agriculture

Systematic Review

Bacterial Endophytes and Their Contributions to Alleviating Drought and Salinity Stresses in Wheat: A Systematic Review of Physiological Mechanisms

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Abstract: Drought and salinity stresses significantly threaten global wheat productivity, limiting growth and reducing yields, thus endangering food security worldwide. These stresses disrupt physiological processes, impair photosynthesis, and hinder optimal growth and yield by diminishing water uptake, causing osmotic stress, ion toxicity, and oxidative stress. In response, various mitigation strategies have been explored, including breeding for stress-tolerant cultivars, improved irrigation techniques, and the application of exogenous osmoprotectants and soil amendments. Among these strategies, the emergence of rhizospheric and endophytic growth-promoting microorganisms has attracted significant attention. Therefore, a systematic review was undertaken to illustrate the role of endophytic bacteria in enhancing wheat tolerance to drought and salinity stresses. This review analyzes physiological mechanisms and research trends, identifies gaps, and discusses implications for sustainable agriculture. An analysis of the literature related to endophytic bacteria in wheat was conducted using databases of major publishers from 2004 to 2023. The review explores their mechanisms, such as phytohormone production and stress-responsive gene induction, emphasizing their contribution to plant growth and stress resilience. The current research trends indicate a growing interest in utilizing endophytic bacteria to mitigate these stresses in wheat cultivation, with studies focusing on understanding their physiological responses and interactions with wheat plants. Future research should concentrate on elucidating the role of endophytic bacteria in enhancing host plant tolerance to multiple stressors, as well as aspects like endophytic mechanism of action, endophytic lifestyle, and transmission pathways. Overall, endophytic bacteria offer promising avenues for sustainable agricultural practices, aiding in crop resilience and food security amid environmental challenges.

Keywords: endophytes; abiotic stress; drought; salinity; nitrogen fixation; siderophore production; phosphate solubilization; IAA production

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1. Introduction

Wheat holds great significance as a staple crop worldwide, serving as a primary source of sustenance for a substantial portion of the global population. Its high nutritional value and versatility make it a key component in various diets, particularly in regions heavily reliant on cereal grains [1]. However, wheat productivity faces significant challenges from both abiotic and biotic stresses. Abiotic stresses, such as extreme temperatures, water scarcity, and soil salinity, can significantly impede wheat growth and yield [2–4]. Climate change exacerbates these challenges, leading to unpredictable weather patterns that further threaten productivity. Dryland agriculture involves rainfed crop cultivation in semiarid/arid conditions, relying solely on often scarce and variable rainfall, with Mediterranean systems exemplifying this pattern, emphasizing the crucial role of water management for improved productivity and sustainability [5]. On the biotic front, pests and diseases pose persistent threats, causing substantial losses in wheat crops [6]. Addressing these stressors is crucial for ensuring food security and sustaining global wheat production, highlighting the importance of research and agricultural practices aimed at mitigating these challenges [7].

Over the past few decades, plant breeders have focused on boosting crop productivity, especially enhancing resilience to drought and salinity stresses [8–10]. Advances in breeding genetically adapted varieties have significantly contributed to sustainable crop production [3,8]. However, further exploration of genetic, environmental, and management strategies is necessary to improve productivity and stability of major food and feed resources under elevated environmental stresses [11]. The integration of growth-promoting microorganisms has emerged as a valuable option, harnessing beneficial interactions between plants and specific microbes to promote growth, induce systemic resistance, and enhance nutrient uptake [12].

Deciding between endophytic and rhizospheric microorganisms depends on the desired mode of action. Endophytes offer systemic protection within plant tissues, while rhizospheric microorganisms influence nutrient availability and promote plant health in the root zone [13–15]. Selection should align with specific stressors and plant interaction preferences. Ultimately, an integrated approach combining bacterial and fungal mechanisms, along with endophytic and rhizospheric microorganisms, may offer a comprehensive solution [16–19]. Such an approach acknowledges the multifaceted nature of biotic stresses and aims to leverage the synergistic benefits of diverse microbial communities to enhance crop resilience and productivity [11,16].

