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**ARTICLE**

# Isolation and Characterization of Plant Growth Promoting Endophytes from Linum Usitatissimum

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## ABSTRACT

This present study identifies endophytic bacteria from *Linum usitatissimum* with multidimensional plant growth-promoting attributes, positioning them as ecological engineers for sustainable agriculture. Plant growth-promoting bacteria (PGPB) are present in symbiotic associations with plants or rhizosphere. These microbes enhance crop productivity and resilience under different environmental conditions. Endophytes are a type of PGPB that inhabit inside plant tissues and contribute to plant growth by phytohormone production, phosphate solubilisation, zinc solubilisation, siderophore production, ammonia production, nitrogen fixation, stress tolerance, and biocontrol mechanisms. Twelve bacterial strains were isolated from *Linum usitatissimum* exhibiting plant growth-promoting attributes such as ammonia and indole-3-acetic acid (IAA) production, siderophore synthesis, phosphate solubilisation, and extracellular enzyme synthesis. The isolated endophytes were also assessed for different enzymatic activities such as; cellulase, pectinase, xylanase, amylase, and gelatinase, which contribute to development of a symbiotic relationship and are crucial for the degradation of plant cell wall components The most efficient endophytes identified in the present study were *Pseudomonas* sp. strain JL-1 (ESL1) and Staphylococcus sciuri

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ARTICLE INFO

Received: 7 April 2025 | Revised: 6 May 2025 | Accepted: 15 May 2025 | Published Online: 30 May 2025

DOI: https://doi.org/10.30564/re.v7i2.9406

CITATION

Choudhary, S., Bhandari, G., Deogaonkar, A., et al., 2025. Isolation and Characterization of Plant Growth Promoting Endophytes from Linum Usitatissimum. Research in Ecology. 7(2): 129–143. DOI: https://doi.org/10.30564/re.v7i2.9406

(ESL2), both of which displayed strong plant growth-promoting potential. ESL1 and ESL2 demonstrated promising plant growth-promoting characteristics and cellulase, pectinase, xylanase, amylase, and gelatinase, activity. ESL2 (Staphylococcus sciuri) enhanced nutrient cycling (phosphate solubilisation: 196–209 µg/ml; siderophores: 68–71%) and stress tolerance (IAA: 11–12 µg/ml), reducing reliance on synthetic inputs. By integrating flax microbiomes into agro-ecosystems, we demonstrate a scalable approach to reconcile crop productivity with soil biodiversity conservation. These results demonstrate the potentiality of these endophytic microbes in sustainable agriculture, environmental management, and microbial biotechnology. Further studies on their metabolic pathways may expand their applications in bioremediation and plant-microbe interactions.

***Keywords:*** *Linum usitatissimum*; Bacteria; Plant Growth; Biochemical; Siderophore

# 1. Introduction

The eradication of global hunger due to population explosion is amongst the United Nations Sustainable Development Goals and feeding this increased population is a prime societal challenge. The intensive application of chemical fertilizers for crop development results in long-term detrimental impact of soil health and microbial diversity and ecosystem stability [1]. Moreover, accumulation of these chemical-based fertilizers contributes to soil degradation, groundwater pollution, and loss of native microbiota [2,3]. Thus, the pursuit of environment friendly and sustainable methods to improve agronomic productivity without endangering the soil's native microbiota is essential [4]. Plant growth promoting endophytic microbes exists in the intra- and extracellular compartments of plant tissues without having any deleterious effect on plant health and is vital to the ecosystem [5]. These endophytes consisting of both bacterial and fungal species have co-evolved with plants resulting in a synergistic relationship that enhance plant development through gene regulation and metabolic interaction [6]. Endophytic microorganisms are estimated to be found in over 300,000 plant species worldwide [7]. Endophytic bacteria promote plant health through a range of direct and indirect processes such as; IAA and siderophore synthesis, phosphate and zinc solubilisation, Hydrogen cyanide (HCN) and ammonia production etc. Plant growth-promoting endophytes (PGPE) include *Pseudomonas, Flavobacterium, Clostridium, Azotobacter, Rhizobium, Serratia, Bacillus* and *Burkholderia* etc.[8,9]. Endophytes interact closely with their host plants more than phyllosphere and rhizosphere bacteria. As keystone species within the plant holobiont, endophytes serve a critical function in mediating plant and soil quality, nutrient exchange and stress response. Endophytic establishment in internal host tissues gives them access to host metabolic pathways, allowing them to influence host development and environmental responses from within. Unlike rhizosphere or phyllosphere microbes, endophytes inhabit nutrient-rich niches where they can modulate plant hormone levels, activate stress-related signalling pathways, and enhance systemic resistance to pathogens. Endophytes aid plants by limiting weed growth, improving nutrient intake, germination rate, water movement, chlorophyll, leaf area, nitrogen, and protein contents along with ability to mitigate abiotic stress including salinity, alkalinity, and drought [6,10,11]. Furthermore endophytes enhance soil quality and sustainability by producing antibiotic, siderophore, and specific enzymes that build plant resistance and mitigate environmental pollutants [12]. Plant growth-promoting endophytes confer a sustainable alternate to chemical and synthetic fertilizers by improving plant growth naturally while preserving soil quality and ecosystem balance [1]. In contrast to chemical fertilizers which deteriorate soil quality and microbiome diversity, endophytes enhance nutrient cycling, organic matter and support beneficial microorganisms [7]. They also offer low carbon, biologically integrated approach to maintain soil fertility and ecosystem function. The employment of endophytes reduces carbon footprint by minimising dependency on energy-intensive fertilizers and lowering nitrous oxide emissions a potent greenhouse gas associated with over-fertilization [9]. Furthermore, endophytic microbes promote root development and carbon sequestration. Endophytes are not merely passive colonizers but active ecological bio-agents that enhance plant growth and balance soil health and fertility under stressed environmental conditions, supporting climate-resilient and sustainable agriculture.

*Linum usitatissimum*, commonly referred to as flax or linseed, is a dicot crop of family Linaceae. It is a well-known fibrous plant and has been cultivated for more than 5000 years, making it one of the oldest medicinal crops across the globe [13]. Flaxseeds are rich in short-chain omega-3 fatty acids and have a multitude of other nutritional benefits. Although *Linum* mostly grown for its fibre, but its seeds are rich in nutritional and therapeutic worth and fend off from diabetes, cancer and cardiovascular diseases [14,15]. Flax is a highly significant crop in the commercial sector, utilized for high content of vitamins, proteins, linseed oil, polyunsaturated fatty acids, lignans, phytosterols, squalene and fibre [15]. Furthermore, nowadays it is also used in wound dressings, biodegradable packing material, tissue engineering scaffolds, and surgical threads

[16]. In addition to its inherent nutritional and commercial value, recent research has demonstrated that the benefits of flax can be further enhanced through the application of endophytic microbes in an economical and sustainable manner [16, 17]. Flax associated endophytic microbiomes represent an untapped reservoir for ecological intensification. Flax associated endophytes not only boost crop yields but also mediate critical ecosystem functions such as nitrogen fixation, phosphate solubilisation, iron mobilization and pathogen suppression making them vital for designing climate-resilient agro-ecosystem [7]. Moreover, these microbiomes synthesize plant growth hormones such as auxins, gibberellins, and cytokinins that promote root and shoot development [9]. These microbes also assists in developing plant resistance to different abiotic stresses such as drought, salinity, and heavy metal toxicity, as well as biotic stresses by suppressing plant pathogens by producing antimicrobial agents [11]. Flax associated endophytic microbiome has emerged as potential model for enhancing crop growth, soil quality, intraspecific biodiversity and resilience under climate stress. Inoculation of endophytic microbes including *Azospirillum brasilense and Pseudomonas geniculata* to salinity-stressed flax plants significantly improved various growth characteristics and chlorophyll, carotenoids, soluble sugars, free proline, total phenolic, ascorbic acid, potassium, proteins, and antioxidant enzymes in *Linum* [18]. In flax, the occurrence of diverse endophytic communities has been associated to enhanced antioxidant activity, secondary metabolite production, and stress tolerance—traits that are vital for safeguarding plant yield and nutritional quality under adverse climatic conditions. Endophytic consortia significantly enhanced the shoot-root biomass, seed yield, and levels of protein, flavonoid, and phenolic compounds of flaxseed when applied through seed inoculation [6]. The present study investigates the application of endophytes on *Linum* growth properties due to its economical, medicinal, and nutritional qualities, as well as the paucity of research on *Linum* endophytes.

