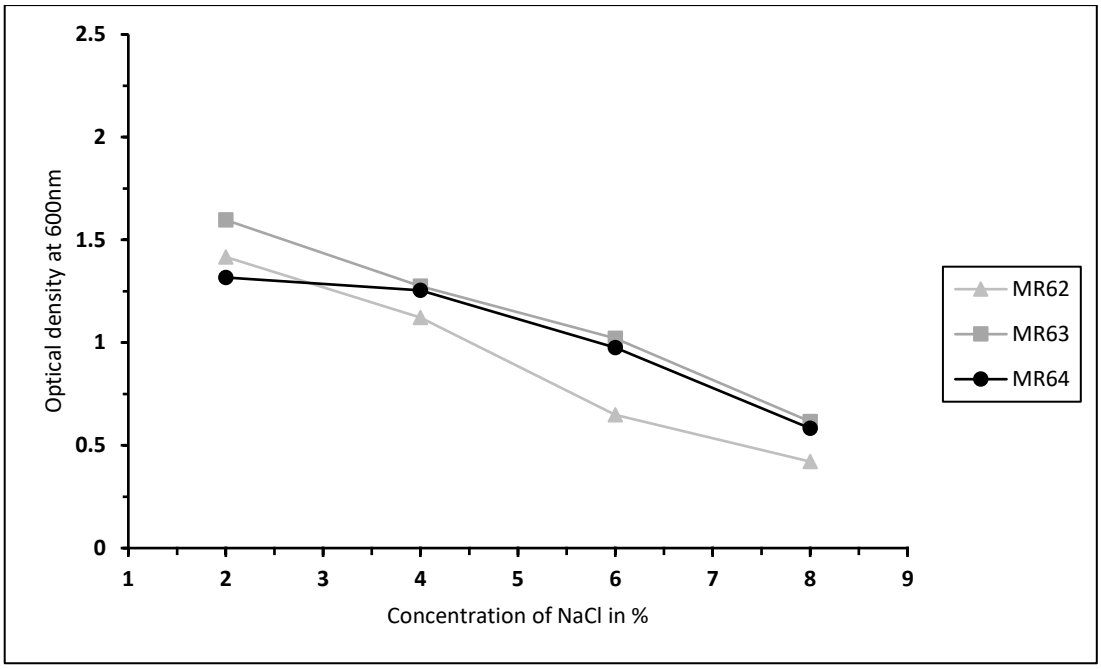

Figure 19: Effects of different concentrations of NaCl on the optical density (600 nm) of the three rhizobacterial strains, namely: MR62, MR63 and MR64.

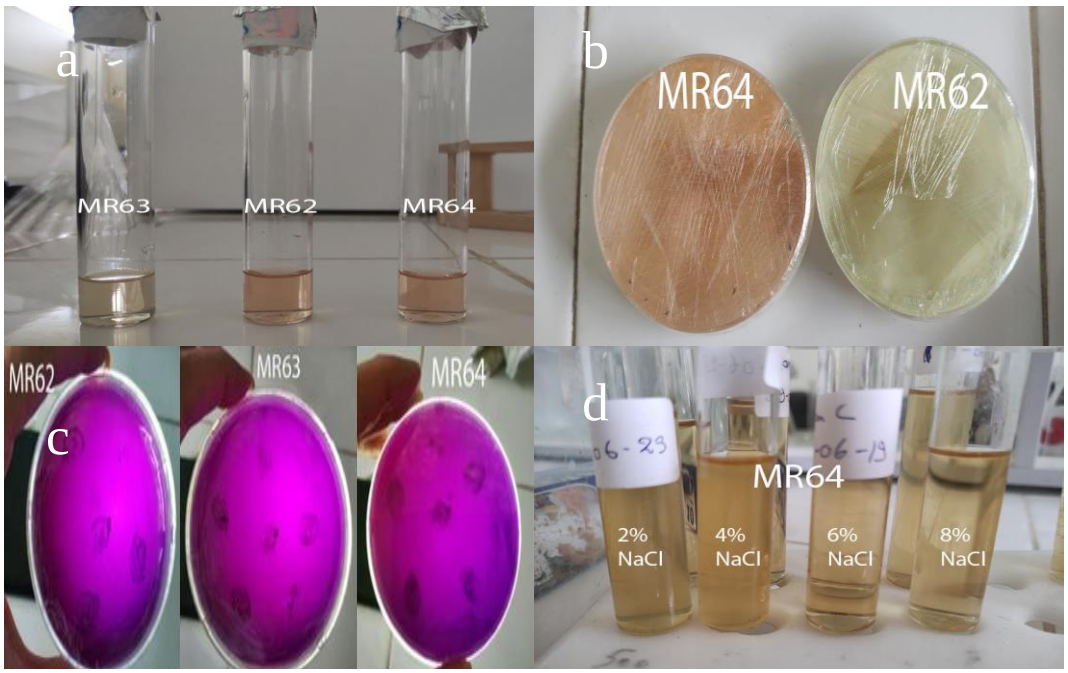

Figure 20: Results of PGP traits screening and halotolerance of the rhizobacterial strains MR62, MR63, and MR64., (**a**): IAA production, (**b**): HCN production, (**c**): phosphate solubilization (**d**): halotolerance.

Table 7: The results of the PGP traits screening tests for the three rhizobacteria strains, namely MR62, MR63, and MR64.

Test	MR62	MR63	MR64
Production of the IAA	+	-	+
Phosphate solubilization	-	-	-
HCN production	-	-	+

2.2. Molecular identification of selected bacterial strain with 16S rRNA sequencing

The bacterial strain MR64 was identified through 16S rRNA sequencing performed by Macrogen Europe, using a similarity score comparison with known sequences. The partial sequence of the 16S ribosomal RNA of the bacterial strain is available on GenBank at the following link: https://www.ncbi.nlm.nih.gov/nuccore/PP266913.1

Blastn analysis revealed significant alignments with the Bacillus cereus strains group as shown in Figure 21. A majority of sequences within this group exhibited identities exceeding 97%. Specifically, the sequence of MR64 (GenBank: PP266913.1) demonstrated a similarity of 97.75% with Bacillus cereus strain VMI2 (GenBank: ON680844.1) and a similarity score of 97.60% with Bacillus cereus strain S1-C (GenBank: MK185697.1).

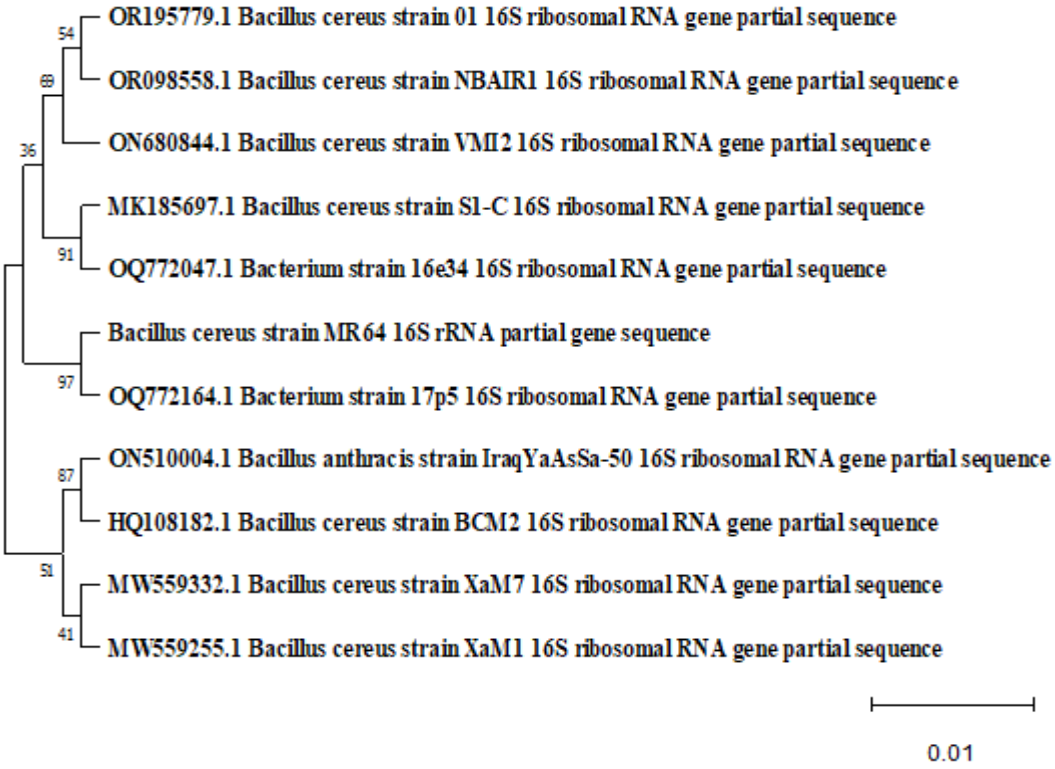

Figure 21: A phylogenetic tree based on the 16S rRNA gene sequence reveals the relationships between *Bacillus cereus* MR64 and the top 10 closest strains of the *Bacillus* species with the highest similarity score. Bootstrap percentages, derived from a neighbor-joining analysis with 1000 replicates, are indicated at the nodes. The bar represents a sequence divergence of 1%. The tree is generated using MEGA software version 11 following alignment by ClustalW.

3. Effect of *C. compressa* aqueous extract and/or *Bacillus cereus* MR64 on different Tomato plants parameters under salinity stress

3.1. Morpho-physiological parameters

The morphological and physiological responses of tomato plants to treatments with different concentrations (5%, 10%, and 15%) of aqueous extract of *Cystoseira compressa* (CLE), the PGPR *Bacillus cereus* MR64, and their synergistic application under saline stress (150 mM NaCl) are presented in Figure 22, Figure 23, Figure 24, and Table 8. The co-application of both biostimulants had a significant effect on the growth parameters of tomato plants, including shoot and root length, fresh and dry weights, as indicated in Figure 22 and Figure 23, while causing a notable improvement in physiological responses, such as an increase in total chlorophyll and chlorophyll A, as well as an enhancement in electrolyte leakage, as illustrated in Figure 24. However, it is noteworthy that no significant

effect was observed on the number of leaves, chlorophyll B, and the relative water content of the leaves.

The interactive treatments particularly improved several morphological variables. Specifically, treatments T8 (PGPR + 15% CLE) and T7 (PGPR + 10% CLE) showed respective shoot lengths of 89.8 ± 5.64 cm and 23.3 ± 0.43 cm, compared to control plants (70.8 ± 4.49 cm and 19.57 ± 2.12 cm). Additionally, treatment T8 exhibited higher fresh and dry shoot weights (93.3 ± 10.1 g and 26.23 ± 1.81 g, respectively) than the control (76 ± 7.81 g and 19.29 ± 2.81 g, respectively). The fresh and dry root weights for T8 and T7 were 26.11 ± 5.62 g and 10.88 ± 0.08 g, respectively, contrasting with the control (17.48 ± 1.62 g and 8.85 ± 0.48 g).

The individual application of algal extracts led to higher values for shoot length (82.6 ± 8.81 cm) at 15% CLE, fresh and dry shoot weights (83.7 ± 9.60 g and 22.69 ± 1.50 g) at 15% CLE, and dry root weight (9.61 ± 0.38 g) at 10% CLE compared to treatment with PGPR alone. Conversely, the individual application of the PGPR *Bacillus cereus* MR64 improved root length and fresh weight (22 ± 0.8 g and 21.71 ± 1.75 g, respectively) compared to the sole use of algal extract (21.27 ± 0.814 g) at 15% CLE and (17.98 ± 1.12 g) at 10% CLE.

Regarding physiological responses, the co-application of the PGPR strain with algal extract showed notable improvements, with the highest means (1.043 ± 0.161 mg/g FW, 1.93 ± 0.155 mg/g FW) observed respectively for chlorophyll A and total chlorophyll, recorded with T8 compared to the control (0.551 ± 0.032 mg/g FW, 1.217 ± 0.134 mg/g FW), respectively. Additionally, the lowest mean in terms of % electrolyte leakage (69.29 ± 5.956) was observed under treatment T6, contrasting with the control (80.95 ± 2.07). Furthermore, algal extract alone proved to be more effective than PGPR alone. Specifically, all treatments with algal extract (T3, T4, and T5) recorded higher means (0.933 ± 0.067 mg/g FW, 0.873 ± 0.114 mg/g FW, 0.977 ± 0.173 mg/g FW) at concentrations of 5%, 10%, and 15% CLE, respectively for chlorophyll A and (1.537 ± 0.099 mg/g FW, 1.707 ± 1.64 mg/g FW, 1.663 ± 0.160 mg/g FW) at 5%, 10%, and 15% CLE concentration, respectively for total chlorophyll, compared to the same variables observed with the PGPR treatment T2 (0.65 ± 0.254) for chlorophyll A and (1.44 ± 0.277 mg/g FW) for total chlorophyll. However, only treatment T5 showed lower electrolyte leakage (69.46 ± 0.371) compared to the PGPR treatment (70.78 ± 2.115).