Research on endophytic bacteria's role in mitigating drought and salinity in wheat has significantly advanced, yet knowledge gaps persist, notably in understanding specific mechanisms enhancing wheat resilience to these stressors [20]. Identifying these mechanisms at molecular and physiological levels is crucial for effective application. Additionally, comprehensive studies assessing the long-term impacts of endophytic bacteria under varying conditions are necessary [21], as they can inform sustainable strategies for stress management. This paper conducts a systematic analysis of wheat growth and productivity, emphasizing the need for integrated approaches to enhance resilience.

Bacterial endophytes exert noticeable effects as growth promoters, presenting an opportunity to enhance crop productivity. These symbiotic microorganisms inhabit various parts of plants, including flowers, leaves, roots, seeds, and stems [22,23]. Colonization by bacteria occurs at specific stages of plant development, with a potentially stable endophytic bacterial community already established during the seed stage [24]. Utilizing the plant's internal environment, known as the endosphere, these endophytes find a unique niche that shields them from significant alterations in external conditions [25].

This study aims to comprehensively assess how endophytic bacteria contribute to enhancing wheat's resilience to drought and salinity stresses. Objectives include synthesizing existing literature, analyzing physiological mechanisms, evaluating emerging research trends, identifying gaps in understanding, and proposing future research directions. Additionally, we discuss the potential implications of utilizing endophytic bacteria as a sustainable agricultural strategy to enhance crop resilience against environmental challenges, particularly drought and salinity stresses.

2. Materials and Methods

2.1. Data Collection

This systematic review analyzed over 120 studies on the role of endophytic bacteria in host plants. Various research methods were employed to address gaps in knowledge, with a focus on the impact of bacterial endophytes in reducing stress effects. Meta-analyses were conducted to assess their efficacy [26,27].

In addition, systematic analyses were performed on the literature from various publishers, including Wiley, MDPI, Taylor and Francis, and ScienceDirect. These analyses aimed to discern trends in publications related to the keywords under study. Furthermore, a thorough literature search was performed on ISI Web of Science and Google Scholar to gather data exploring the impact of endophytic bacteria on the physiological responses of host plants and their subsequent effects on growth parameters [28,29].

The selection criteria for suitable studies included the following: (1) the host plant being wheat, (2) the inclusion of bacterial inoculation along with a control group without inoculation, and (3) the provision of mean, standard deviation, and the number of replicates for both treatment and control groups. Data were collected for various parameters including grain yield, shoot length, root length, shoot fresh weight, root dry weight, shoot dry weight, root dry weight, proline content, chlorophyll a, chlorophyll b, and total chlorophyll. However, not all growth parameters had sufficient data, so the analysis focused on shoot length, root length, shoot fresh weight, root fresh weight, shoot dry weight, and root dry weight. After thorough searching and screening, the data were analyzed to assess the impact of bacterial endophyte inoculation on wheat [28,29].

2.2. Data Analysis

2.2.1. Systematic Analysis

Systematic studies were employed to analyze connections between research and recent trends across various publishers' databases. This systematic methodology offers a clear and static representation of research trends [30]. Systematic analysis, a well-established form of meta-analytical study and statistical technique, was utilized to examine the breadth and depth of different research areas, facilitating qualitative and quantitative insights into specific topics [31]. This approach has been widely used to evaluate vast amounts of publications across diverse disciplines [32].

Systematic analysis tools were employed across Wiley, MDPI, Taylor and Francis, and ScienceDirect databases in three sequential steps; the search was performed with the whole database each time. The first step involved assessing the frequency of publications on various types of endophytes from 2004 to 2023 using keywords such as "endophytes", "bacterial endophytes", and "fungal endophytes" as shown in Figure 1. Subsequently, the second step focused on analyzing the number of publications across each publisher's database regarding the role of endophytes in host plant stress tolerance from 2004 to 2023. This analysis was conducted using keywords like "endophytes and stress" and "endophytes and biotic stress", among others as shown in Figure 2. Finally, the third step addressed gaps in research articles pertaining to specific types of bacterial endophytes and their mechanisms of action in enhancing physiological responses and growth parameters from 2004 to 2023 as shown in Figure 3. Keywords utilized in this step included "nitrogen-fixing endophytes", "phosphate-solubilizing endophytes", and others, aiming to identify areas warranting further investigation and understanding [33–35].