# 2. Material and Methods

## 2.1. Isolation of Endophytes from Plant Sample

Fresh and healthy *Linum* plants were collected; detritus and epiphytic germs were removed from the plant samples by rinsing with sterile distilled water. Plant samples were surface sterilized for one minute by 70% ethanol, two minutes with 2% sodium hypochlorite on the surfaces of the leaves and stems, and three minutes with 2% sodium hypochlorite on the surfaces of the roots and then washed six times by autoclaved distilled water and kept for drying in laminar flow cabinet. The final wash was applied to the tryptic soy agar medium for sterility testing and kept for incubation at 28 ℃ for 5 days to check the sterility. For isolating microbial endophytes from surface sterilized *Linum* plant samples i.e., leaves, stems, and roots were crushed in autoclaved mortar and pestle to form a uniform mixture. Later the supernatant was separated and diluted in 12.5 mM phosphate buffer (pH 7.1). Different dilutions were then spread on tryptic soy agar and incubated for seven days at 28 ℃ [3]. Individual endophytes were then purified from the mixed culture on the basis of colony characteristics. The isolated endophytes were characterized by gram's staining, biochemical test, and 16s rRNA sequencing.

## 2.2. Biochemical and Molecular Characterization of Endophytes

To identify the isolated endophytic bacteria, morphological and biochemical characterization was performed [19]. The biochemical assays such as catalase, coagulase, IMViC, and urease tests were carried out [19]. Genomic DNA was isolated and was used for amplification of 16S rDNA by employing universal primer: 27F and 1492R. A clear and specific amplicon of 1500 bp was detected following PCR and was purified using QIAGEN QIAquick PCR Purification Kit. Purified samples were taken for sequencing by Applied BiosystemsTM MiniAmpTM Plus Thermal cycler using Big Dye TM Terminator V3.1 kit. BLAST was performed for the 16S rRNA gene sequence using NCBI GenBank database's 'nr' database. The first ten sequences were chosen based on the maximum identity score and Clustal W, a multiple alignment software program was employed for aligning the sequences [19].

## 2.3. Screening of Selected Isolate for Plant Growth Promoting Characteristics

### 2.3.1. IAA Production

IAA production by endophytes was determined by method explained by Gordon and Weber [20]. Fresh endophytic cultures (24 hr old) were cultivated in Luria Bertini (LB) broth having 0, 2, and 5 mg/ml L-tryptophan and kept for incubation in dark shaking conditions for 7 days at 28 ± 2 ℃. After incubation, 2 drops of orthophosphoric acid and 4 mL Salkowaski's reagent (50 ml of 35% perchloric acid and 1 ml of 0.5 M $FeCl_3$) in 2:1 ratio was added to the microbial culture. Then it was kept for 30 minutes in dark and presence of pink colour shows synthesis of IAA. The absorbance was measured at 530 nm and the amount of IAA synthesized by each isolate was determined by using standard IAA graph in range of 0.01 to 0.4 g $ml^{-1}$.

### 2.3.2. Siderophore Production

Based on competition for iron between ferric complexes of chrome azurol S (CAS), an indicator dye, and a siderophore synthesized by the microbe, the qualitative determination of siderophore can be performed. On a CAS agar plate, a 50 µl aliquot of an isolated endophyte was spotted in triplicate and kept for incubation for three to four days at 30 °C [21]. Siderophore, which binds iron more firmly, extracts the iron from CAS, and a positive result is shown by the CAS reagent changing from blue to orange in colour [21].

### 2.3.3. Phosphate Solubilisation

The phosphate solubilisation test was performed on pikovskaya media. 50 µl aliquot of the isolated endophyte were inoculated on pikovskaya agar plate and kept for incubation at 28 ºC for 48–78 hours, clear zone observed around the culture shows phosphate solubilisation [22, 3].

### 2.3.4 Ammonia Production

The capability of endophytes to synthesize ammonia was determined by method discussed by Marques et al. [23]. Isolated endophytes were inoculated in peptone water and grown for 48 h at 28 °C. Fifty microliter of nesseler's reagent was mixed in the culture supernatant and the change in colour was observed. A yellow colour in the culture depicts ammonia production whereas the intensity of colour indicates the quantity of ammonia synthesized by the endophytes. The quantitative determination of ammonia produced by each isolate was assessed from standard plot of ammonium sulphate solution (0.1–5.0 µmol $ml^{-1}$).

## 2.4. Determination of the Extracellular Enzymatic Activity of Bacterial Endophytes

### 2.4.1. Cellulase Activity

Cellulase synthesis by endophytes were determined by inoculating the culture on M9 MS medium having (g $l^{-1}$) $Na_2HPO_4$ (33.9), $KH_2PO_4$ (15), NaCl (2.5), $NH_4Cl$ (5), agar (15) supplemented with carboxy methyl cellulose (10) and yeast extract (1.2). The culture was incubated for 8 days at 28 °C, after which the plates were flooded with 1 ml Gram's iodine production of blue coloured complex with un-hydrolysed cellulose so that a distinct, clear zone around the cellulase producing colonies can be observed after 3–5 min.

### 2.4.2. Amylase Activity

The amylase activity of endophytes was determined inoculating the culture on LB media containing 1.5% (w/v) starch and kept for incubation at 28 ºC for 48 h. After that, the plates were flooded with Lugol's iodine. A clear zone is formed around amylase producing microorganisms.

### 2.4.3. Protease activity

Protease activity by endophytes was determined by inoculating the culture on skim milk agar medium having (g $l^{-1}$) casein (5), skim milk powder (28) yeast extract (2.5), glucose (1), and agar (15). The plates were kept for incubation at 28°C for 48 hrs and protease activity was depicted by the clear zones formed around the inoculated culture [24].

### 2.4.4. Lipase Activity

Lipase activity of the endophytes was assessed y inoculating in tributyrin agar medium containing (g $l^{-1}$): peptone (5), yeast extract (3), agar (15) and 10ml tributyrin. The plates were kept for incubation at 28ºC for 48 hours and clear zone around the bacterial growth was checked. The clear zone indicates lipase activity, where the enzyme has hydrolysed the tributyrin, causing a zone of clearance in the otherwise opaque medium.

### 2.4.5. Esterase Activity

LB media containing 1.0% tributyrin (v/v) were inoculated with isolated bacterial endophytes, and kept for incubation at 30 ºC for 48 hours. The plates were then flooded with solution with Fast Blue RR salt in 0.1 M phosphate buffer (pH 7.0). The development of a purple to dark blue colour around the inoculated culture are indicative for lipase production.