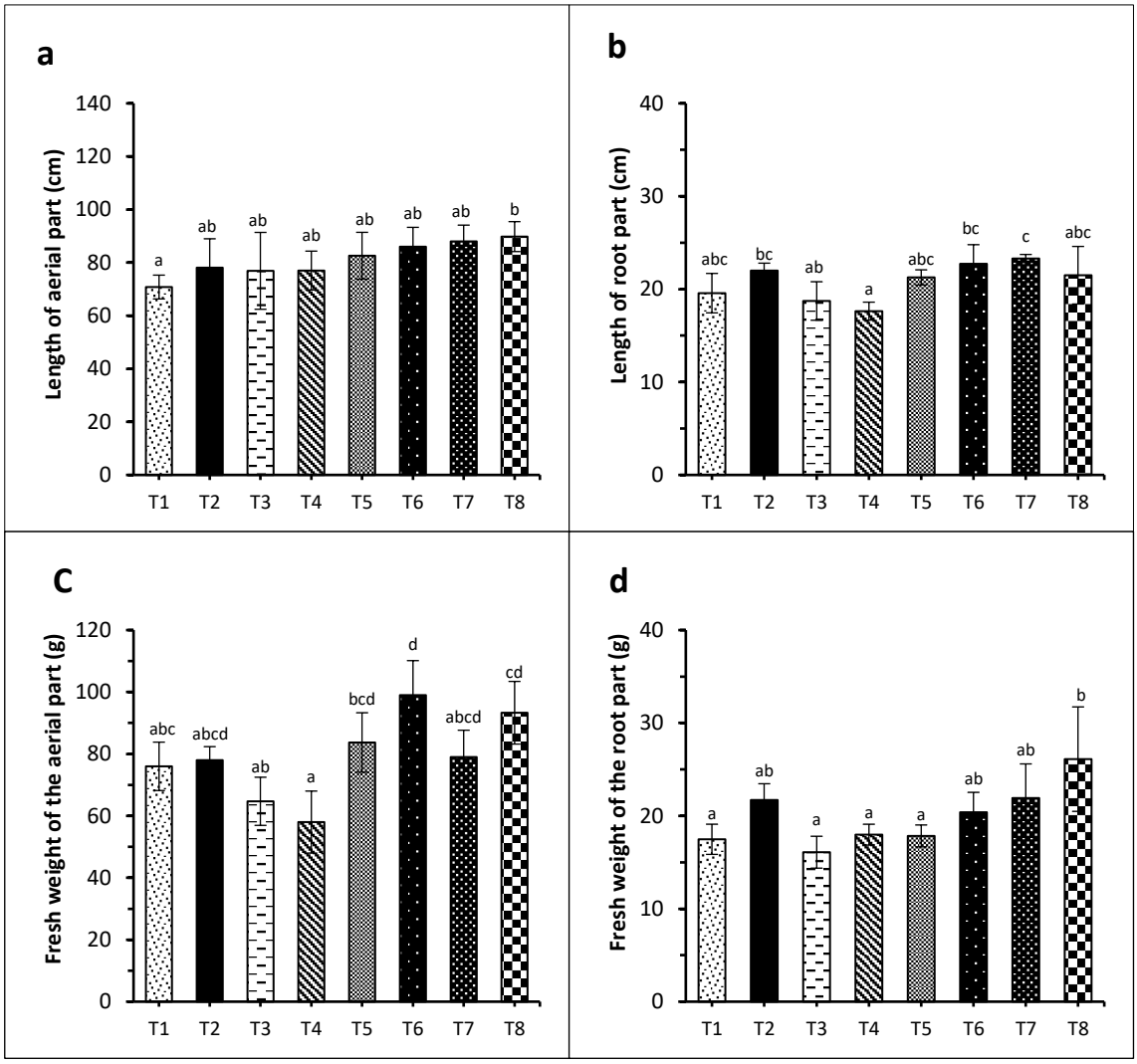

Figure 22: Effects of the single and combined use of PGPR *Bacillus cereus MR64* and three doses (5%, 10% and 15%) of aqueous extract of *C. compressa* under saline stress (NaCl 150 mM) on the morphological and physiological parameters of tomato (*Solanum lycopersicum L.*) plants. (**a, b**) length of shoots and roots, (**c, d**) fresh weight of shoots and roots, **T1**: control (150 mM NaCl); **T2**: *Bacillus cereus MR64* + 150 mM NaCl; **T3, T4** and **T5**: 5%, 10%, and 15% aqueous extract of *C. compressa* + 150 mM NaCl, respectively; **T6**, **T7**, and **T8**: 5%, 10%, and 15% aqueous extract of *C. compressa* + *Bacillus cereus MR64* + 150 mM NaCl, respectively. Results are represented as mean ± SD. Two-way ANOVA was applied at the 5% significance level. Values followed by the same letter are not significantly different according to the Tukey test ($P < 0.05$).

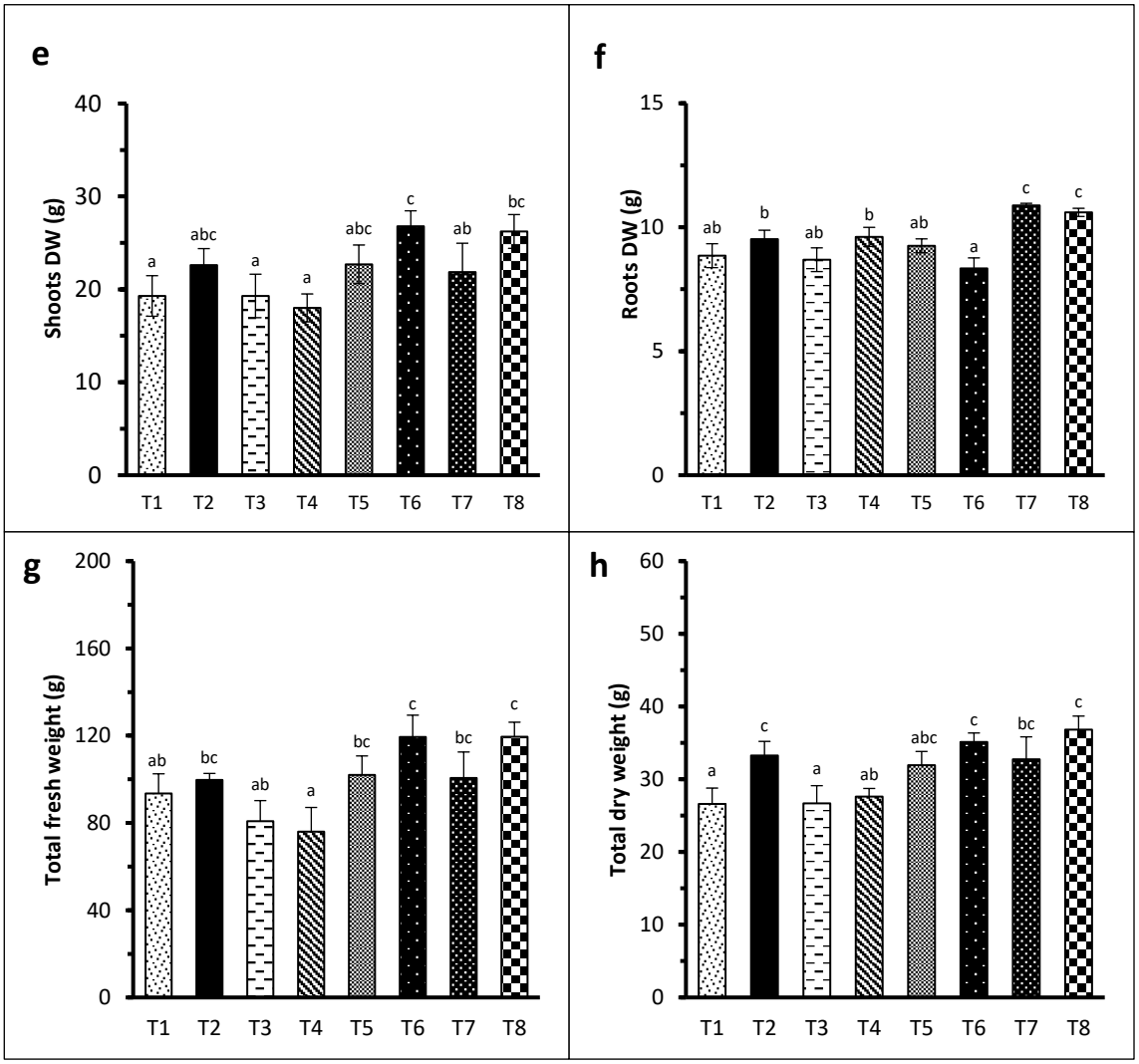

Figure 23: Effects of the single and combined use of PGPR *Bacillus cereus MR64* and three doses (5%, 10% and 15%) of aqueous extract of *C. compressa* under saline stress (NaCl 150 mM) on the morphological and physiological parameters of tomato (*Solanum lycopersicum L.*). (**e, f**) dry weight of shoots and roots, (**g, h**) total fresh and dry weight, **T1**: control (150 mM NaCl); **T2**: *Bacillus cereus MR64* + 150 mM NaCl; **T3**, **T4** and **T5**: 5 %, 10% and 15% of aqueous extract of *C. compressa* + 150 mM NaCl, respectively; **T6**, **T7**, and **T8**: 5%, 10% and 15% of aqueous extract of *C. compressa* + *Bacillus cereus MR64* + 150 mM NaCl, respectively. Results are represented as mean ± SD. Two-way ANOVA was applied at the 5% significance level. Values followed by the same letter are not significantly different according to the Tukey test ($P < 0.05$).

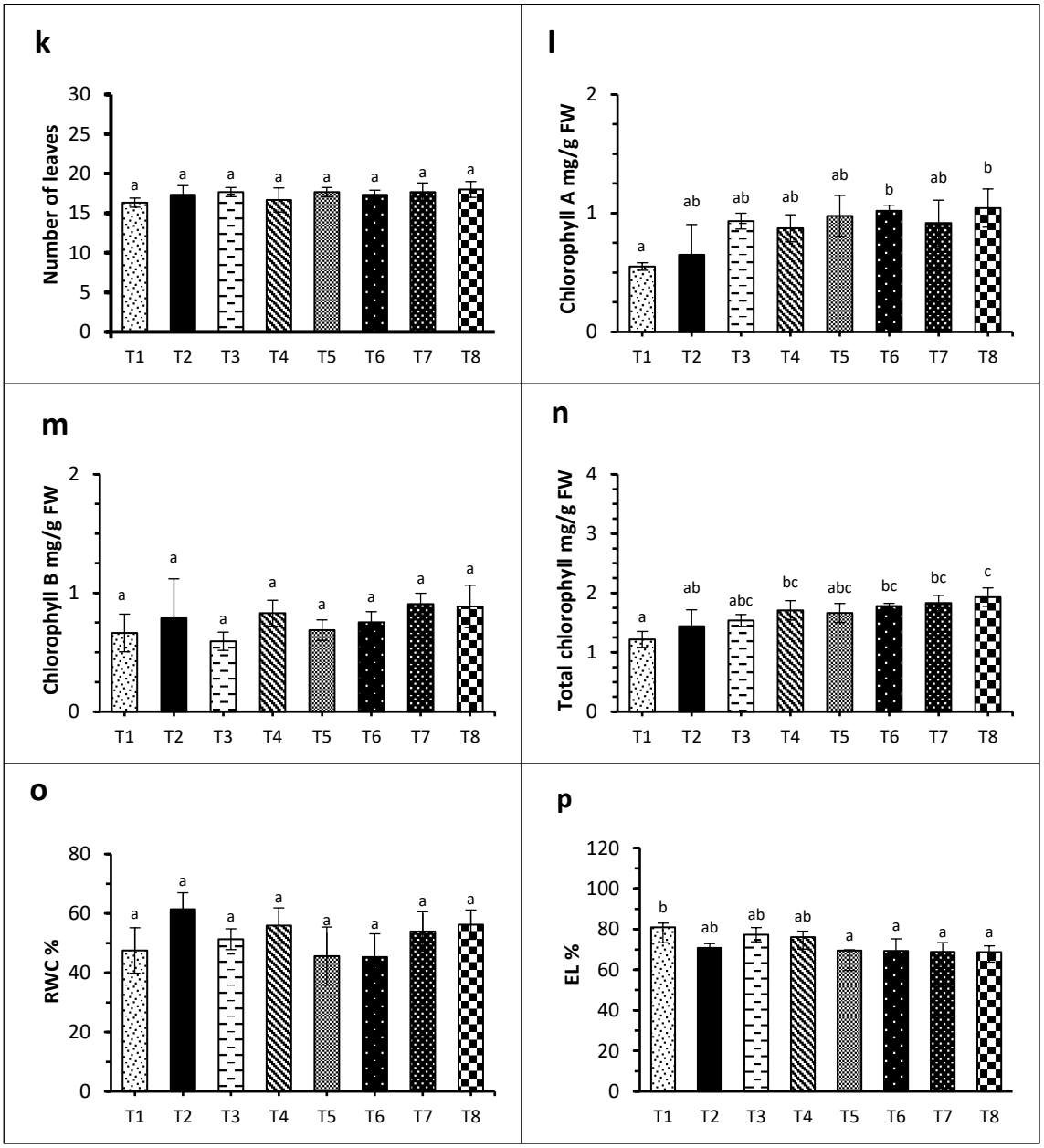

Figure 24: Effects of the single and combined use of PGPR *Bacillus cereus MR64* and three doses (5%, 10% and 15%) of aqueous extract of *C. compressa* under saline stress (NaCl 150 mM) on the morphological and physiological parameters of tomato (Solanum lycopersicum L.). (**k**) number of leaves, (**l**, **m**, **n**) chlorophyll A, B, Total, (**o**) relative water content of leaves %, (**p**) electrolyte leakage from leaf %, **T1**: control (NaCl 150 mM); **T2**: *Bacillus cereus MR64* + 150 mM NaCl; **T3**, **T4** and **T5**: 5%, 10% and 15% aqueous extract of *C. compressa* + 150 mM NaCl, respectively; **T6**, **T7** and **T8**: 5%, 10%, and 15% aqueous extract of *C. compressa* + *Bacillus cereus MR64* + 150 mM NaCl, respectively. Results are represented as mean ± SD. Two-way ANOVA was applied at the 5% significance level. Values followed by the same letter are not significantly different according to the Tukey test ($P < 0.05$).