2.2.2. Descriptive Analysis

The crucial and physiological role of the endophytes that bacterial endophytes play in the host plant was described and measured through the growth parameters. The cited research articles were extracted narratively aligning with the statistical analysis as explained in the Section 2.2.1.

This section focuses on the physiological role of endophytic bacteria and their mechanisms of action in mitigating abiotic stresses and enhancing growth. This section illustrates the contribution of endophytic bacteria to enhancing host plant tolerance to different abiotic stresses.

2.2.3. Statistical Analysis

Statistical analysis was employed to assess the effect of bacterial inoculation on host plant stress tolerance, utilizing data extracted from published research articles. Six parameters (shoot length, root length, shoot fresh weight, root fresh weight, shoot dry weight, and root dry weight) were examined across drought and salinity stresses as compared to no-stress conditions. The performance of bacterial endophytes was evaluated according to the following equation:

$$((\text{Inoculated} - \text{control})/\text{control}) \times 100\%)$$

This equation provides a summary of bacterial endophyte performance in wheat, illustrating the effects of inoculation while disregarding differences. Variables such as plant stage, measurement units (e.g., mg or g), and salinity levels are standardized for analysis. Percentages were initially depicted using box and whisker charts in Microsoft Excel 2016 to visualize changes and variations in growth parameters under major abiotic stresses, with Figure 5a,b representing drought and salinity, respectively. Data of percentages were analyzed using a mixed procedure of SAS OnDemand for Academics (SAS Institute Inc., Cary, NC, USA) according to the following model:

$$Y_{ij} = \mu + \tau_i + \varepsilon_{ij}$$

where Y_{ij} is the observation of dependent variables, μ represents the population mean, t_i is the fixed effect of stresses, and e_{ij} is the residual error.

3. Results and Discussion

3.1. Performance Analysis

Data extracted from databases of various publishers were organized into year intervals ranging from 2004 to 2023, and keywords across platforms. Figure 1 illustrates the total publications over the last two decades, revealing a greater focus on fungal endophytes compared to bacterial counterparts. This preference for studying fungal endophytes over bacteria can be attributed to their rapid growth rates, straightforward propagation methods, observable growth patterns, and distinctive morphological characteristics, as outlined in references [34,35].

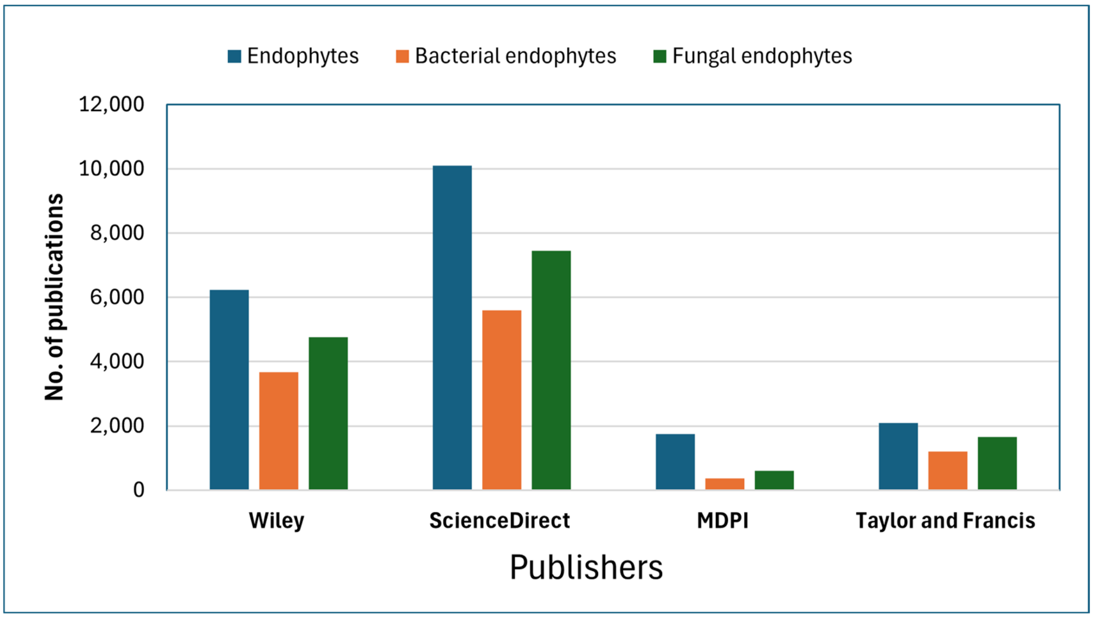

Figure 1. Total publications on different types of endophytes from 2004 to 2023 across multiple publishers.