### 2.4.6. Pectinase Activity

The endophytes were assessed for pectinase activity by spot inoculating in Minimal Salt (MS) medium having pectin (1% w/v). The MS medium consisted of g $l^{-1}$ $KH_2PO_4$ (1.36), $Na_2HPO_4$ (2.13), $MgSO_4.7H_2O$ (0.2) and trace elements. After 5 days of incubation at 28 °C, bacterial colonies were flooded with Congo red (0.12%). Positive bacterial isolates formed a clear halo around the colonies [25].

# 3. Results

## 3.1. Isolation of Endophytic Bacteria

The *Linum usitatissimum* plants were obtained during summer season. The soil characters were loamy soil with a pH range of 6.8–7.2. Prior to collection, no chemical fertilizers or pesticides were used to the field for at minimum three months, ensuring a relatively undisturbed environment. A total of twelve endophytic bacterial strains were successfully isolated from the different parts such as leaves, stem, and root of *Linum usitatissimum* plant. This indicates the rich diversity and abundance of endophytic bacterial strains harbouring within various part of the *Linum usitatissimum* plant. The occurrence of different endophytes in plant tissues indicates a well-established symbiotic

interaction amongst the Linum plant and its internal microbiome. The isolated bacterial strains were characterized on the basis of colony morphology (shape, size, colour, margin, elevation) and biochemical characterization **(Table 1**, **Figure 1)**. Amongst the twelve isolates, nine were gram-positive and three were gram-negative suggesting a dominance of gram-positive bacteria within the plant tissues.

Biochemical profiling such as positive catalase activity indicated the capability of these strains to tolerate oxidative stress. Coagulase activity present in seven isolates, suggests potential virulence or biofilm-forming ability **(Figure 2)**. Moreover, seven strains were urease-positive, suggesting their capability to hydrolyse urea into ammonia.

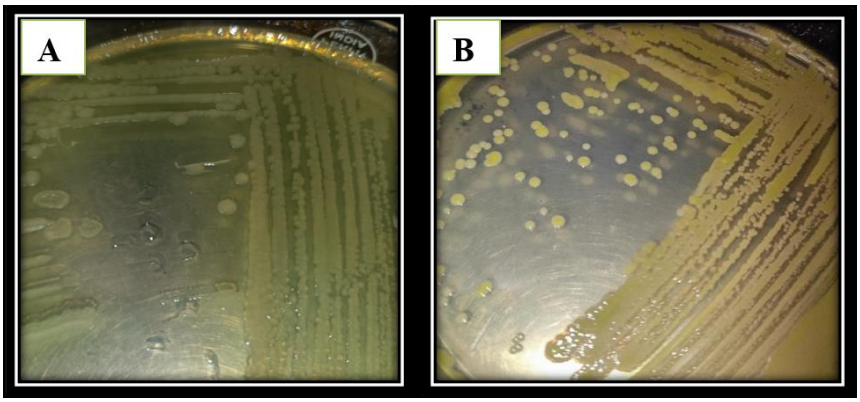


**Figure 1.** Culture morphology of endophytic bacterial isolates on Tryptic soya agar medium; (**A**): Culture morphology of ESL 1; (**B**): Culture morphology of and ESL 2.

**Table 1.** Biochemical characterization of the isolates

| S.no. | Isolated bacteria | Gram's stain | Indole | MR | VP | Citrate | Catalase | Coagulase | Oxidase | Urease |
|---|---|---|---|---|---|---|---|---|---|---|
| 1. | ESL1 | Pink | - | - | - | + | + | + | + | + |
| 2. | ESL2 | Purple | - | + | - | - | + | + | + | + |
| 3. | ESL3 | Purple | - | - | + | + | + | + | + | + |
| 4. | ESL4 | Purple | - | + | + | + | + | + | + | - |
| 5. | ESL5 | Pink | + | + | - | - | + | - | - | + |
| 6. | ESL6 | Purple | - | - | + | + | + | + | + | + |
| 7. | ESL7 | Purple | + | + | - | _ | + | - | + | - |
| 8. | ESL8 | Pink | - | _- | + | + | - | - | + | - |
| 9. | ESL9 | Purple | + | - | - | + | + | - | - | + |
| 10. | ESL10 | Purple | + | - | + | + | - | + | + | - |
| 11. | ESL11 | Purple | - | - | + | - | + | - | - | + |
| 12. | ESL12 | Purple | - | + | + | - | - | + | - | - |