Table 8: Effects of single and combined use of PGPR *Bacillus cereus* MR64 and three doses (5%, 10%, and 15%) of aqueous *Cystoseira compressa* extract under salt stress (150 mM NaCl) on morphological and physiological parameters of tomato (*Solanum lycopersicum L.*) plants. Shoot length, root length, shoot fresh weight, shoot dry weight, root fresh weight, root dry weight, total fresh weight, total dry weight, number of leaves, Chlorophyll A, Chlorophyll B, total chlorophyll, relative water content %, and electrolyte leakage %., **T1**: control (NaCl 150 mM); **T2**: *Bacillus cereus MR64* + 150 mM NaCl; **T3**, **T4** and **T5**: 5%, 10% and 15% aqueous extract of *C. compressa* + 150 mM NaCl, respectively; **T6**, **T7** and **T8**: 5%, 10%, and 15% aqueous extract of *C. compressa* + *Bacillus cereus MR64* + 150 mM NaCl, respectively. Results are represented as mean ± SD. Two-way ANOVA was applied at the 5% significance level. Values followed by the same letter are not significantly different according to the Tukey test ($P < 0.05$).

Parameters	T1	T2	T3	T4	T5	T6	T7	T8
	Control (150 mM NaCl)	BT	5% CLE	10% CLE	15% CLE	BT+5% CLE	BT+10% CLE	BT+15% CLE
Shoot L (cm)	70.8 ± 4.49a	78.1 ± 10.87ab	76.9 ± 14.48ab	77 ± 7.32ab	82.6 ± 8.81ab	86 ± 7.29ab	88 ± 6.13ab	**89.8 ± 5.64b**
Root L (cm)	19.57 ± 2.12abc	22 ± 0.8bc	18.73 ± 2.07ab	17.63 ± 0.97a	21.27 ± 0.81abc	22.73 ± 2.05bc	23.3 ± 0.43c	21.5 ± 3.1abc
Shoot FW (g)	76 ± 7.81abc	78 ± 4.35abcd	64.7 ± 7.76ab	58 ± 10.0a	83.7 ± 9.60bcd	**99 ± 11.13d**	79 ± 8.66abcd	93.3 ± 10.11cd
Shoot DW (g)	19.29 ± 2.81a	22.61 ± 1.77abc	19.29 ± 2.34a	18.01 ± 1.5a	22.69 ± 1.50abc	**26.79 ± 1.66c**	21.86 ± 3.10ab	**26.23 ± 1.81bc**
Root FW (g)	17.48 ± 1.62a	21.71 ± 1.75ab	16.09 ± 1.71a	17.98 ± 1.12a	17.84 ± 1.17a	20.39 ± 2.14ab	21.92 ± 3.67ab	**26.11 ± 5.62b**
Root DW (g)	8.85 ± 0.48ab	9.52 ± 0.36b	8.69 ± 0.47ab	9.61 ± 0.38b	9.25 ± 0.28ab	8.34 ± 0.42a	**10.88 ± 0.08c**	**10.60 ± 0.16c**
Total FW (g)	93.48 ± 9.00ab	99.71 ± 2.98bc	80.76 ± 9.42ab	75.98 ± 11.08a	102.01 ± 8.70bc	**119.39 ± 9.97c**	100.59 ± 11.9bc	**119.49 ± 6.64c**
Total DW (g)	26.61 ± 2.18a	**33.27 ± 1.94c**	26.69 ± 2.43a	27.62 ± 1.11ab	31.94 ± 1.89abc	**35.13 ± 1.23c**	**32.75 ± 3.08bc**	**36.83 ± 1.86c**
Leaves number	16.33 ± 0.57a	17.33 ± 1.15a	17.67 ± 0.57a	16.67 ± 1.52a	17.67 ± 0.57a	17.33 ± 0.57a	17.67 ± 1.15a	18 ± 1a
Chl A (mg/g FW)	0.55 ± 0.03a	0.65 ± 0.25ab	0.93 ± 0.06ab	0.87 ± 0.11ab	0.97 ± 0.17ab	**1.02 ± 0.04b**	0.91 ± 0.19ab	**1.04 ± 16b**
Chl B (mg/g FW)	0.66 ± 0.15a	0.78 ± 0.33a	0.59 ± 0.07a	0.83 ± 0.10a	0.68 ± 0.08a	0.75 ± 0.08a	0.90 ± 0.09a	0.88 ± 0.17a
Chl total (mg/g FW)	1.21 ± 0.13a	1.44 ± 0.27ab	1.53 ± 0.09abc	**1.70 ± 1.64bc**	1.66 ± 0.16abc	**1.78 ± 0.04bc**	**1.83 ± 0.12bc**	**1.93 ± 0.15c**
RWC %	47.5 ± 7.65a	61.4 ± 5.54a	51.3 ± 3.50a	55.9 ± 5.95a	45.6 ± 9.79a	45.3 ± 7.81a	53.9 ± 6.64a	56.2 ± 4.93a
EL %	80.95 ± 2.07b	70.78 ± 2.11ab	77.3 ± 3.51ab	76.1 ± 2.91ab	**69.46 ± 0.37a**	**69.29 ± 5.95a**	**68.83 ± 4.54a**	**68.71 ± 3.09a**

Results are represented as means ± SD. Two-way ANOVA was applied at the 5% significance level, Values followed by the same letter are not significantly different according to Tukey's test ($P<0.05$).

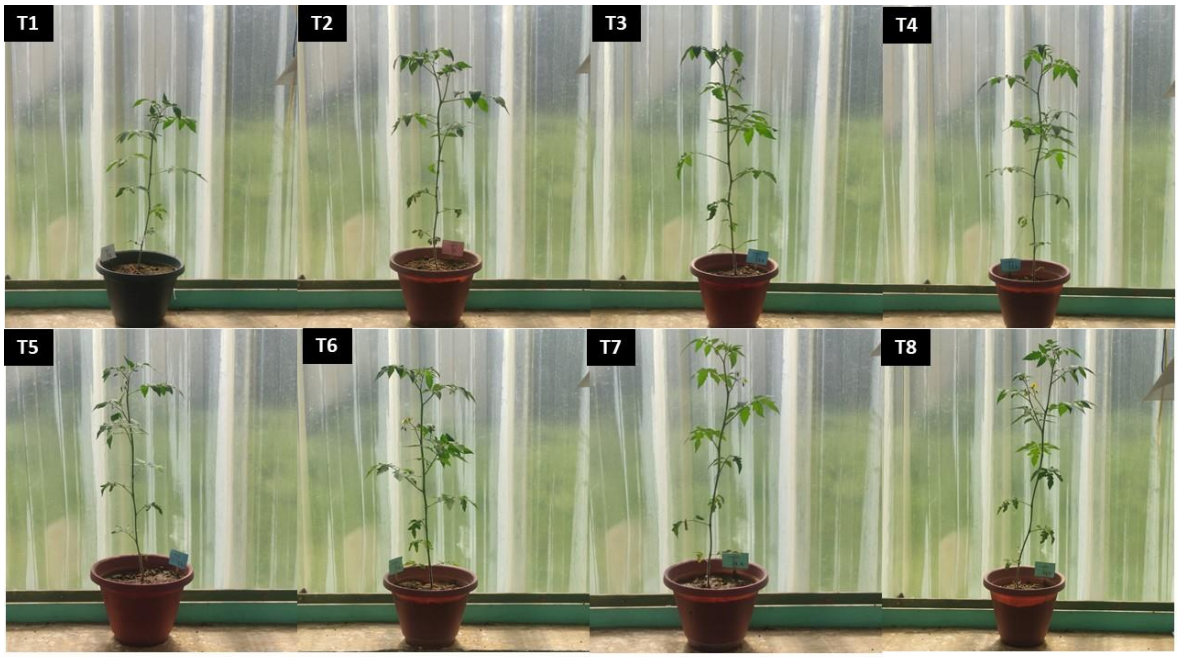

Figure 25: The aerial parts of tomato plants, photographed 10 days after the 2nd application of the treatments in a greenhouse under semi-controlled conditions. The treatments were as follows: **T1**: control (150 mM NaCl); **T2**: *Bacillus cereus* MR64 + 150 mM NaCl; **T3**, **T4**, and **T5**: 5%, 10%, and 15% aqueous extract of *Cystoseira compressa* + 150 mM NaCl, respectively; **T6**, **T7**, and **T8**: 5%, 10%, and 15% aqueous extract of *Cystoseira compressa* + *Bacillus cereus* MR64 + 150 mM NaCl, respectively.

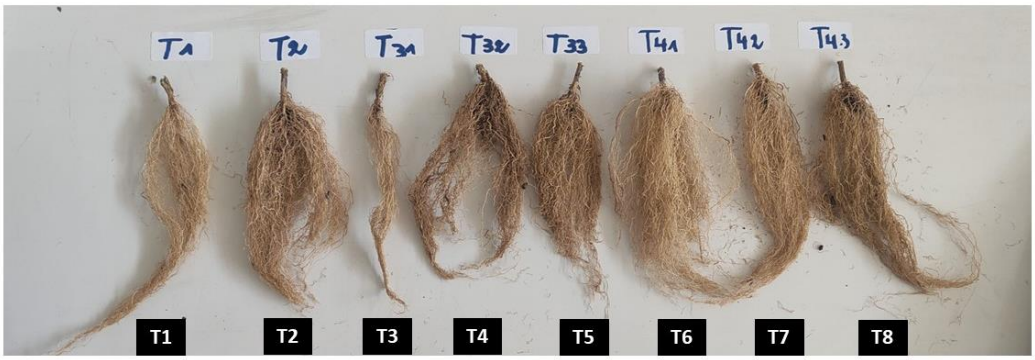

Figure 26: The roots of tomato plants, photographed 10 days after the 3rd application of the treatments in a greenhouse under semi-controlled conditions. The treatments were as follows: **T1**: control (150 mM NaCl); **T2**: *Bacillus cereus* MR64 + 150 mM NaCl; **T3**, **T4**, and **T5**: 5%, 10%, and 15% aqueous extract of *Cystoseira compressa* + 150 mM NaCl, respectively; **T6**, **T7**, and **T8**: 5%, 10%, and 15% aqueous extract of *Cystoseira compressa* + *Bacillus cereus* MR64 + 150 mM NaCl, respectively.

3.2. Biochemical parameters

The mineral content, notably Na+ and K+, proline content, and total soluble sugars of tomato plants subjected to various treatments, including the application of the PGPR strain *Bacillus cereus* MR64, the aqueous extract of *Cystoseira compressa* (CLE) at different doses (5%, 10%, and 15%), as well as their combined effects under saline stress conditions (150 mM NaCl), are illustrated in Figure 27 and Table 9. According to the results of two-way ANOVA and Tukey's test, the algae extract (CLE) significantly influenced the sodium (Na+) content and proline levels ($p < 0.05$). On the other hand, the PGPR had a significant influence on potassium (K+) levels and proline content ($p < 0.05$). Specifically, the combined application of both treatments also had a significant impact on potassium (K+) content and proline levels ($p < 0.05$).

The highest concentrations of potassium (K+) (8.19 ± 1.019 mg/g DW) and proline (115.7 ± 17.13 µg/g FW) were observed in treatments T7: 10% CLE + PGPR and T8: 15% CLE + PGPR, respectively. These levels exceeded the control values for potassium (K+) (4.7 ± 1.443 mg/g FW) and proline (84.4 ± 11.24 µg/g FW). Additionally, treatment T6: 5% CLE + PGPR exhibited the highest total soluble sugars content (87.2 ± 5.90 mg/g FW) compared to the control (74.7 ± 13.81 mg/g FW). Furthermore, the concentration of sodium (Na+) showed significant reductions in response to treatments T6: 5% CLE + PGPR, T7: 10% CLE + PGPR, and T8: 15% CLE + PGPR (17.21 ± 1.108 mg/g DW, 17.21 ± 2.863 mg/g DW, and 17.12 ± 1.173 mg/g DW, respectively) compared to the control group (24.24 ± 1.085 mg/g DW). However, the individual application of the algal extract also resulted in a decrease in Na+ concentrations (18.72 ± 4.554 mg/g DW, 19.88 ± 3.020 mg/g DW, and 15.59 ± 2.217 mg/g DW) compared to the control (24.24 ± 1.085 mg/g DW).