Over the twenty-year period from 2004 to 2023, each publisher exhibited distinct research focuses based on their total publications. Wiley led with over 6230 publications on endophytes overall, while ScienceDirect had the highest number of papers specifically on bacterial endophytes, totaling around 5600. Conversely, ScienceDirect featured the most publications on fungal endophytes, with approximately 7500 papers. This rapid increase in endophyte-related publications over the past twenty years reflects their significant roles in plant physiology and diversity. Fungal endophytes have attracted significant attention due to their capacity to enhance plant growth and tolerance by secretion of secondary metabolites and enhancing nutrient absorption [36]. This emphasis on fungal endophytes derived from their extensive association with host plants, facilitating the secretion of plant growth-promoting metabolites, including phytohormones, throughout their life cycle [37]. Conversely, bacterial endophytes have received less attention, with limited specific reviews, as shown in Figure 1. Notably, systematic review articles over the past two decades have predominantly focused on fungal endophytes and their commercial applications, as indicated by [38].

The selected publishers discussed in this paper exhibit distinct historical backgrounds, with varying dates of establishment and differing numbers of journals. These differences account for the fluctuations in the number of publications related to the selected keywords, as depicted in Figure 2. Wiley, founded in 1807, and Taylor and Francis, established in 1852, have longstanding histories. In contrast, MDPI was established in 1996, followed by ScienceDirect in 1997. Additionally, these publishers differ in their accessibility to the public, with some being available online.