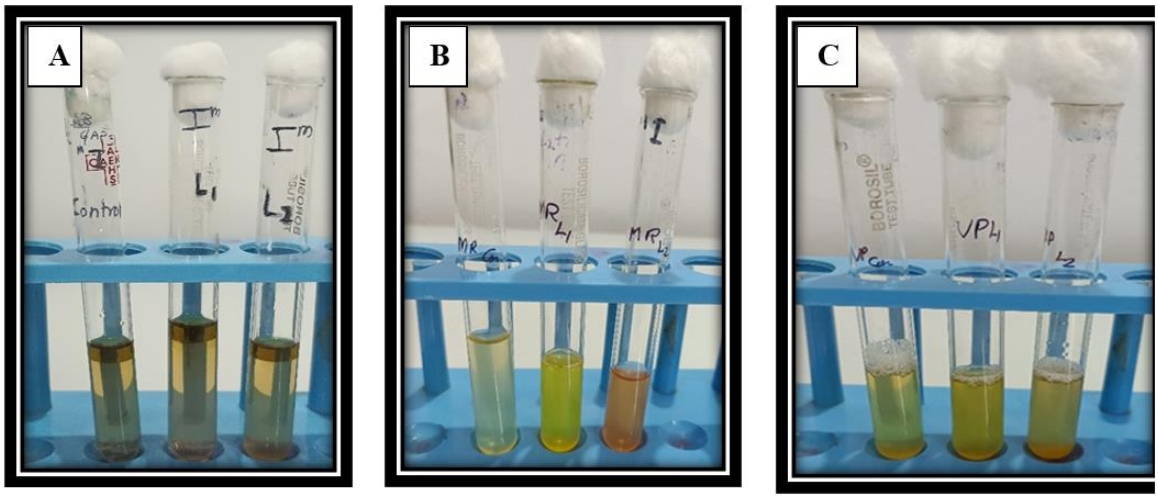


**Figure 2.** *Cont.*

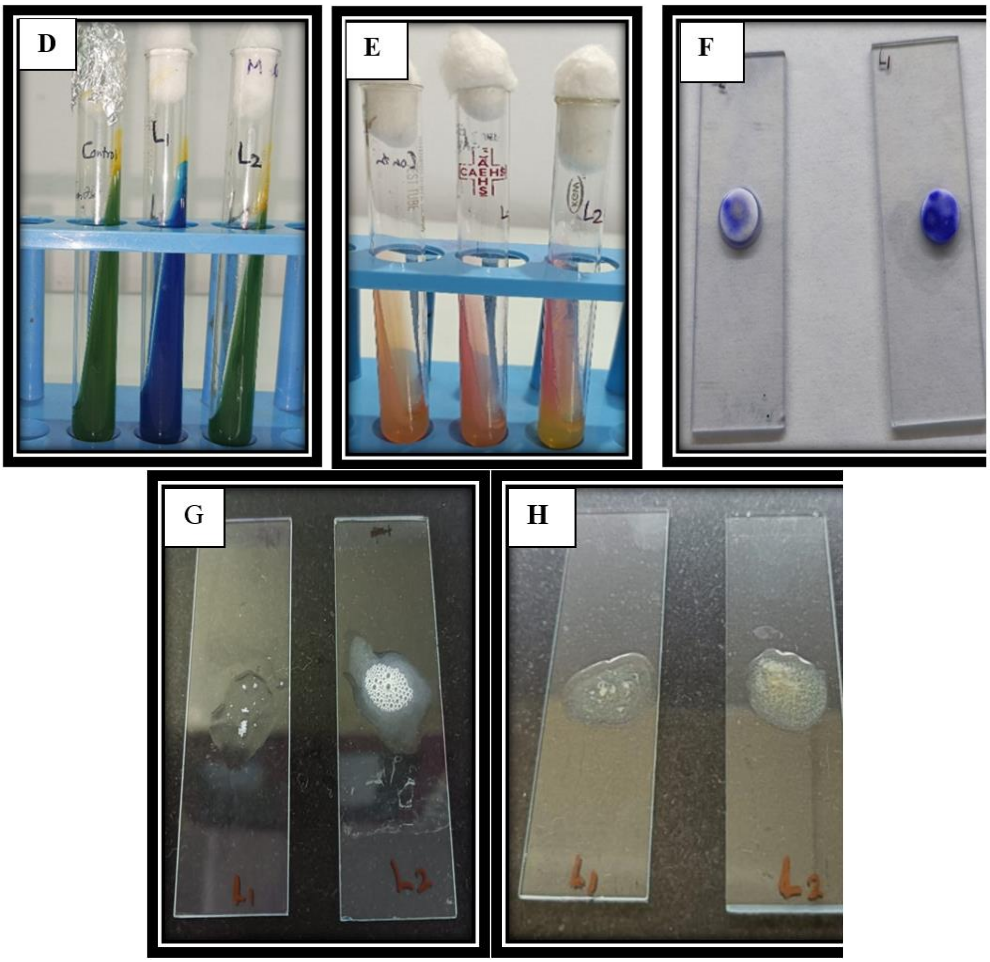


**Figure 2.** Biochemical profiling of endophytes ESL1 & ESL2; (**A**): Indole production by ESL 1 & ESL2; (**B**): Methyl Red Test of ESL 1 & ESL2; (**C**): Voges Proskauer Test of ESL 1 & ESL2; (**D**): Citrate Solubilization by ESL 1 & ESL2; (E): Urease Test of ESL 1 & ESL2; (F): Oxidase Test of ESL 1 & ESL2; (**G**): Coagulase Test of ESL 1 & ESL2; (**H**): Catalase Test of ESL 1 & ESL2.

These findings highlight the biochemical and physiological diversity amongst the isolated strains. All the experiments, consisting of microbial isolation and biochemical analysis, were performed in sterile laboratory conditions. The microbial isolates were cultivated at $28 \pm 2$ °C for 24–48 hours on nutrient-rich agar media and optimized for endophyte growth.

Screening for Plant Growth Promoting Trait:

The results of this study highlight the variability in plant growth promoting capabilities of endophytic bacterial strains. ESL1, ESL2 and ESL8 demonstrated a great potential to improve root development and overall plant growth by synthesizing 11.5 µg/ml, 12.1 µg/ml and 6.3 µg/ml of indole-3-acetic acid (IAA) respectively. IAA is a vital phyto-hormone for plant cell elongation and root differentiation, demonstrating that these endophytes can significantly support plant growth regulation. Furthermore, six strains solubilize phosphate highlighting their significance in increasing phosphorus availability to plants. The high phosphate solubilisation ability of the ESL1 isolate (196 µg/ml) and ESL2 (209.4 µg/ml) suggests its strong potential to improve phosphorus availability in soils, especially in sandy or nutrient-deficient environments where phosphorus leaching is common. By transforming insoluble forms of phosphate into bioavailable forms, ESL1 and ESL2 can assist in mitigating phosphorus losses, thus decreasing the nutrient runoff into nearby water bodies and minimizing the eutrophication of aquatic ecosystems. Additionally, ESL1, ESL2, ESL8, ESL11 produced significant amount of siderophore, underscoring their function in facilitating iron acquisition, a vital micronutrient often limited in bioavailability, generally in calcareous and degraded soils. The synthesis of siderophores by ESL1 and ESL2 demonstrates an increased capability to chelate and mobilize iron in iron-deficient soils. This not only supports optimum plant growth and development but also contributes to effective nutrient cycling, especially in degraded or heavily weathered soils [3]. Notably, none of the strains produced any HCN, indicating that these endophytic bacteria could stimulate plant development without the possible phytotoxic consequences of HCN **(Figure 3)**. The fact that all strains produce ammonia suggests a

characteristic in common that may help increase the availability of nitrogen in the plant rhizosphere. Moreover, the ammonia production observed in ESL9 and ESL5 highlights their function in biological nitrogen turnover. This microbial-mediated nitrogen input can minimize the reliance on synthetic nitrogen fertilizers, lowering the agricultural carbon footprint, and promoting eco-friendly and sustainable nutrient management [5].

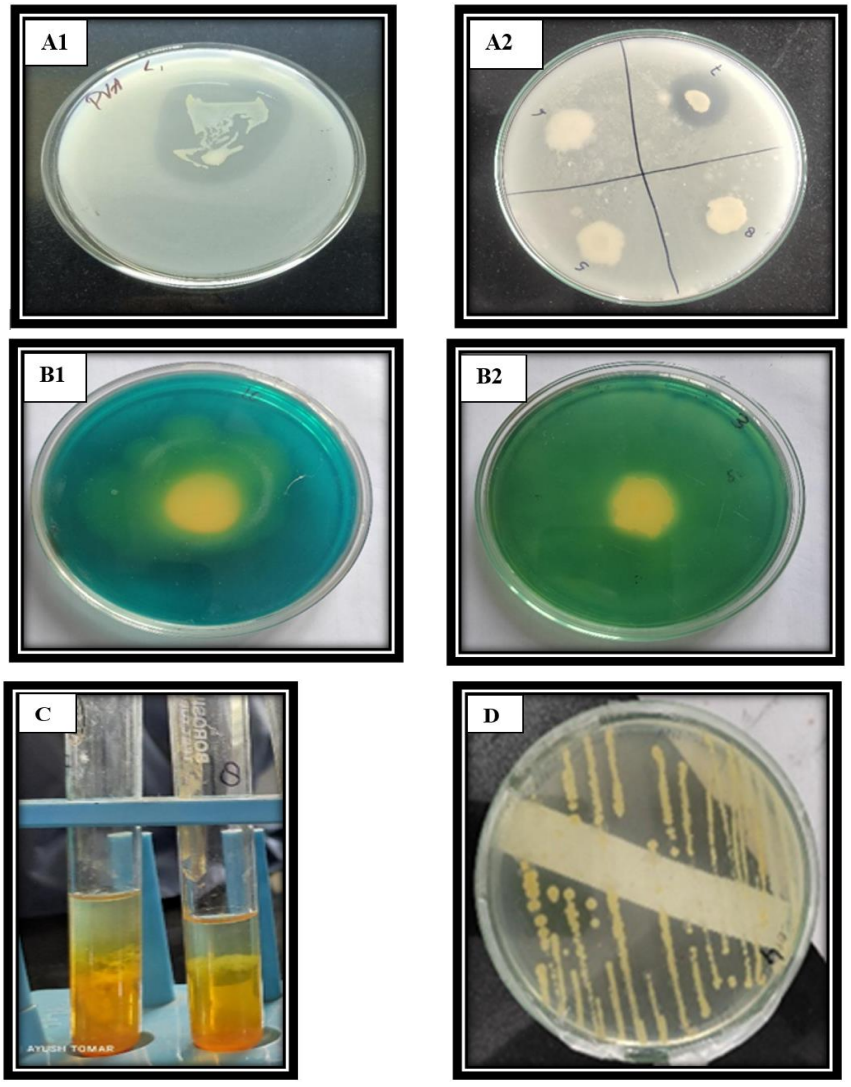


**Figure 3.** Plant growth promoting activity of isolated endophytic bacteria ESL1 and ESL2; (**A1**): Phosphate solubilisation by ESL1; (**A2**): Phosphate solubilisation by ESL2; (**B1**): Siderophore production by ES1; (**B2**): Siderophore production by ES2; (**C**): Ammonia production by ESL1 & ESL2; (**D**): HCN production by ESL1.