Table 9: Effects of single and combined use of PGPR *Bacillus cereus* MR64 and three doses (5%, 10%, and 15%) of aqueous *Cystoseira compressa* extract under salt stress (150 mM NaCl) on biochemical parameters of tomato (*Solanum lycopersicum L.*) plants. Sodium content, Potassium content, Proline content, Total soluble sugars content. **T1**: control (NaCl 150 mM); **T2**: *Bacillus cereus MR64* + 150 mM NaCl; **T3**, **T4** and **T5**: 5%, 10% and 15% aqueous extract of *C. compressa* + 150 mM NaCl, respectively; **T6**, **T7** and **T8**: 5%, 10%, and 15% aqueous extract of *C. compressa* + *Bacillus cereus MR64* + 150 mM NaCl, respectively. Results are represented as mean ± SD. Two-way ANOVA was applied at the 5% significance level. Values followed by the same letter are not significantly different according to the Tukey test ($P < 0.05$).

Parameters	T1	T2	T3	T4	T5	T6	T7	T8
	Control (150 mM NaCl)	BT	5% CLE	10% CLE	15% CLE	BT+5% CLE	BT+10% CLE	BT+15% CLE
Sodium (NA+) content (mg/g DW)	24.24 ± 1.085b	20.74 ± 1.133ab	18.72 ± 4.554ab	19.88 ± 3.020ab	**15.59 ± 2.217a**	**17.21 ± 1.108a**	**17.21 ± 2.863a**	**17.12 ± 1.173a**
Potassium (K+) content (mg/g DW)	4.7 ± 1.443a	6.3 ± 0.463ab	5.89 ± 1.988ab	4.78 ± 0.704a	6.74 ± 1.991ab	4.93 ± 0.208a	**8.19 ± 1.019b**	7.19 ± 1.578ab
Proline content (µg/g FM)	84.4 ± 11.24ab	83.8 ± 11.87ab	86.7 ± 11.72abc	68.8 ± 15.02a	94.7 ± 7.22abc	76.4 ± 12.08a	**115.7 ± 17.13c**	109 ± 10.42bc
Total soluble sugars (mg/g FM)	74.7 ± 13.81a	64.5 ± 12.46a	72.3 ± 4.09a	83.2 ± 14.64a	72.5 ± 0.33a	87.2 ± 5.90a	77.6 ± 11.49a	79.9 ± 9.49a

Results are represented as means ± SD. Two-way ANOVA was applied at the 5% significance level, Values followed by the same letter are not significantly different according to Tukey's test ($P<0.05$).

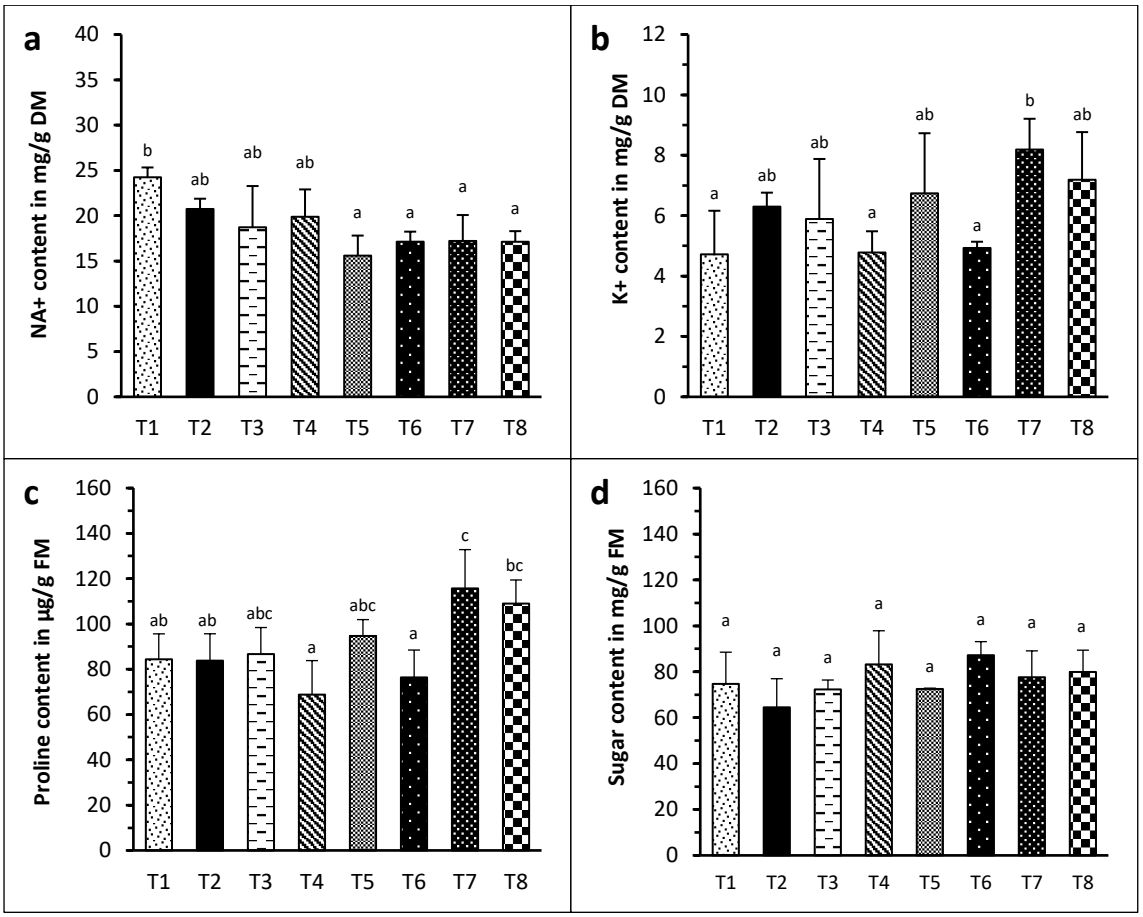

Figure 27: Effects of the individual and combined use of PGPR *Bacillus cereus MR64* and three doses (5%, 10% and 15%) of aqueous extract of *C. compressa* under salt stress (NaCl 150 mM) on the biochemical parameters of tomato (*Solanum lycopersicum L.*). (**a**): the sodium content (Na+) in the leaves in mg/g of dry matter, (**b**): the potassium content (K+) in the leaves in mg/g of dry matter, (**c**): the content in leaf proline in µg/g of fresh plant material, (**d**): the total soluble sugar content in mg/g of fresh plant material. **T1**: control (150 mM NaCl); T2: *Bacillus cereus MR64* + 150 mM NaCl; **T3**, **T4** and **T5**: 5%, 10% and 15% aqueous extract of *C. compressa* + 150 mM NaCl, respectively; **T6**, **T7** and **T8**: 5%, 10%, and 15% aqueous extract of *C. compressa* + *Bacillus cereus MR64* + 150 mM NaCl, respectively. Results are represented as mean ± SD. Two-way ANOVA was applied at the 5% significance level. Values followed by the same letter are not significantly different according to the Tukey test ($P < 0.05$).

3.3. Development and production parameters

The average number of flowers per plant, the average number of fruits per plant, and the average distance between floral clusters of tomato plants under treatments of different concentrations (5%, 10%, and 15%) of aqueous extract of *Cystoseira compressa* (CLE), PGPR *Bacillus cereus MR64*, and their synergistic application under saline stress (NaCl 150 mM) are presented in Figure 28 and Table 10.

According to the results of the two-way ANOVA and Tukey's test, all treatments showed no statistical significance for the average number of flowers per plant, the average number of fruits per plant and the average distance between floral clusters of tomato plants ($P > 0.05$). In the control group, plants had an average of 10 flowers per plant with 9 fruits and an average distance of 46.17 cm between flower clusters. The bacterial treatment alone increased the number of flowers and fruits (11.67 ± 0.58 and 11.33 ± 0.58, respectively) with a reduced distance between flower clusters (42.9 ± 6.58 cm).

The 5% extract treatment showed similar effects on flowers and fruits, but with a slightly increased distance (48.5 ± 6.31). The 10% extract treatment exhibited the highest number of flowers (12.33 ± 1.53) and fruits (11.67 ± 2.52), but a reduced distance (40.27 ± 4.84). The 15% extract treatment showed effects similar to those of the bacterial treatment alone. The combinations of bacterial treatments and extracts produced varied effects. Specifically, the (*B. cereus MR64* + 15% CLE) treatment resulted in an increase in the number of flowers and fruits per plant compared to the control (11.67 ± 1.53 and 11.67 ± 1.53, respectively). The (*B. cereus MR64* + 10% CLE) treatment recorded the shortest distance between clusters (37.63 ± 1.23).

Table 10: Effects of the individual and combined use of PGPR *Bacillus cereus MR64* and three doses (5%, 10% and 15%) of aqueous extract of *C. compressa* under saline stress (150 mM NaCl) on development and production of tomato (*Solanum lycopersicum L.*). (**a**): the average number of flowers in each plant, (**b**): the average number of fruits in each plant, (**c**): the average distance between floral clusters. **T1**: control (150 mM NaCl); **T2**: *Bacillus cereus MR64* + 150 mM NaCl; **T3**, **T4** and **T5**: 5%, 10% and 15% aqueous extract of *C. compressa* + 150 mM NaCl, respectively; **T6**, **T7** and **T8**: 5%, 10%, and 15% aqueous extract of *C. compressa* + *Bacillus cereus MR64* + 150 mM NaCl, respectively. Results are represented as mean ± SD. Two-way ANOVA was applied at the 5% significance level. Values followed by the same letter are not significantly different according to the Tukey test ($P < 0.05$).

Parameters	T1	T2	T3	T4	T5	T6	T7	T8
	Control	BT	5% CLE	10% CLE	15% CLE	BT+5% CLE	BT+10% CLE	BT+15% CLE
AVG number of flowers	10 ±1.73a	11.67± 0.58a	11.67± 0.58a	12.33± 1.53a	11.67± 0.58a	9.67± 1.15a	11± 1.00a	11.67± 1.53a
AVG number of fruits	9± 1.00a	11.33± 0.58a	10± 1.00a	11.67± 2.52a	11± 1.00a	9.67± 1.15a	10.67± 1.53a	11.67± 1.53a
AVR distance between clusters (cm)	46.17± 2.48a	42.9± 6.85a	48.5± 9.15a	40.27± 4.84a	42.7± 3.84a	45.83± 4.29a	37.63± 1.23a	42.4± 0.52a

Results are represented as means ± SD. Two-way ANOVA was applied at the 5% significance level, Values followed by the same letter are not significantly different according to Tukey's test ($P<0.05$).