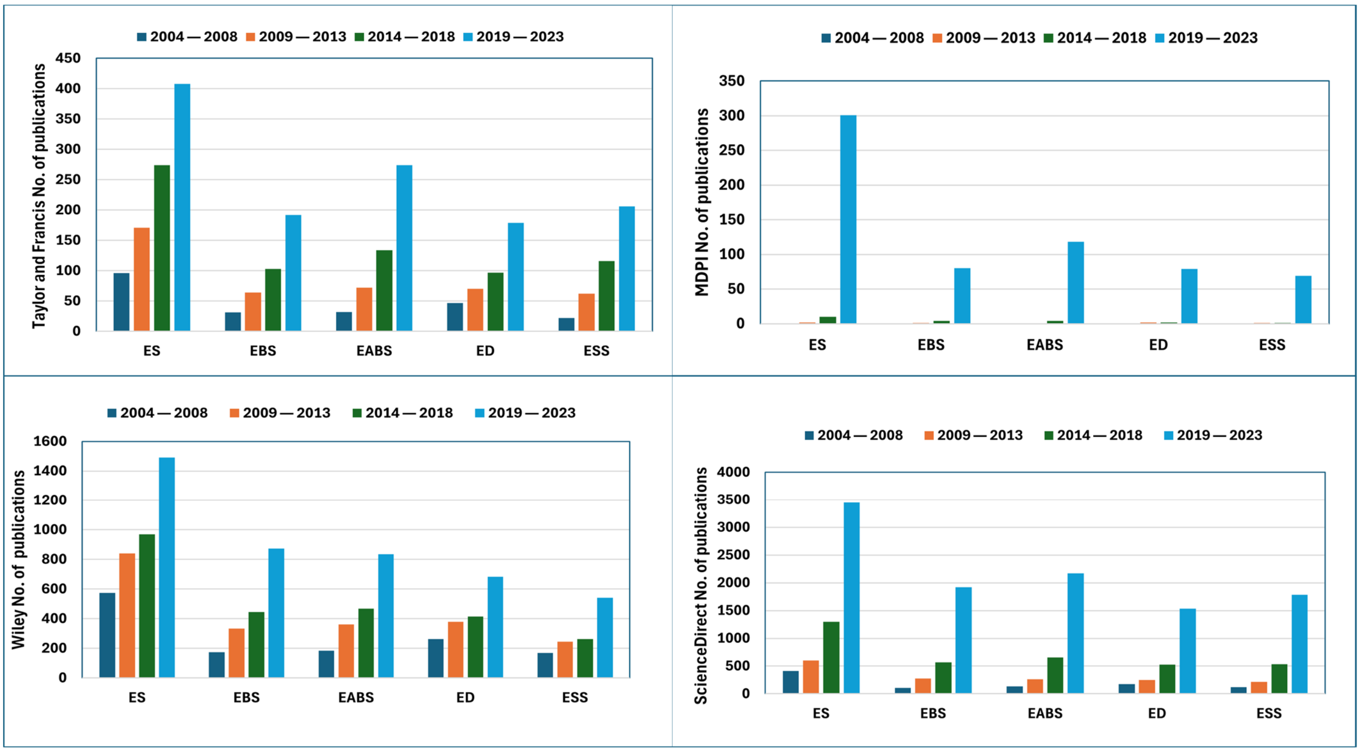

Figure 2. Distribution of endophyte-related publications and their correlation with stress (ES: endophytes and stress, EBS: endophytes and biotic stress, EABS: endophytes and abiotic stress, ED: endophytes and drought, ESS: endophytes and salinity) from 2004 to 2023 across various publishers (MDPI, Wiley, Taylor and Francis, and ScienceDirect).

Figure 2 presents a systematic analysis illustrating the total publications addressing endophytes and their role under various types of stresses. These figures elucidate the evolution of endophytes as a trending research topic from 2019 to 2023 across various publishers' databases. Exploring publishers' websites, including MDPI, Elsevier, Taylor and Francis, and Wiley, provides a comprehensive insight into recent research on endophytic bacteria and their contribution to enhancing plant stress tolerance. Analysis reveals a notable surge in interest in endophytes between 2014 and 2018, with a threefold increase in publications observed between 2019 and 2023, as depicted in Figure 2. Endophytic bacteria employ a multifunctional approach on the host plant, facilitated by the symbiotic relationship between the bacteria and the plant [39,40]. This symbiosis leads to improvements in plant growth, including the stimulation of plant growth regulators' production [41–43] and nutrient acquisition [44]. Furthermore, endophytes play a crucial role in enhancing plant adaptation to abiotic stresses such as drought and salinity by regulating plant hormone signaling [20,43], and mitigating cellular damage caused by low temperatures while augmenting photosynthetic activity in response to cold stress-related metabolism [45].

Figure 3 illustrates the number of publications focusing on specific keywords within the timeframe of the last five years (2019–2023). This figure provides insight into the publications concerning the traits of endophytic bacteria that contribute to the tolerance and mitigation of stress effects in host plants. It reveals variations in publication numbers based on the type of endophytes. The response of endophytes and their mechanism of action relies on the coordination among the microbial community within the plant, a process known as "quorum sensing" [46]. Quorum sensing involves microorganisms interacting with plants based on signals and signal perception mechanisms adopted by both parties [47,48]. Microbes produce sensing signals that trigger intensive action.