Thus, these plant growth-promoting traits demonstrate the ecological significance of these endophytes in improving soil quality, fertility, nutrient efficiency, and environmental protection. Out of all isolated bacterial strains, two endophytic bacteria (ESL1 and ESL2) showed the most prominent plant growth promoter activity and were selected for further studies (**Table 2**).

Extracellular Enzymatic Activity of Isolated Endophytes:

The enzymatic profiling of the twelve isolated endophytic bacterial strains demonstrates a wide range of abilities, with several strains demonstrating a great potential for biotechnological applications (**Table 3**). The enzyme and plant growth-promoting assays were conducted in controlled laboratory conditions while maintaining temperature, humidity, and air parameters suitable for microbial activity. These conditions ensured the natural expression of microbial traits and reduced stress-induced variability. Notably, ESL2 produced five of the six examined enzymes, demonstrating its adaptability in a variety of processes. This broad enzyme activity suggests its strong metabolic adaptability and role in organic matter decomposition, nutrient cycling, and plant growth promotion. Significant enzymatic activity was also demonstrated by ESL1, especially in the synthesis of lipase, amylase, protease, and pectinase. Conversely, other strains such as ESL4, ESL6, ESL9, ESL10 and ESL12 exhibited

reduced or absent enzymatic activity, which could potentially impact their suitability for particular uses. For instance, ESL10 displayed protease and lipase activity, indicating potential function in nitrogen turnover and lipid degradation, whereas ESL8 showed lipase and pectinase production, reflecting role in carbon cycling and root colonization. In contrast, endophytes such as ESL7 and ESL5 exhibited minimal enzymatic activity, limiting their employment in nutrient cycling or rhizospheric interactions. These results imply that depending on their enzyme profiles, specific strains might be given priority for more study and improvement (**Figure 4**).

**Table 2.** Plant growth promoting activity of endophytic bacteria.

| S.No. | Endophytic Bacteria | IAA (µg ml$^{-1}$) | Siderophore (%) | P Solubilisation (µg ml$^{-1}$) | Ammonia (µmol ml$^{-1}$) |
|---|---|---|---|---|---|
| 1. | ESL1 | 11.5±0.3 | 71.4±2.5 | 196.2±2.9 | 2.4±0.1 |
| 2. | ESL2 | 12.1±0.2 | 68.7±1.6 | 209.4±3.8 | 1.6±0.07 |
| 3. | ESL3 | - | - | - | 3.2±0.4 |
| 4. | ESL4 | - | - | 182.4±2.5 | 2.3±0.2 |
| 5. | ESL5 | - | - | + | 3.5±0.2 |
| 6. | ESL6 | - | - | - | 0.9±0.003 |
| 7. | ESL7 | - | - | - | 2.6±0.2 |
| 8. | ESL8 | 6.3±0.3 | 29.2±0.9 | - | 1.3±0.02 |
| 9. | ESL9 | - | - | 125.6±2.1 | 3.9±0.5 |
| 10. | ESL10 | - | - | - | 3.1±0.4 |
| 11. | ESL11 | - | 41.5±1.3 | - | 0.4±0.002 |
| 12. | ESL12 | - | - | 148.2±2.6 | 1.7±0.02 |

**Table 3.** Extracellular enzymatic activity of endophytic bacteria.

| S.No. | Isolated Bacterial Strains | Cellulase | Amylase | Protease | Lipase | Esterase | Pectinase |
|---|---|---|---|---|---|---|---|
| 1. | ESL1 | | | + | + | | + |
| 2. | ESL2 | + | + | + | + | + | |
| 3. | ESL3 | | | + | | | |
| 4. | ESL4 | + | + | | | | |
| 5. | ESL5 | | | | | | + |
| 6. | ESL6 | | + | | | | |
| 7. | ESL7 | | | | | | |
| 8. | ESL8 | | | | + | | + |
| 9. | ESL9 | + | | | | | |
| 10. | ESL10 | | | + | + | | |
| 11. | ESL11 | | | | + | | |
| 12. | ESL12 | | | | | + | |