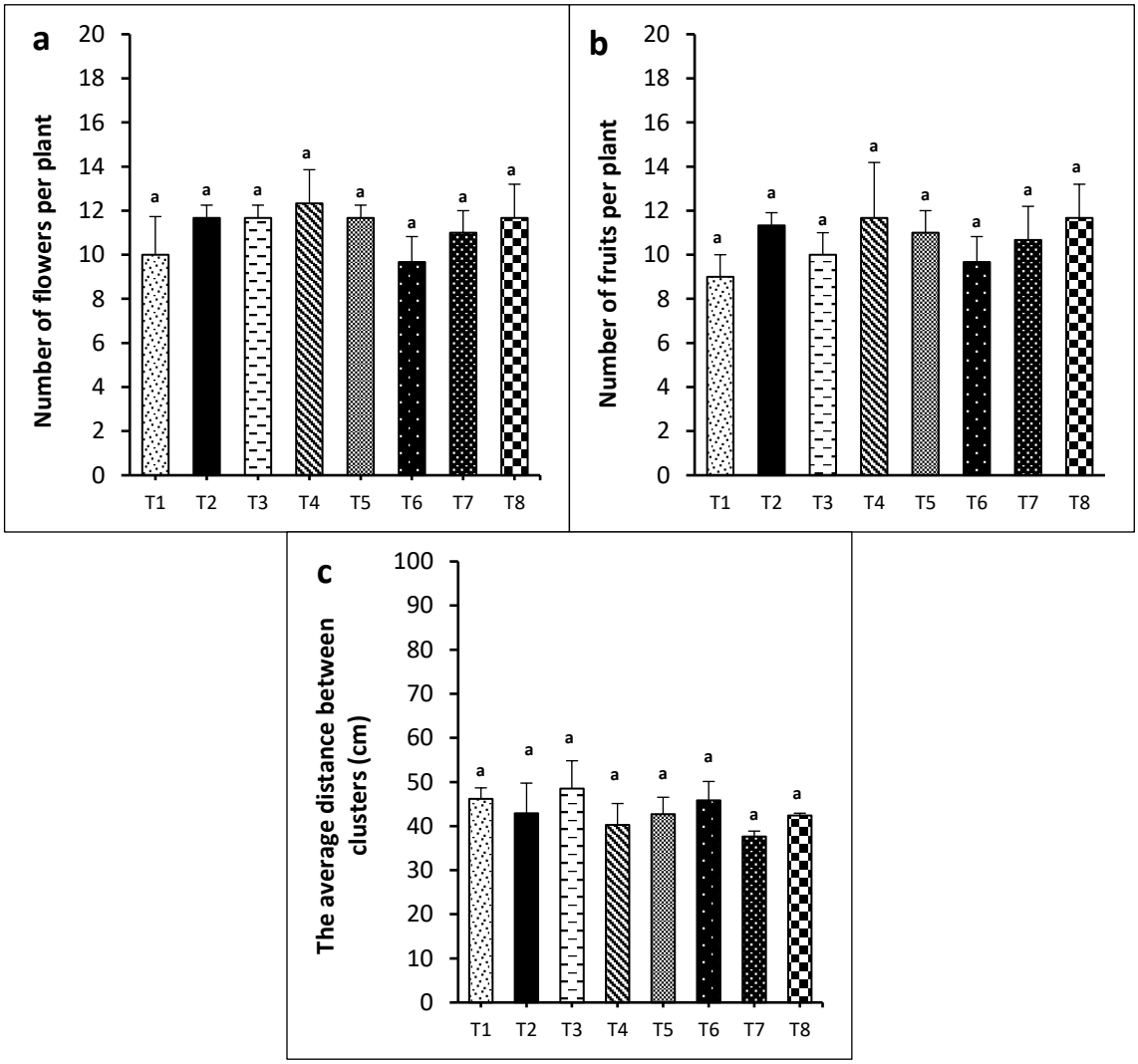

Figure 28: Effects of the individual and combined use of PGPR *Bacillus cereus MR64* and three doses (5%, 10% and 15%) of aqueous extract of *C. compressa* under saline stress (150 mM NaCl) on the development and production responses of tomato (*Solanum lycopersicum L.*). (**a**): the average number of flowers in each plant, (**b**): the average number of fruits in each plant, (**c**): the average distance between floral clusters in cm. **T1**: control (150 mM NaCl); **T2**: *Bacillus cereus MR64* + 150 mM NaCl; **T3**, **T4** and **T5**: 5%, 10% and 15% aqueous extract of *C. compressa* + 150 mM NaCl, respectively; **T6**, **T7** and **T8**: 5%, 10%, and 15% aqueous extract of *C. compressa* + *Bacillus cereus MR64* + 150 mM NaCl, respectively. Results are represented as mean ± SD. Two-way ANOVA was applied at the 5% significance level. Values followed by the same letter are not significantly different according to the Tukey test ($P < 0.05$).

3.4. FT-IR analysis of Tomato plants under different treatments

The stacked and normalized FT-IR analysis spectra in the range of 4000 to 500 cm^{-1} for tomato plants treated with the PGPR strain *Bacillus cereus MR64* and/or three doses (5%, 10%, and 15%) of aqueous extract of the brown seaweed *C. compressa* under salinity stress (150 mM NaCl) are illustrated in Figure 27, Figure 28, and Table 11, respectively. The FT-IR spectrum of the sample T1A (Control) exhibits intense vibrational peaks at wavenumbers 1606 and 1044 cm^{-1}, with moderate vibrational peaks at wavenumbers 3232, 1732, 1418, 1316, and 1235, 778.8 cm^{-1}. Sample T2A (*Bacillus cereus* MR64 + 150 mM NaCl) shows intense vibrational peaks at wavenumbers 3272, 1609, 1012, and 651 cm^{-1}, with moderate vibrational peaks at wavenumbers 2921, 1420, 1315, and 778.8 cm^{-1}. Samples T3A, T4A, and T5A (aqueous extract of *C. compressa* at 5%, 10%, and 15% + 150 mM NaCl, respectively) exhibit intense vibrational peaks at wavenumbers 3270, 1610, and 1009 cm^{-1}, with moderate vibrational peaks at wavenumbers 2920, 1420, 1316, 779, and 651 cm^{-1}. Samples T6A, T7A, T8A (aqueous extract of *C. compressa* at 5%, 10%, and 15% + *Bacillus cereus* MR64 + 150 mM NaCl, respectively) show intense vibrational peaks at wavenumbers 3270, 1617, and 1010, with moderate vibrational peaks at wavenumbers 3854, 3737, 3649, 2376, 1421, 1316, 778, and 651 cm^{-1}.

It is noteworthy that the vibrational peaks at wavenumbers 3851, 3737, and 3649 are present only in the plants subjected to treatments T6A, T7A, and T8A. The spectra of tomato plant leaves treated with both biostimulants and their combination exhibited remarkable structural alterations in several key regions. Specifically, significant changes were observed in the aliphatic region from 3500 to 4000 cm^{-1}, as well as in the region of from 1700 to 1800 cm^{-1}. Moreover, distinct shifts were evident in the region from 900 to 1250 cm^{-1} compared to the control samples (T1A). Particularly, a marked difference was observed in the aliphatic region from 3500 to 4000 cm^{-1} of the spectra of plants treated with combinations of *C. compressa* and the *B. cereus MR64* strain, characterized by prominent peaks distinct from those treated with either *C. compressa* aqueous extract or the *B. cereus* strain individually and the control.

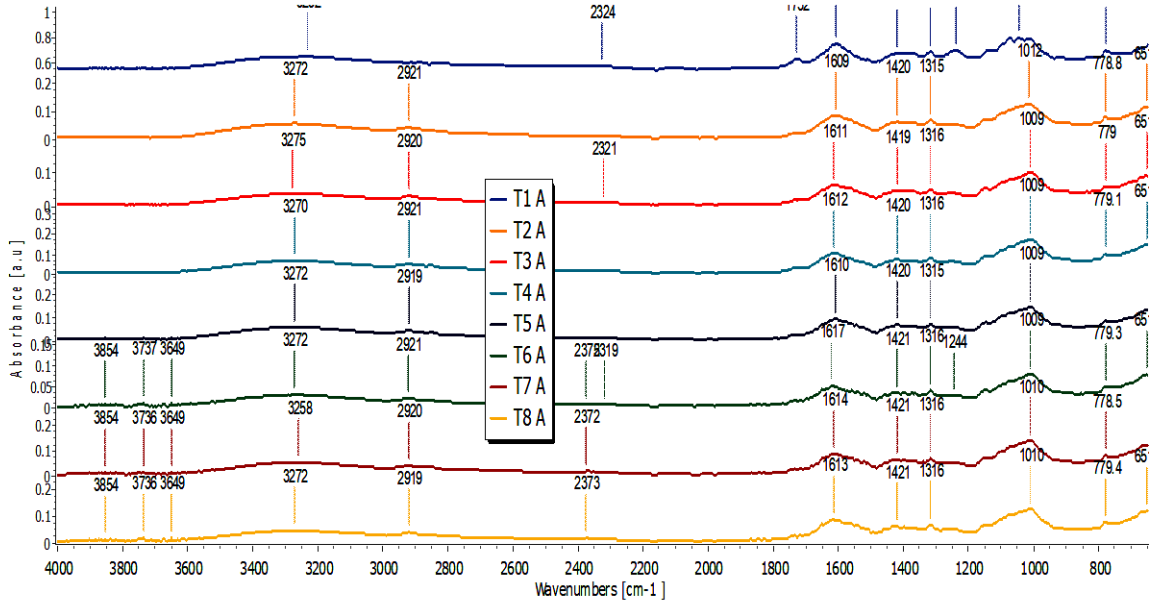

Figure 29: The stacked FT-IR spectrum in the range of 4000 to 500 cm^{-1} for tomato plants where: **T1A**: control (150 mM NaCl); **T2A**: *Bacillus cereus MR64* + 150 mM NaCl; **T3A**, **T4A** and **T5A**: 5%, 10% and 15% aqueous extract of *C. compressa* + 150 mM NaCl, respectively; **T6A**, **T7A** and **T8A**: 5%, 10%, and 15% aqueous extract of *C. compressa* + *Bacillus cereus MR64* + 150 mM NaCl, respectively.

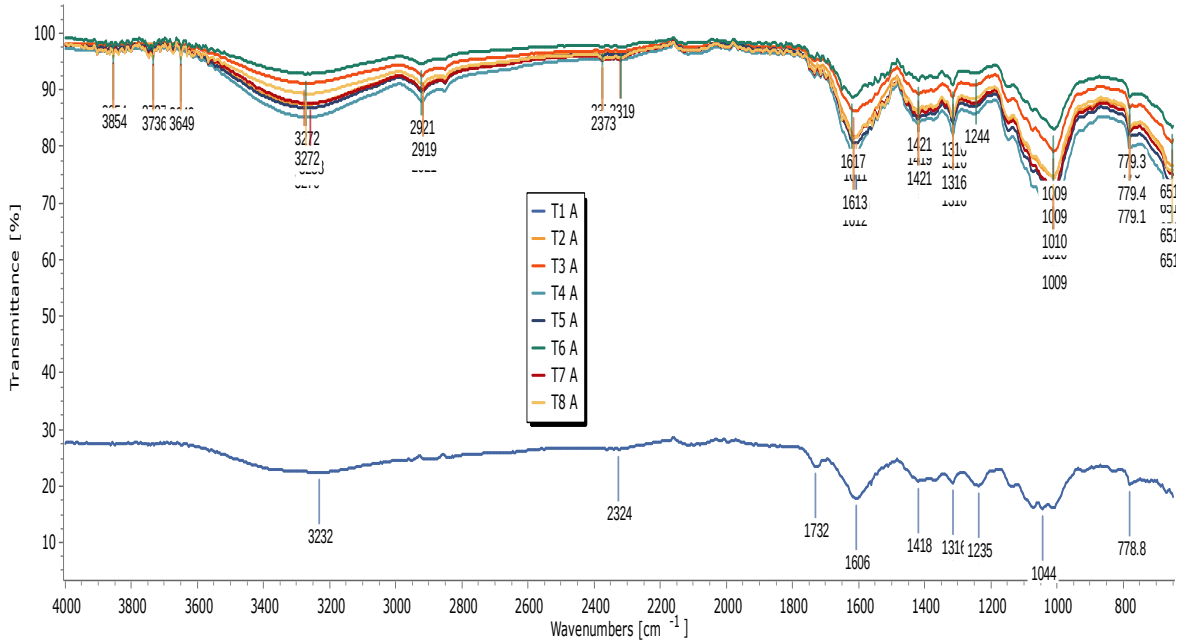

Figure 30: The normalized FT-IR spectrum in the range of 4000 to 500 cm^{-1} for tomato plants where: **T1A**: control (150 mM NaCl); **T2A**: *Bacillus cereus MR64* + 150 mM NaCl; **T3A**, **T4A** and **T5A**: 5%, 10% and 15% aqueous extract of *C. compressa* + 150 mM NaCl, respectively; **T6A**, **T7A** and **T8A**: 5%, 10%, and 15% aqueous extract of *C. compressa* + *Bacillus cereus MR64* + 150 mM NaCl, respectively.

Table 11: Functional groups associated with the vibrational peaks in tomato plants under salinity stress subjected to different biostimulant treatments.

Peak vibration	**Functional group**	**Associated compounds**
3854, 3737, 3649, 3270, 3272, 3232, 2920, 2921	O-H, C-H, and N-H	alcohols, phenols, polysaccharides, amino acids and absorbed water (Feng et al., 2014; Lingegowda et al., 2012; Prodan et al., 2021).
2376	C≡N, C≡O, and C≡C	aldehydes, amides, amino acids, anhydrides, carboxylic acids (Bankar et al., 2010; Rahman & Sathasivam, 2015).
1732, 1609, 1617	C=O and N=O	Acid halides, aldehydes, amides, amino acids, anhydrides, carboxylic acids, esters, ketones, lactams, lactones, quinones (Selmi et al., 2021; Yuen et al., 2005).
1420, 1421, 1418, 1316, 1315,	C-C, C-N, and C-O	Nitrogen compounds, alkanes, alkenes, etc. (Hernández-Garibay et al., 2019; Kannan, 2014; Yuen et al., 2005).
1235, 1044, 1012, 1010, 778, 651	S=O, and aromatic rings	Alkenes and aromatic compounds (Socrates, 2004; Yuen et al., 2005).