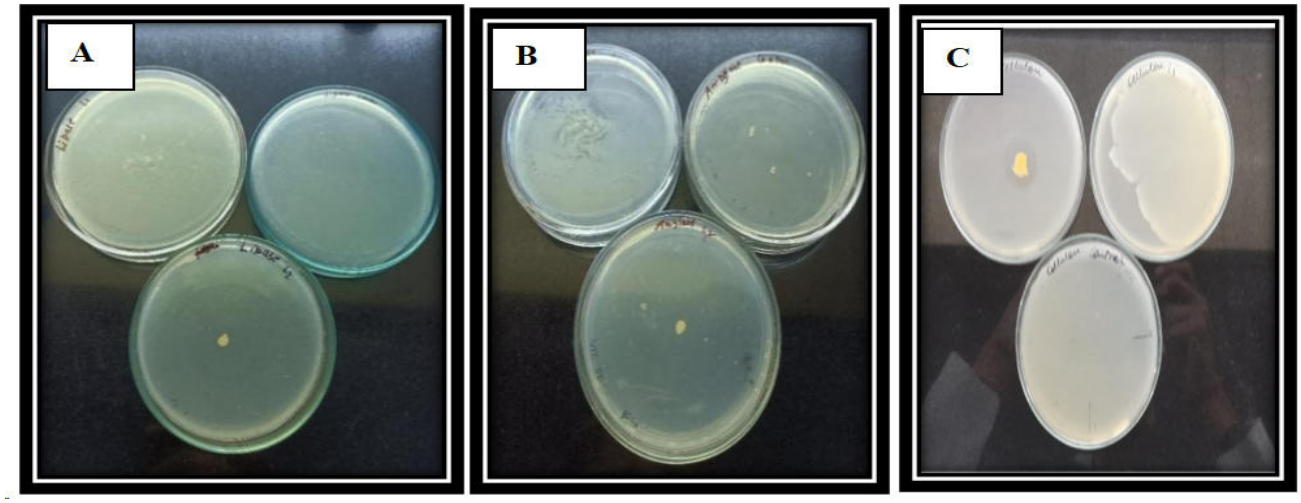


**Figure 4.** *Cont.*

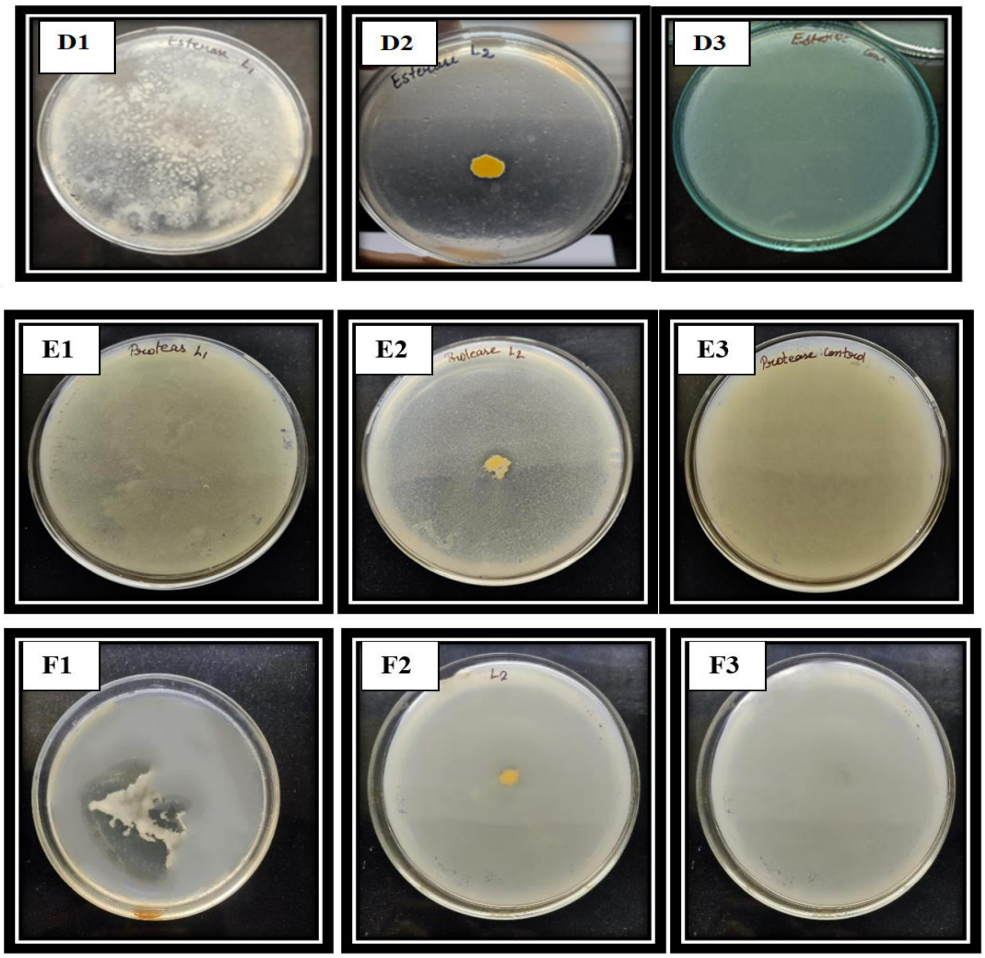


**Figure 4.** Enzymatic activity of isolated endophytic bacteria; (**A**) Lipase activity; (**B**) Amylase activity; (**C**) Cellulase activity; (**D**) Esterase activity; (**E**) Protease activity; (**F**) Pectinase activity.

The production of different extracellular enzymes by ESL1 and ESL2 support their role in the organic matter decomposition in the rhizosphere. This assists in nutrient cycling and improves soil organic carbon dynamics and soil health. Lipase and protease support cycling of organic nitrogen and lipid compounds improve soil nutrient availability and also assist in bioremediation of contaminated soils [6]. Amylase and esterase assist in starch and ester hydrolysis, connecting microbial activity to broader biochemical pathways. Cellulase and pectinase are vital for breakdown of plant-derived polymers and promote carbon turnover, enhancing soil organic matter formation [6]. These traits not only help in nutrient cycling but also improve soil organic carbon dynamics, thereby improving soil health and fertility [5]. Extracellular enzyme contribute towards nutrient cycling and stress mitigation, supporting ecological resilience and agro-ecosystem sustainability. Collectively, these results support the role of ESL1 and ESL in promoting agro-ecosystem sustainability through enhanced enzymatic activity. Prioritizing these endophytes for additional functional analysis, formulation, or field trials can support the emergence of efficient bio-inoculants aimed at sustainable agriculture and environmental restoration.

Phylogenetic Characterization of Bacterial Endophytes:

The phylogenetic identification of isolates ESL1 and ESL2 was carried out based on their 16S rRNA gene sequences, a widely employed molecular marker for microbial taxonomy and evolutionary analysis. Sequence alignment and phylogenetic analysis revealed that endophytic isolate ESL1 showed high sequence similarity to *Pseudomonas* sp. strain JL-1, a bacterium known for its metabolic versatility and environmental adaptability. *Pseudomonas* sp. inhabits diverse ecological niches, and possesses plant growth-promoting activities including phosphate solubilisation, siderophore production, and bio-control activity. ESL1 also demonstrates similar functional attributes valuable for application in different agro-ecosystem and environmental remediation. On the other hand, ESL 2 was closely related to *Staphylococcus sciuri*, a species typically found in soil, animals, and environmental niches and is known for its ability to acquire resistance to various antibiotics. The phylogenetic analysis of these isolates provides insights into their evolutionary relationships and potential ecological roles (**Figures 5** and **6**).

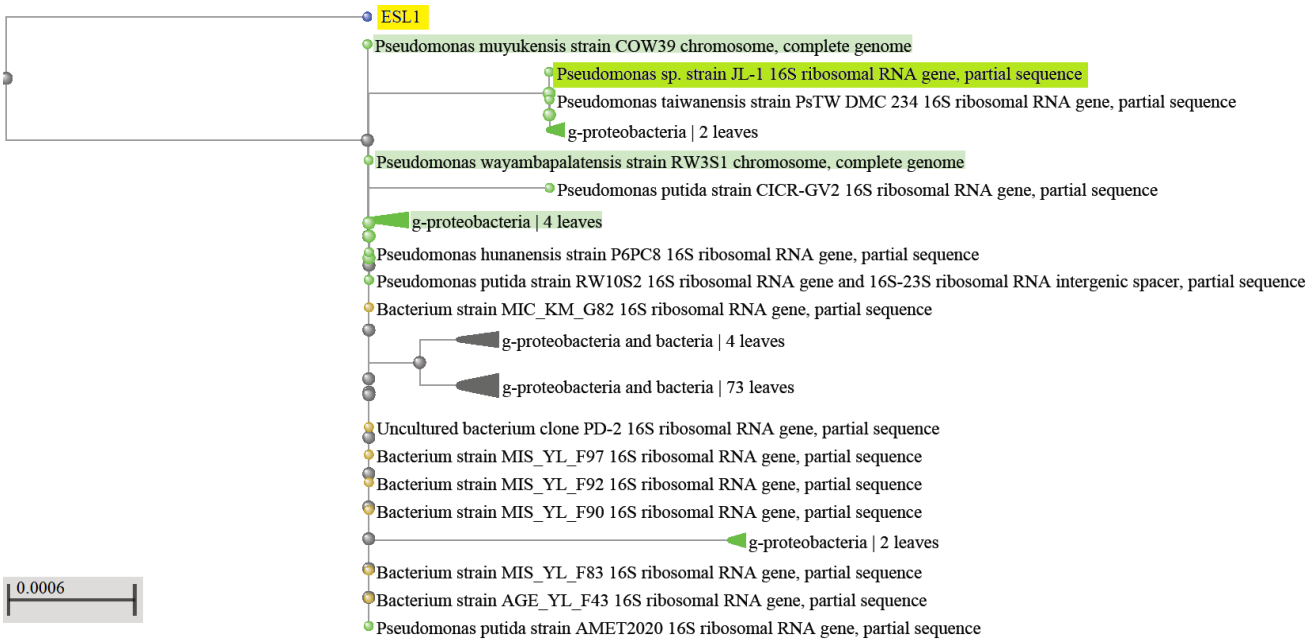


**Figure 5.** Phylogenetic analysis of ESL1.

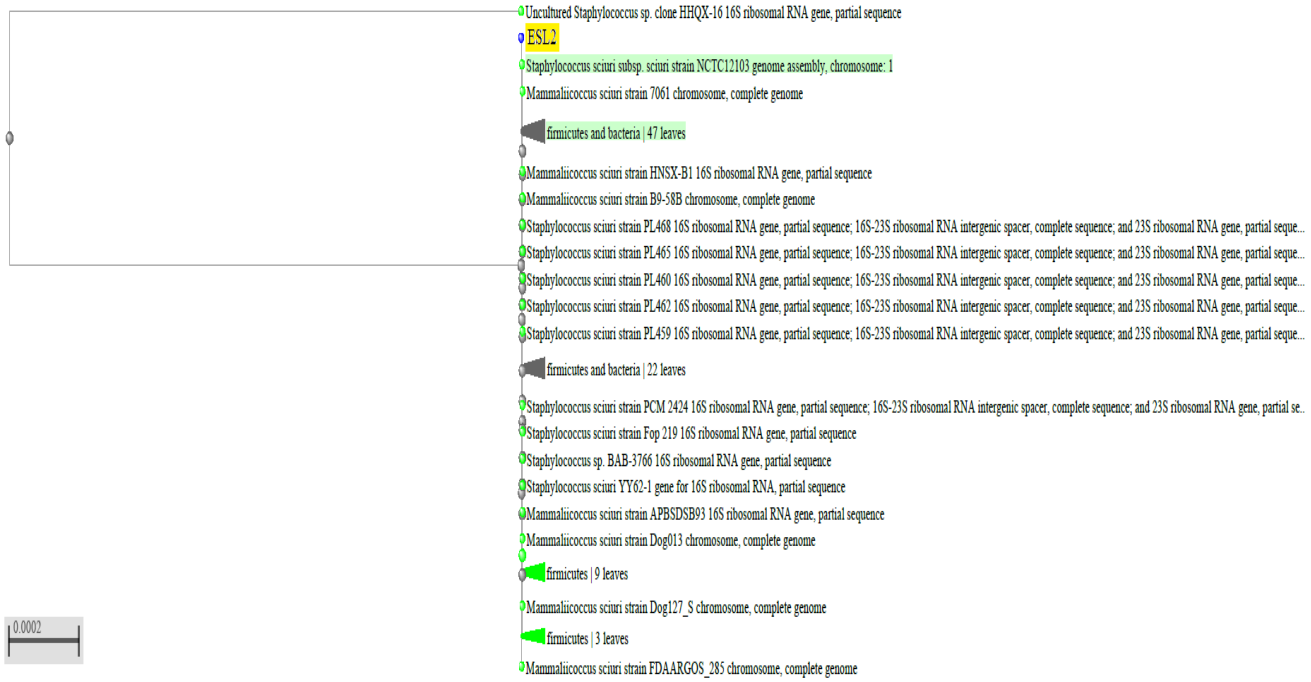


**Figure 6.** Phylogenetic analysis of ESL2.

# 4. Discussion

Endophytic microbes have been demonstrated as a group of beneficial free-living microbes which show symbiotic association with plant tissues. Endophytic bacteria probably have closer interactions with their host than phyllosphere and rhizosphere bacteria. Through direct or indirect mechanisms, endophytic bacteria improve plant health. Twelve endophytic bacterial strains were isolated and identified from the *Linum* plant during this study work. Endophytic microbial strains have been isolated and identified from desert plants, Linum, and wheat [3,6,8]. The nutritional and therapeutic qualities of the *Linum* plant are well-established. The ESL1 and ESL2 strains of endophytic bacteria have more promising characteristics that promote plant growth when compared to other strains. The bacterial strains were found to exhibit various plant growth promoting activities, such as producing ammonia and IAA, siderophore, ammonia, Phosphate solubilisation and producing extracellular enzymes. Bacterial strain producing ammonia and IAA-perform important role in endophytes by enhancing plant growth parameters through $N_2$ availability,

root development by auxin, nutrient uptake and elevate stress or increase stress tolerance [26–30]. Siderophores help to sequester iron and promote plant growth, suppress the surrounding pathogen, and increase nutrient availability, which improves plant stress tolerance power. Endophytes, having the characteristics of Ammonia- and phosphate production, help plant growth and yield by making available nitrogen for them. While phosphate solubilizing bacteria aid in plant nutrient uptake and enhance stress resilience [31–35]. The absence of HCN production further supports their ecological compatibility by mitigating the risks associated with phyto-toxicity. These functional traits demonstrate ESL1 and ESL2 as ecologically important inoculants which assist in nutrient cycling, improving plant resilience under environmental stress, and contributing to the long-term sustainability and stability of agro-ecosystems.

Bacterial endophytes produce many enzymes, including cellulase, pectinase, xylanase, amylase, and gelatinase [36, 37]. Microorganisms can enter plant tissues and form a symbiotic connection with their host plants through the use of cellulolytic and pectinolytic activities. According to Garg et al. [38], *Bacillus* spp. exhibited strong proteolytic and cellulose hydrolysing activity. Similarly, several endophytic strains of *Bacillus* were proven to be potent makers of cellulase and pectinase. Bacterial cellulase, pectinase, xylanase, amylase, and gelatinase are indispensible in endophytic interactions and play crucial role in promoting plant development, nutrient acquisition, and stress tolerance. These hydrolytic enzymes break down complicated plant polymers, thereby increasing the bioavailability of nutrients for the microbial population as well as the host plant. Endophytic bacteria producing cellulase and xylanase help to break down cellulose and hemicellulose and improve carbon cycling and root colonization. Pectinase helps plant cell walls to become more flexible, therefore allowing bacterial access and endophytic development. Bacterial amylase breaks down the starch into their simple monomers and offering easily accessible sugars that support microbial survival and plant metabolism. Protein breakdown by gelatinase increases nitrogen cycling and improves plant health. These enzymatic activities taken together not only help plants growth and withstand but also create a mutualistic relationship between endophytes and their host, therefore promoting a dynamic and sustained plant-microbe interaction [39–42]. These enzymes facilitate the entry of microorganisms into plant tissues, forming a symbiotic relationship. These enzyme-producing endophytes can function as key ecological components in sustainable agriculture practices by improving soil functionality, plant-microbe interactions, and minimizing dependence on chemical fertilizers. Genetic recombination amongst the endophytic microbes and their host plants during evolution may have led to the evolution of enzyme synthesis and control. Bhutani et al. [31] assessed the production of hydrolytic enzymes by endophytes obtained from Pigeon pea and Mung bean. Nine isolates was reported to synthesize pectinase, cellulase, protease, and amylase. ARDRA profiling and 16S rDNA sequencing demonstrated that the isolates belonged to Bacillus species. With the exception of nodulation, these isolates remarkably improve plant growth and displayed plant growth-promoting attributes [31]. 52 endophytic fungal isolates were reported from five epiphytic orchid species [37]. The isolates synthesized lipase, cellulase, pectinase, protease, and amylase [37]. The ability of sixty endophytic strain obtained from Ethiopian pepper plants to inhibit *Phytophthora capsici* and synthesize hydrolytic enzymes was assessed [38]. These isolates demonstrated their potential to function as bio-control agents against *P. capsici* by synthesizing enzymes including lipase, chitinase, cellulase, and protease [38]. Various industrial sectors employ microbial enzymes with high catalytic efficiency since they are more affordable, stable, and can be produced by fermentation in large quantities.