4. Discussion

4.1. The phytochemical composition of the brown alga *C. compressa*

4.1.1. FT-IR analysis

The FT-IR analysis revealed intense peaks at 2928, 3437, 3850, and 3734 cm^{-1}, in the single bound region indicating stretching vibrations associated with the C-H, O-H and N-H groups. These vibrations can be attributed to various compounds, including alcohols, phenols, polysaccharides, amino acids, and absorbed water (Feng et al., 2014; Lingegowda et al., 2012; Prodan et al., 2021). The vibrational band at 2353 cm^{-1} in the triple bound region is attributed to functional groups such as C≡N (Nitriles) and C≡C (Alkynes) bonds found in carboxylic acids and organic acids (Bankar et al., 2010; Rahman & Sathasivam, 2015). The absorption peaks at 1531, 1639 cm^{-1} are related to C=O stretching and asymmetric N=O stretching and C=C, indicating the presence of carbohydrates (polysaccharides), proteins, amino acids, esters, aldehydes and ketones compounds (Selmi et al., 2021). The peaks at 1447, 1258, 1045, and 818 cm^{-1} are related to C-O and S=O

bonds, characteristic of carbohydrates, nitrogen compounds, sulfates, and phenols (Hernández-Garibay et al., 2019; Kannan, 2014). The peak at 679 cm^{-1} is associated with C-S and C=S stretching vibrations, indicating the presence of sulfide compounds (Socrates, 2004). These results are consistent with a previous study (Kumari et al., 2022).

4.1.2. Characterization of the amino acid profile of the seaweed by LC-MS/MS

The analysis of amino acids in the brown seaweed *C. compressa* using LC-MS/MS unveiled the detection of eight primary compounds, featuring notably high levels of L-alanine, L-glutamic acid, and L-aspartic acid. Moreover, lower quantities of L-valine, L-proline, L-leucine, L-threonine, and L-lysine were detected. Brown seaweeds constitute a substantial reservoir of amino acids, displaying considerable variations in composition across distinct species (Pangestuti & Kim, 2015). Particularly, the main amino acids identified in *C. compressa* were L-alanine, L-glutamic acid, and L-aspartic acid. The results of this study correspond with the outcomes of a prior investigation carried out by Manns et al. (2017) on the brown algae *Saccharina latissima*, which recognized glutamic acid, aspartic acid, and alanine as the predominant amino acids. Likewise, Peinado et al. (2014) documented a noteworthy alanine content of 4.1 ± 0.2 mg/g dry weight in the brown algae *Laminaria digitata*. In addition, *Pelvetia canaliculata* and *Fucus spiralis* categorized as brown macroalgae, displayed elevated levels of glutamic acid, with *Fucus spiralis* showcasing aspartic acid as the primary amino acid. It is crucial to recognize that the amino acid composition of algae can be impacted by diverse factors, such as species, preservation techniques, extraction methods, seasonal fluctuations, and environmental growth conditions (Biancarosa et al., 2017; A. Y. Zhou et al., 2015).

4.1.3. Characterization of the phytohormone profile of *C. compressa* by HP-LC

High-performance liquid chromatography (HP-LC) examination of the same seaweed, revealed the presence of five phytohormones, with zeatin (Z) identified as the predominant phytohormone. Zeatin (Z) is categorized within the group of cytokinins belonging to plant hormones, with its primary role being the stimulation of cell division in non-meristematic tissues (Gul et al., 2023). Furthermore, the analysis detected other notable phytohormones, such as gibberellic acid (GA), salicylic acid (SA), abscisic acid (ABA), and indole-3-acetic acid (IAA).

These results align with a prior study on algae *Petalonia fasci*a and *Caulerpa racemosa*, where a high abundance of phytohormones was observed. Particularly, *Caulerpa racemosa*

exhibited the highest abundance of the phytohormone indole-3-acetic acid (IAA). Moreover, it was observed that brown seaweed like *Sargassum vulgare*, *Cystoseira montagnei*, and *Dictyota dichotoma* predominantly contained indole-3-acetic acid (IAA), along with cytokinins such as zeatin (Z) and 6-benzylaminopurine (BAP). It's noteworthy to mention that among brown algae, the macroalgae *Cystoseira foeniculacea* displayed the highest concentration of gibberellic acid (GA) as reported by Yalçın et al. (2020). In a separate inquiry, the analysis of phytohormone composition in *Cystoseira spp*. unveiled the presence of indole-3-acetic acid (IAA), zeatin (Z), benzyladenine (BA), indole-3-butyric acid (IBA), and the highest concentration of gibberellic acid (GA) compared to other studied algae species (Hashem et al., 2019).

4.1.4. Analysis of the sugar composition of *C. compressa* by HP-LC

The analysis conducted using High-Performance Liquid Chromatography (HP-LC) on the brown algae *Cystoseira compressa* revealed the presence of substantial levels of sugars, among which significant quantities of arabinose and sucrose were identified as the predominant types of carbohydrates present within the seaweed. It was also noted that lower concentrations of glucose and maltose were detected. These findings are consistent with previous studies (Apostolova et al., 2022; Ben Gara et al., 2017; Dobrinčić et al., 2021).

The study outcomes reveal the considerable abundance of carbohydrates contained in brown seaweed *C. compressa*, with sugars such as arabinose, sucrose, glucose, and maltose possibly serving as constituents of the algal polysaccharides, as suggested by García-Ríos et al. (2012). Prior investigations into the hydrolysates of brown algae species have highlighted a diverse array of monosaccharide combinations that contribute to the overall sugar content. Furthermore, it has been reported that disaccharides, including sucrose, which is formed through the association of glucose and fructose molecules, play a pivotal role in both nutrient storage and structural functions within the algae, as pointed out by Stiger-Pouvreau et al. (2016). Additionally, polysaccharides like alginic acid, fucoidan, and laminarin, which can collectively make up to 76% of the dry weight, are significant contributors to the overall sugar content found in brown algae species like *C. compressa*, as highlighted by Kadam et al. (2015).

4.2. Characterization and screening of the bacterial strain

The halotolerance test revealed that both strains MR63 and MR64 were capable of moderately tolerating up to 6% NaCl in LB medium, while strain MR62 showed the ability to tolerate approximately 4% NaCl. Additionally, the selected rhizobacterial strain MR64 demonstrated the ability to produce certain important traits promoting plant growth such as indoleacetic acid (IAA) and hydrogen cyanide HCN. Analysis of the bacterial 16S rRNA gene sequence by phylogenetics indicated that the strain belongs to the species *Bacillus cereus* with 98% similarity. *Bacillus* strains constitute a substantial portion of soil microorganisms and are commonly used in agriculture to enhance plant growth (Han et al., 2006; Lee et al., 2021).

Similar results have been reported by Upadhyay et al. (2009) regarding *Bacilli* strains capable of tolerating up to 8% NaCl and showing PGP activities. According to Abdelmoteleb and Gonzalez-Mendoza (2020), *Bacillus megaterium* and *Bacillus cereus* have shown viability in environments containing up to 14% NaCl. Halotolerant bacteria can withstand high salt concentrations due to their ability to accumulate compatible osmolytes, thus preserving intracellular osmotic balance (Duc et al., 2006; Singh et al., 2013). Indole-3-acetic acid (IAA) stands out as an important phytohormone, serving as a signaling molecule in the control of plant growth and development. Studies have noted that IAA production by plant growth-promoting rhizobacteria can vary among species and strains, and it is also affected by factors such as culture conditions, growth stage, and substrate availability. Dong et al. (2023) documented that *Bacillus cereus DW019* has been recognized as a plant growth-promoting rhizobacterium (PGPR) due to its synthesis of indole-3-acetic acid (IAA). Additionally, it has been suggested that rhizobacteria producing hydrogen cyanide (HCN) could play a significant role in plant disease suppression (Voisard et al., 1989). These findings underscore the potential of the bacterial strain *Bacillus cereus* MR64 importance as a beneficial plant growth-promoting rhizobacterium, offering valuable traits for enhancing agricultural productivity in diverse environments.

4.3. Responses of tomato plants to the application of *Bacillus cereus MR64* and the aqueous extract of the brown alga *Cystoseira compressa* under salt stress

Salinity induces osmotic stress, ionic toxicity, nutritional imbalances, and excessive production of reactive oxygen species (ROs). These effects have substantial repercussions on cellular components and biological membranes, resulting in decreased growth and

biomass (Alzahrani et al., 2019; Loudari et al., 2020). The impact is manifested by a reduction in leaf relative water content (RWC) and decreased levels of photosynthetic pigments due to decreased water potential. Additionally, NaCl impedes the absorption of crucial elements such as nitrogen (N) and magnesium (Mg), which are essential for chlorophyll structure (Kaya et al., 2009). The accumulation of Na+ ions from salinity in NaCl disrupts the ionic balance inside plant cells, potentially damaging cell membranes and increasing permeability to ions, especially sodium ions and chloride (Cl-). Consequently, this leads to increased electrolyte leakage and reduced K+ content (Shelke et al., 2019).

The results of this research indicated that the simultaneous application of the PGPR strain *B. cereus* MR64 and *C. compressa* extract led to improved plant growth responses. Increased shoot and root lengths, higher biomass, and notable improvements in physiological indicators such as chlorophyll A levels, total chlorophyll content, and electrolyte leakage were observed. Additionally, biochemical analyses revealed a decrease in Na+ levels, an increase in K+ concentrations, and an increase in proline content. These results suggest that the synergistic application of these components may facilitate better adaptation to saline stress through the modulation of key parameters such as improved root lengths and more efficient photosynthesis, which is consistent with previous research (Aremu et al., 2022; Aydi-ben-abdallah et al., 2021; Ngoroyemoto et al., 2020; Santana et al., 2022). Conversely, compared to the exclusive use of the PGPR strain, the use of only *C. compressa* extract demonstrated superior efficacy in improving growth parameters, increasing chlorophyll levels, and enhancing membrane integrity by reducing electrolyte leakage. Additionally, *C. compressa* extract increased proline levels and improved flower and fruit production per plant, while reducing the distance between floral clusters, especially at concentrations of 15% and 10%, compared to plants inoculated with PGPR and controls. In contrast, the PGPR treatment exerted a more favorable influence on root parameters, such as length and biomass, as well as the highest percentage of leaf relative water content and a notable reduction in sodium absorption, compared to plants treated with the extract and controls.

Algae extracts possess stimulating characteristics known to enhance plant growth and productivity in saline environments (Ali et al., 2021; Deolu-Ajayi et al., 2022). These extracts comprise various bioactive components, including phytohormones, polysaccharides, polyphenols, vitamins, amino acids, peptides, and proteins (Khan et al.,

2009). FT-IR analysis of C. compressa revealed the presence of functional groups such as O-H, N-H, C-H, and C-C. These groups are associated with bioactive molecules such as amino acids (AA), polysaccharides, proteins, phenols, alcohols, and various other organic compounds (Kumari et al., 2022). Analysis of the amino acid profile by LC-MS/MS demonstrated the presence of various important amino acids, including L-alanine, L-glutamic acid, L-aspartic acid, L-valine, and L-proline. The application of amino acids (AA) before or during different abiotic stresses has been found to be beneficial for plants (Godoy et al., 2021). They serve as osmoprotectants to plants facing saline stress conditions. Major constituents such as proline, aspartate, glutamate, glycine, valine, lysine, histidine, and arginine have been recognized for their significant roles in osmotic regulation in response to saline stress challenges (Hosseini et al., 2023). Amino acids contribute to maintaining cell turgor pressure, modulating stomatal opening, and reducing reactive oxygen species (ROS). Consequently, they likely contribute to the beneficial effects of algae extract (Ramzan et al., 2023). In a study on amino acid-based biostimulants, Abdelkader et al. (2023) observed that essential amino acids (EAAs) effectively alleviated saline stress in affected lettuce plants. Specifically, the application of exogenous amino acids reduced EC levels to 469–558 μS/g. Amino acids decreased Cl- anions in lettuce leaves by 25% and mitigated Na+ cations. Additionally, amino acid application improved K+ absorption and increased chlorophyll concentrations compared to the control treatment. Furthermore, quantification of sugars contained in *C. compressa* revealed the presence of important monosaccharides and disaccharides. These sugars are potential constituents of algae polysaccharides (García-Ríos et al., 2012). Algae polysaccharides have been demonstrated to promote plant growth, reduce lipid peroxidation of membranes, increase chlorophyll content, enhance antioxidant activity, and regulate intracellular ion concentration (Zou et al., 2019). In general, algae sugars and polysaccharides have the potential to improve plant salt tolerance and prevent damage due to saline stress, which has been proven and well-documented in previous studies (Zou et al., 2018, 2021). Furthermore, analysis of phytohormones revealed significant concentrations of zeatin (Z) and gibberellic acid (GA), as well as other key phytohormones at lower levels. Zeatin (Z) and gibberellic acid (GA) are known to stimulate cell division and elongation, thereby contributing to overall plant growth (de Souza Vandenberghe et al., 2014). However, indole-3-acetic acid (IAA), salicylic acid (SA), and abscisic acid (ABA) participate in root development, plant defense mechanisms, and regulation of organ size and stomatal closure (Haverroth et al., 2023; Li et al., 2014; War et al., 2011). Furthermore,

adequate levels of indole-3-acetic acid (IAA) and zeatin (Z) positively influence floral bud differentiation (Yan et al., 2019). The presence of these essential phytohormones in the extract suggests their potential role in enhancing overall responses and mitigating salinity effects in tomato plants (Hernández-Herrera et al., 2022). The improvements observed in tomato parameters may be attributed to various beneficial components present in algae extracts, including essential macro and micronutrients, vitamins, amino acids, and phytohormones (Hussein et al., 2021). These compounds collectively influence the plant cellular metabolism, resulting in a significant increase in growth and development (Khan et al., 2009). Furthermore, the presence of osmoprotectants such as free amino acids and polysaccharides in algae extracts plays a vital role in supporting and enhancing plant physiology, leading to increased photosynthetic activity and reinforced membrane integrity, reduced electrolyte leakage, and improved metabolomics, thus resulting in enhanced flowering and fruiting (Wang et al., 2017). According to the results of the study conducted by Patel et al. (2018), the application of *Kappaphycus alvarezzi* extract to different varieties of wheat subjected to saline and drought stress led to several positive outcomes. These included increased root length, elevated levels of chlorophyll and carotenoids, and improved tissue water content. Furthermore, the extract significantly reduced electrolyte leakage and lipid peroxidation, lowered the Na+/K+ ratio, and increased calcium content, thus mitigating ion imbalances in the plants. In another study conducted by Hussein et al. (2021), seed priming in liquid algae extracts, including *Cystoseira compressa*, enhanced the growth of *V. sinensis* and *Z. mays* under saline stress. Godlewska et al. (2016) suggest that the ability of algae to promote growth may depend on the concentration and extraction methods used. This is correlated with the results of this study where the application of liquid extract of *Cystoseira compressa* at concentrations of 10% and 15% improved most of the growth and physiological parameters of tomato plants despite saline stress, these results are in agreement with previous studies (Bensidhoum & Nabti, 2021; Chanthini et al., 2022; Latique et al., 2017).