Khan et al. [6] evaluated the impact of different endophytes (PsJN, MN17, and MW4C), applied individually and as a consortium as seed and foliar inoculation on Linum plant growth and development. The results indicated that MW4C and the bacterial consortium, when applied through seed inoculation, remarkably improved shoot-root biomass, seed yield, and biochemical activities including protein, flavonoids, and phenolic content. This study supports the potentiality of endophytes as efficient bioinoculants to enhance growth, yield, and physiological quality of flaxseed [6]. Inoculating of salinity-stressed Linum plants with endophytic strains *Azospirillum brasilense* and *Pseudomonas geniculata* remarkably improves the plant development, chlorophyll, carotenoid, ascorbic acid, soluble sugar, protein, free proline, potassium and total phenolic content [18]. The treated plants displayed reduced levels of malondialdehyde, sodium, and hydrogen peroxide. Furthermore, antioxidant enzyme activities such as superoxide dismutase, ascorbate peroxidase and peroxidase were increased; implying enhances stress tolerance [18]. This study indicates that endophytes can mitigate the adverse impact of salt stress and stimulate plant development. Al-Amri, [43] aimed to enhance the growth and production of Phaseolus vulgaris L. in different water stress employing biofertilizers, such as arbuscular mycorrhizal fungi and endophytic microbe *Bacillus amyloliquefaciens*. The combined employment of AMF and *Bacillus amyloliquefaciens* significantly improved growth, water-use efficiency, photosynthesis, and yield especially under moderate stress conditions [43]. Moreover, the plants generated seeds having high nutritional content, essential nutrients, vitamins, protein, and fiber, in comparison to

untreated plants [43]. Candida albicans-silver nanoparticles exhibited significant antifungal activity against *Candida glabrata* [44]. The biogenic nanoparticles remarkably decreased the fungal viability and $H^+$-ATPase activity. Naveed et al. [45] identified potential endophytic strains able to improve yield in maize plant and mitigate different stresses. Five different endophytes were isolated from maize roots and were assessed for plant growth-promoting activities. Amongst these strains, *Enterobacter* sp. strain FD17 displayed highest growth-promoting activities and efficient plant colonization. Plant inoculation of *Enterobacter* sp. strain FD17 significantly enhanced maize biomass, and grain yield by up to 39%, and 42%, respectively, in comparison to control plants [45]. The endophyte inoculation also improved photosystem II efficacy and expedited flowering. *Enterobacter* sp. strain FD17 was confirmed to colonize the rhizosphere, roots, and stems efficiently and thus it emerged as a potent bio-inoculant for improving maize performance under natural environments [45].

Microbes stimulate plant development and stress tolerance by different methods: (i) improving their population in the rhizospheric zone, (ii) synthesizing iron chelating molecules such as siderophore for iron acquisition, (iii) mineralizing important nutrients such as NPK, (iv) producing lytic enzymes like cellulases and catalases, (v) producing plant growth hormones such as IAA, cytokinin, and gibberellins, and (vi) synthesizing ACC deaminase, which mitigates reactive oxygen species (ROS) and regulates ethylene levels under stress environments [6]. Endophytes produce different biologically active components which colonize plant tissues and promote root, and shoot development, and modulate plant defence systems [9]. The improved capability plant roots to absorb nutrients from soil can be attributed to improved root function due to associated endophytic microbes [1]. These findings suggest that these bacterial endophytes can be harnessed for sustainable agricultural practices to improve plant health and productivity.

# 5. Conclusion

This present study emphasizes the importance of multifaceted role of endophytic bacteria improving plant development, nutrient uptake, and stress tolerance thus contributing to the resilience and productivity of different agro-ecosystems. Endophytic microbes reside symbiotically in the internal plant tissues and establish intricate interactions with their host plants and providing a range of physiological and biochemical advantages. Two endophytic bacterial strains investigated in this study; ESL1 (*Pseudomonas* sp.) and ESL2 (*Staphylococcus sciuri*) exhibit superior a wide range of plant growth promoting attributes. These consist of ammonia biosynthesis, that functions as a supplementary source of plant nitrogen; IAA production, a plant growth hormone which stimulates root elongation and root formation. Both the endophytes also showed phosphate solubilisation capacity, enabling them to transform insoluble phosphorus to available form which is vital for plant development. Additionally, ESL1 and ESL2 produced siderophore which enables them to chelate iron and assist it's uptake by plant especially in iron limiting conditions. This attribute also confers competitive benefit against pathogenic organisms by minimizing iron availability to them. The synthesis of hydrolytic enzymes, such as cellulases, proteases, and amylases, further underlines the potential of these endophytes to degrade complex organic compounds. This improves nutrient cycling and stimulates microbial colonization by degrading plant cell walls in a controlled manner. These enzymatic activities also help in decaying organic matter in the rhizospheric zone, thereby improving soil health and structure, and supporting a more active and diverse soil microbiome. Through these synergistic activities, the endophytic strain facilitates symbiotic associations with the host plant's internal and external microbiome, promoting homeostasis and resilience against biotic and abiotic stress conditions. The employment of these microbial endophytes in agro-practices represents a promising bio-based solution for minimizing the over dependence on chemical and synthetic fertilizers. The present study estimates that ESL1 and ESL2 have the potential to minimize the chemical fertilizers and pesticides requirement by approximately 30–50%, resulting in low cost production and minimized environmental pollution. Moreover, their employment as bio-inoculants can rejuvenate soil heath, enhance soil microbiome richness, and support long-term sustainability of different agro-ecosystems. The interaction of these endophytes with flax (*Linum usitatissimum*), a crop of both high nutritional and industrial significance, provides an added benefit. As flax is generally grown in marginal soils with minimal inputs, the employment of these beneficial endophytes can substantially improve plant yield and quality, while restoring ecosystem functions in low-input systems.

The results of the study also highlight the ecological and agronomic significance of ESL1 and ESL2 as potential bio-functional agents. Their application aligns with the principles of sustainable agriculture and the United Nations Decade on Ecosystem Restoration, which emphasizes on adoption of nature-based solutions to restore degraded landscapes, combat climate change, and ensure food security. By promoting climate-resilient farming, enhancing plant-soil-microbe interactions, and minimizing environmental impact, flax-associated microbial endophytes present a transformative tool for long-term ecosystem stewardship and the development of a greener,

more sustainable agricultural paradigm.

## Author Contributions

Conceptualization, S.C. and G.B.; Methodology, S.C. and K.M.; Software, A.D. and D.K.; Validation, G.B.; Formal analysis, A.D. and D.K.; Investigation, S.C.; Resources, G.B. and S.G.; Data curation, A.M.; Writing—original draft preparation, G.B.; Writing—review and editing, S.G., S.J., S.G.; Supervision, G.B.; Project administration, S.C. and K.M. All authors have read and agreed to the published version of the manuscript.

## Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

## Institutional Review Board Statement

Not applicable.

## Informed Consent Statement

Not applicable.

## Data Availability Statement

Not applicable.

## Acknowledgment

The authors would like to express their gratitude to Swami Rama Himalayan University, Dehradun, Uttarakhand, India for providing the all the necessary facilities to conduct the experimental work.

## Conflict of Interest

The authors declare no conflict of interest.

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