The rhizobacterial strain used in this study which was identified as *Bacillus cereus* MR64 demonstrated salt tolerance characteristics and produced essential traits promoting plant growth, including the production of indole acetic acid, likely contributing to the observed improvements in tomato plants, in line with previous research (Cordero et al., 2018; Kaloterakis et al., 2021; Zameer et al., 2016). The application of plant growth-promoting rhizobacteria (PGPR) offers various benefits through hormone synthesis, phosphate

solubilization, and nitrogen fixation (Gamalero & Glick, 2011). The improvements observed in plant parameters in our study align with confirmed responses to inoculation by the *Bacillus* strains. Numerous previous studies have underscored the positive impact of applying halotolerant rhizobacteria, especially Bacillus strains with plant growth-promoting characteristics, on enhancing the growth of treated plants under salinity stress, particularly in root parameters (Ayaz et al., 2022; El-Esawi et al., 2018; Xiong et al., 2020). Additionally, these treatments have been shown to improve photosynthetic activity and overall plant physiology. Furthermore, inoculated plants exposed to saline conditions have exhibited reduced sodium uptake and increased accumulation of endogenous osmoprotectants like proline, resulting in enhanced overall plant health, stress tolerance, and increased flowering and fruiting (Julia et al., 2020; Zhou et al., 2022). Previous studies, such as that of Y. Zhou et al. (2022), have examined the effectiveness of halotolerant *Bacillus cereus* (4% NaCl) producing indole-3-acetic acid (IAA) in promoting the growth of cucumber plants and mitigating saline stress, resulting in increased plant height, stem diameter, fresh and dry weight, as well as root length, biomass, and proline content. Shultana et al. (2020) observed that the application of *Bacillus tequilensis* and *Bacillus aryabhattai* resulted in the highest total chlorophyll content, showing a 28% increase, and the lowest electrolyte leakage of 92%. Additionally, a notable increase of 156% in total dry matter was observed with the inoculation of this bacterial strain. Furthermore, inoculation with these *Bacillus* strains led to the highest increase in relative water content and the most significant reduction in the Na+/K+ ratio, respectively. In another study by Khan et al. (2019), specific halotolerant bacterial strains significantly increased the chlorophyll content of soybean plants compared to plants subjected to saline stress alone. Additionally, electrolyte leakage, an indicator of membrane damage under various stresses, showed reduced levels in salt-stressed radish plants inoculated with PGPR compared to non-inoculated stressed plants (Yildirim et al., 2008).

The interactive use of the PGPR strain *B. cereus MR64* and liquid extract of the brown algae *C. compressa* resulted in the most significant improvements in tomato plant parameters, demonstrating the effectiveness of this combination in promoting plant growth and mitigating saline stress. Biostimulants do not directly reduce sodium (Na+) uptake in plants. Instead, they assist plants in better managing saline stress. This is achieved by enhancing plant functions such as root growth, water balance, and stress response activation (Bulgari et al., 2019). Consequently, plants can better accumulate osmolytes and

antioxidants such as proline, an amino acid that accumulates in plants in response to abiotic factors and helps balance osmotic stress and oxidative stress caused by reactive oxygen species (ROs) and total soluble sugars (Liang et al., 2013). It is also known that plant tissues and cells accumulate soluble sugars in response to saline stress, potentially as an osmotic protection mechanism (Ahmad et al., 2020). Additionally, the accumulation of potassium (K+), which plays a crucial role in regulating turgor within stomatal cells during stomatal movement and detoxifying reactive oxygen species, along with a greater accumulation of K+ in plant tissues, has reduced the concentration of Na+ and resulted in a higher K+/Na+ ratio, enabling improved plant metabolism to cope with saline stress and maintain normal growth (Wang et al., 2013). According to Rinaldelli and Mancuso (1996), preserving membrane integrity can also promote the segregation of sodium (Na+) within vacuoles and the selective absorption of ions, particularly potassium (K+) and calcium (Ca++).

The variance observed across the parameters under different treatments demonstrated a complex interaction between biostimulants and plant physiological responses. In our study, while the application of biostimulants resulted in a notable reduction in the distance between floral clusters, indicating enhanced productivity (Bradea et al., 2015). However, other parameters exhibited varying degrees of change. The number of leaves, leaf relative water content (LRWC), chlorophyll B, total soluble sugar content, number of fruits, and number of flowers did not show statistically significant differences across treatments. This lack of significant variance suggests that these responses may be influenced by additional factors not directly addressed by the biostimulant treatments. The percentage of LRWC% is commonly used to indicate the plant water status (Bowman, 1989). Additionally, Fischer (1973) discovered a direct correlation between relative water content and soil water content, suggesting that relative water content can serve as an indicator of soil water content; therefore, the soil can influence relative water content. The lack of statistical significance in total soluble sugar accumulation and chlorophyll B content could be due to various factors, including variability among individual plant responses or within experimental batches, as well as interactions with soil composition, environmental conditions, or genetic variability, contributing to result variations (Anderson & McNaughton, 1973; Wang et al., 2009). Similarly, the number of leaves, flowers and fruits in addition to the average distance between cluster 1 and 2 can be influenced by factors such as growth stage, environmental conditions, and genetic characteristics (Dieleman &

Heuvelink, 1992). Remarkable improvements were observed in most morphological and physiological aspects of tomato plants treated with T7 (MR64 + 10% extract) and T8 (MR64 + 15% extract). These effects can be attributed to the synergistic interaction between *C. compressa* extract and the PGPR *Bacillus cereus* MR64 (Rouphael & Colla, 2018). Ali et al. (2021) suggested that algal extracts could have a positive impact on the soil microbiome, potentially enhancing the plant growth-promoting (PGP) characteristics of rhizospheric microbes. The rapid and early expansion of roots, coupled with the development of an extensive network of long and dense absorbing hairs following inoculation with PGPRs, enhances the absorption of both macro and micronutrients and improves water absorption efficiency. This, in turn, increases the effectiveness of other amendments such as organic extract, leading to greater efficiency and better adaptability (Bhat et al., 2023).

The complex nature of biostimulant characteristics suggests that the effectiveness of a biostimulant cannot simply be attributed to the combined impact of its individual components. Instead, it is likely that effectiveness arises from synergistic interactions among its components and other elements (Franzoni, 2020). Several factors affect the efficacy of biostimulants, including composition, timing of application, plant species, environmental conditions, interactions with other inputs, soil properties, application rate, and biological interactions. These elements influence how biostimulants interact with plants and their environment, thereby shaping their impact on growth and health, which may explain the variations recorded with different parameters of tomato plants (Sible et al., 2021).

Previous studies have demonstrated the effectiveness of combining various plant biostimulants with PGPR, highlighting their ability to improve plant growth and productivity through additive and synergistic mechanisms. For example, the combination of the microbial biostimulant *Rhizophagus intraradices* BEG72 and *Trichoderma atroviride* MUCL45632 alone or with foliar application of plant-derived protein hydrolysate synergistically improved fresh weight, chlorophyll content, and proline accumulation compared to untreated plants, especially under alkaline and saline conditions (Rouphael et al., 2017). Additionally, the combined application of *Azospirillum brasilense* Az39 bacteria and extracts of *Macrocystis pyrifera* algae had a positive impact on the growth of lettuce plants under water stress compared to the control group. Furthermore, Gupta et al. (2021) demonstrated that the synergistic application of the PGPR

Pseudomonas fluorescens (ATCC 13525) and Kelpak, a commercial seaweed extract from *Ecklonia maxima*, resulted in notable benefits for onion plants. This combined treatment led to extended leaf and root lengths, elevated carbohydrate levels, improved nutrient content, and increased cytokinin levels. Moreover, the study revealed a significant increase in cytokinins derived from the mevalonate (MVA) pathway, suggesting that the combined use of seaweed extract and PGPR holds promise for enhancing both growth and nutritional quality.

These results potentially provide evidence of the positive impact on plant performance resulting from the interactive effects between microbial and non-microbial biostimulants, indicating that these effects are attributable to the complementary action mechanisms of both biostimulants (González-González et al., 2020). Recent studies acknowledge that the intentional combination of microbial biostimulants with other non-microbial substances can lead to interactive and synergistic effects, which may not be achieved by individual application (Rouphael & Colla, 2018). It is important to emphasize that biostimulants are derived from living organisms or natural sources, and their properties may result from the collective interaction of all components. Understanding biostimulants may require examining the combined characteristics of their components rather than studying individual characteristics or specific combinations (Yakhin et al., 2017). Therefore, the synergistic application of plant growth-promoting rhizobacteria (PGPR) and algal extracts holds significant potential as an ecologically sustainable approach to enhancing plant growth and vitality under certain salinity conditions (Ngoroyemoto et al., 2020).

4.4. FT-IR analysis of tomato plants subjected to different treatments

The FT-IR analysis revealed intense peaks at approximate wavenumbers of 3270, 1610, and 1010 cm^{-1} for treatments T2A, T3A, T4A, T5A, T6A, T7A, and T8A, respectively, in contrast to control T1A, which exhibited intense vibrational peaks at wavenumbers of 1606 and 1044 cm^{-1}. It is noteworthy that treatments T6A, T7A, and T8A showed the presence of unique vibrational peaks at wavenumbers of 3854, 3737, and 3649 cm^{-1}. The internal vibrational peaks at wavenumbers of 3854, 3737, 3649, 3272, 3270, and 3232 cm^{-1} In addition to the internal vibrational peaks at wavenumbers of 2921 cm-1 for treatment T2A and 2920 cm-1 for treatments T3A, T4A, and T5A correspond to vibrations correspond to stretching vibrations associated with C-H, O-H and N-H groups. These vibrations may be associated with various compounds, including alcohols, polysaccharides, amino acids, and absorbed water (Feng et al., 2014; Lingegowda et al., 2012; Prodan et al., 2021).

The vibrational peaks at wavenumbers of 2376, 2373, 2372, and 2319 cm^{-1} observed weakly in the plants from treatments T1A, T2A, T3A, T4A, T5A, and more intensely in the plants from treatments T6A, T7A, and T8A correspond to the characteristic of triple bounds groups including C≡O and C≡C characteristic of compounds such carboxylic acids (Bankar et al., 2010; Rahman & Sathasivam, 2015). The internal vibrational peaks at wavenumbers of 1617 cm^{-1} for treatments T6A, T7A, and T8A, 1610 cm^{-1} for treatments T3A, T4A, and T5A, 1609 for treatment T2A, and a peak at 1606 cm^{-1} for control T1A. It is worth noting the presence of a unique peak in the spectrum of the control TA1 at wavenumber 1732 cm^{-1}. These peaks correspond to vibrations associated with the C=O, N=O groups, indicating the possibility of the presence of compounds such as halides, acids, aldehydes, proteins, amides, amino acids, anhydrides, carboxylic acids, esters, ketones, lactams, lactones, and quinones. The peak at wavenumber 1732 cm^{-1} in the double bound region may be associated with one of the compounds that accumulate during the confrontation of stress (Selmi et al., 2021; Yuen et al., 2005).

The peaks of these potential compounds appear similarly in different plants. While the vibrational peaks at wavenumbers 1010 cm^{-1} correspond to the vibrations of C-O-C and C-OH bonds, C-O and S=O bonds may be associated with compounds such as ethers, alcohols, and sugars (Yuen et al., 2005). The observed vibrational peaks may suggest the existence of compounds inherent to the chemical composition of tomato plants. The medium vibrational peaks at wavenumbers 1420 and 1316 cm^{-1} mainly correspond to the vibrations of NO2, CH3, and CH2 groups, indicating the possibility of the presence of nitro compounds or compounds with alkane, alkene groups, etc. While the vibrational bands at wavenumbers 1235, 1044, 1012, 1010, and 1009 cm^{-1} which appeared in plants under treatments T1A, T2A, T3A, T4A, T5A, T6A, T7A, and T8A, respectively, are related to C-O and S=O bonds, characteristic of compounds such as ethers, alcohols, and sugars (Hernández-Garibay et al., 2019; Kannan, 2014; Yuen et al., 2005). While the vibrational peak at the wavenumber 778 cm^{-1} for treatment T1A, 778 and 651 cm^{-1} for treatments T2A, T3A, T4A, T5A, T6A, T7A, and T8A is attributed to C-H, N-H, C-S bonds, as well as aromatic cycles indicating the presence of alkenes, aromatic compounds, and sulfur compounds (Socrates, 2004; Yuen et al., 2005). The recorded modifications in the regions 3500 to 4000, 1700 to 1800, and 900 to 1250 cm^{-1} in the spectra of plants treated with both biostimulants, the aqueous extract of algae, and the PGPR strain, along with the appearance of changes in the regions 3500 to 4000 cm^{-1} in plants treated with the

combination of both biostimulants (T6A, T7A, and T8A) compared to plants treated with each biostimulant individually and to the control, suggest the potential appearance of various compounds including alcohols, polysaccharides, amino acids in tomato plants subjected to these treatments. All these modifications are supported by the results of assays that revealed an increase in proline and sugar content compared to the control T1A, also suggesting the possibility of the presence of other compounds that accumulate following treatment with both biostimulants, including aromatic compounds and absorbed water (Ertani et al., 2018; Vujinović et al., 2020).

CONCLUSION

CONCLUSION

This research demonstrates the potential of using the PGPR strain *Bacillus cereus* MR64 and the aqueous extract from brown seaweed *Cystoseira compressa* to mitigate the negative effects of salinity on tomato plants. These two biostimulants were tested individually and in synergy, and their effects were compared. The combined treatment significantly enhances growth parameters such as shoot and root lengths, biomass, and chlorophyll content, while reducing electrolyte leakage. Biochemical analyses show decreased Na+ levels and increased K+ and proline concentrations, contributing to better osmotic regulation and stress tolerance.

FT-IR analysis of tomato plants showed significant spectral changes in the single bound region characterized by unique vibrational peaks at 3854, 3737, 3649, 3272, 3270, and 3232 cm^{-1}, alongside the peaks at 2921 cm^{-1} for treatment T2A and 2920 cm^{-1} for treatments T3A, T4A, and T5A, correspond to stretching vibrations of C-H, O-H, and N-H groups. These vibrations are indicative of the presence of various compounds, including alcohols, polysaccharides, amino acids, and absorbed water. These findings suggest biostimulant treatments enhance the synthesis of various compounds, increasing organic compounds content, and improving stress resistance.

Algae extracts, rich in bioactive components like phytohormones, polysaccharides, amino acids, and vitamins, play a critical role in enhancing plant growth under saline conditions. The presence of amino acids such as proline and polysaccharides as was revealed via analytical tools such as LC-MS/MS and HP-LC in *C. compressa* extracts contributes to improved osmotic balance, stress mitigation, and enhanced physiological functions like photosynthesis and membrane integrity. The FT-IR analysis confirmed the presence of these bioactive molecules, further supporting their role in stress alleviation.

The PGPR strain *B. cereus MR64* also promotes plant growth by enhancing root development, nutrient absorption, and reducing sodium uptake, thereby improving overall plant health and stress tolerance. The combined application of PGPR and algae extracts leads to synergistic effects, resulting in superior plant growth and productivity compared to individual treatments. This synergy likely arises from the complementary actions of microbial and non-microbial biostimulants, enhancing the plant's ability to cope with salinity stress.

In conclusion, the integrated use of PGPR and algae extracts represents a promising, ecologically sustainable approach to improving plant resilience and productivity in saline environments. This study underscores the potential of biostimulants to enhance crop yields and maintain plant health under abiotic stress conditions, offering a viable strategy for sustainable agriculture. The findings suggest broader applicability beyond tomato plants, potentially benefiting a range of crops crucial for food security. Long-term field studies are necessary to validate efficacy under various climatic and soil conditions, and integrating biostimulants with other sustainable agricultural practices could optimize productivity and ecosystem health. Understanding the molecular mechanisms behind stress tolerance enhancement can guide genetic engineering and selective breeding efforts.

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APPENDIX

APPENDIX

A. Appendix

Liquid LB medium (g/l) (Luria-Bertani, 1956)

Reagent	**Quantity (g/l)**
Peptone	10
Yeast extract	5
NaCl	10
pH	7.0

B. Appendix

Nutrient Agar medium (g/l)

Reagent	**Quantity (g/l)**
Peptone	5
Beef extract	3
Agar	15
pH	7.0

C. Appendix

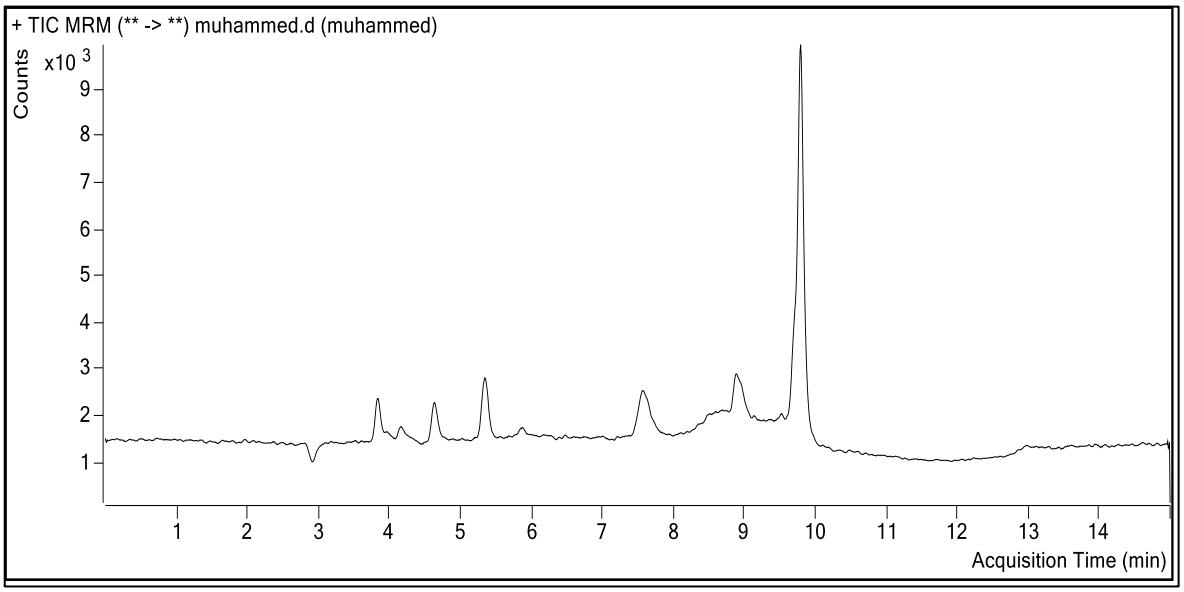
Pikovskaya medium (g/l) (Pikovskaya, 1948)

Reagent	**Quantity (g/l)**
Glucose	10
Tricalcium phosphate	5
Ammonium sulfate	0.5
Potassium chloride	0.2
Magnesium sulphate	0.1
Manganese sulphate	Trace
Ferrous sulphate	Trace
Yeast extract	0.5
Agar	15
pH	7.0

A 0.4% stock solution of bromophenol blue dye was prepared in ethanol and pH was adjusted to 6.7 by using 0.1 N NaOH. 0.4 ml dye was added to Pikovskaya agar to form modified Pikovskaya medium.

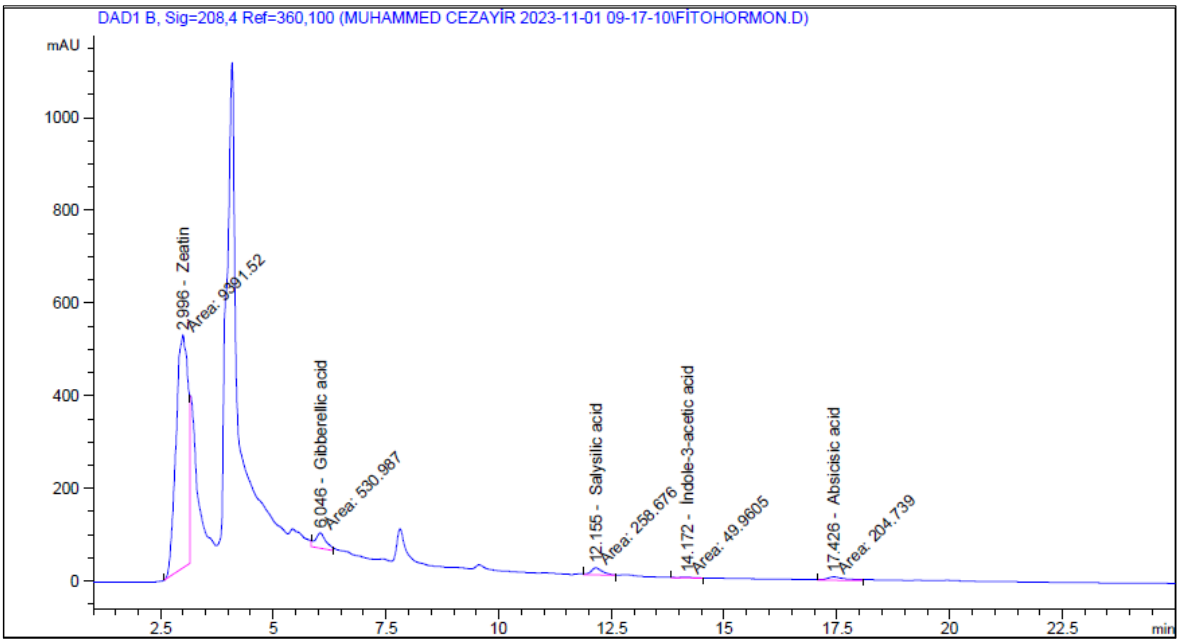
D. Appendix

Chromatogram of LC-MS/MS analysis for amino acids profile of *C. compressa*.



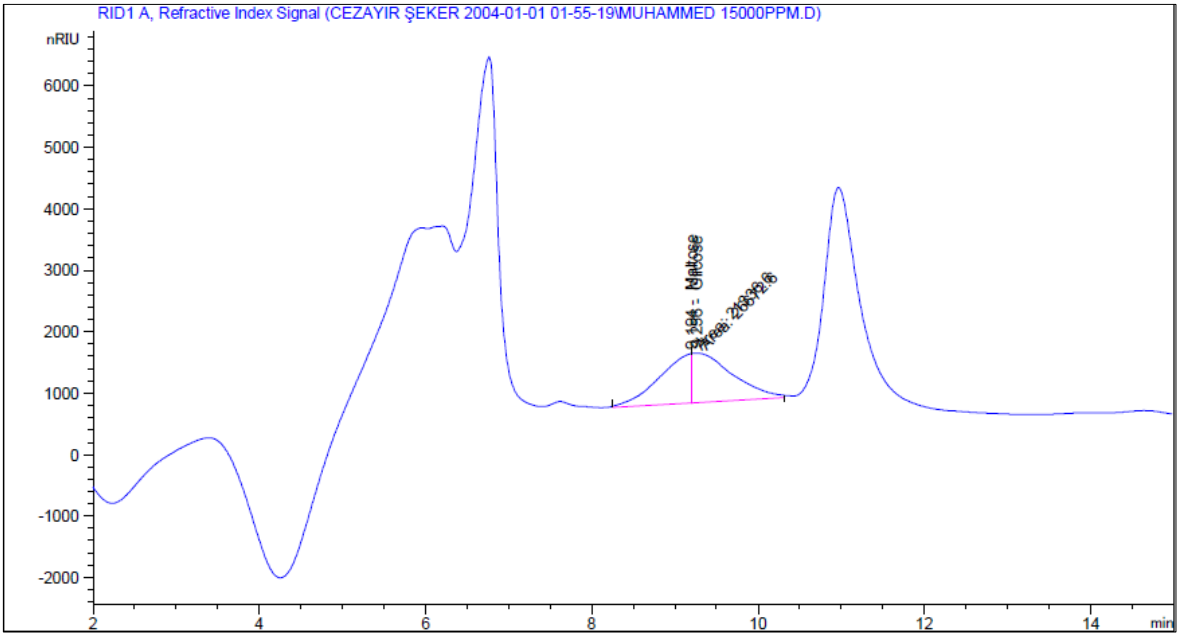
E. Appendix

Chromatogram of HP-LC analysis for phytohormones profile of *C. compressa.*



F. Appendix

Chromatogram of HP-LC analysis showing peaks for Maltose and Glucose in *C. compressa*.



G. Appendix

Chromatogram of HP-LC analysis showing peaks for Sucrose and Arabinose of *C. compressa*.