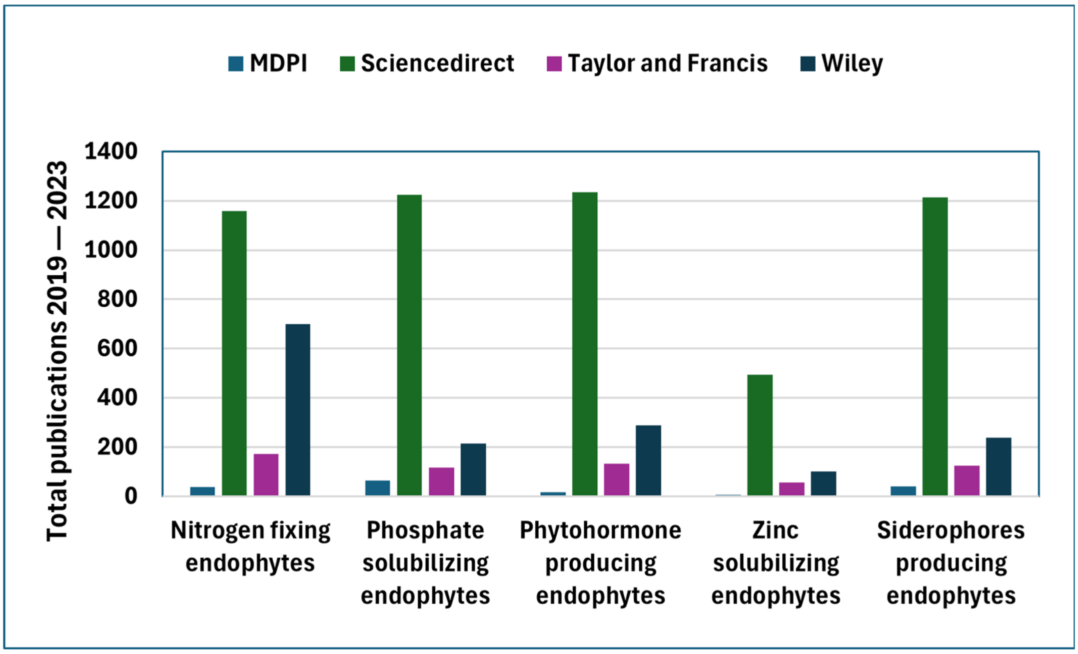

Figure 3. Total publications on the physiological role of endophytic bacteria in publishers' databases from 2019 to 2023.

Publications related to endophyte–micronutrient interactions, particularly those involving zinc-solubilizing endophytes, received relatively less attention, as indicated in Figure 3 The absence of zinc in plants is easily noticeable, affecting crop productivity and nutrition. Zinc-solubilizing bacteria offer a sustainable solution, converting applied inorganic zinc into an accessible form for plant roots [49]. Inoculating zinc-solubilizing bacteria has been shown to enhance plant growth, yield, and nutritional value, serving as bio-inoculants for biofortification [50,51]. *Pseudomonas* sp., a zinc-solubilizing endophytic bacteria, when combined with other zinc-supplying materials, improved wheat grain biofortification. These examples underscore the need for increased research and practical applications of micronutrient-solubilizing endophytic bacteria to enhance crop growth, nutritional value, food security, and environmental sustainability.

3.2. Dynamics of Endophyte–Host Interaction

Bacterial endophytes establish complex interactions with their host plants, influencing various aspects of plant physiology, development, and defense mechanisms. Understanding the dynamics of these interactions is crucial for clarifying their roles in plant health, productivity, and resilience to environmental stresses.

Bacterial endophytes exhibit diverse modes of interaction with their host plants, ranging from mutualistic to commensal and occasionally pathogenic relationships. Many bacterial endophytes are known to promote plant growth and stress tolerance through mechanisms such as nitrogen fixation, phytohormone production, and synthesis of antimicrobial compounds [52]. For example, certain strains of endophytic bacteria belonging to genera like *Rhizobium*, *Azospirillum*, and *Pseudomonas* have been shown to enhance nutrient uptake and improve drought tolerance in various plant species [53,54].

The dynamics of bacterial endophyte–host interactions are influenced by numerous factors, including the specificity of host colonization, environmental conditions, and the genetic makeup of both the host plant and the endophytic bacteria. Some bacterial endophytes exhibit host specificity, preferentially colonizing certain plant species or genotypes, while others display a broader host range [55]. Moreover, environmental factors such as soil composition, moisture levels, and nutrient availability can modulate the abundance and activity of endophytic bacteria within the plant host [56].

Recent advancements in molecular techniques, such as metagenomics and transcriptomics, have provided insights into the diversity and functional capabilities of bacterial endophyte communities associated with different plant species. These studies have revealed the complexity of endophytic microbiomes and their dynamic responses to environmental cues and host physiological changes [57]. Additionally, the advent of high-throughput sequencing technologies has facilitated the identification and characterization of novel bacterial endophytes with potential agricultural and biotechnological applications.

3.2.1. Bacterial Endophyte Entry Mechanisms in Plants

Bacterial endophytes employ various strategies to enter plant tissues, a process crucial for establishing symbiotic relationships with their host plants. The mechanisms through which bacterial endophytes enter plants are diverse and often depend on both the endophyte species and the host plant. Examples of these strategies include the following: (1) Natural plant openings: One common route for bacterial endophytes to enter plants is through natural openings such as stomata, lenticels, or hydathodes. These openings provide direct access to the inner tissues of the plant, allowing bacteria to colonize intercellular spaces or penetrate plant cells [58]. (2) Root colonization: Many bacterial endophytes colonize plants through the roots. They can navigate through the soil, utilizing chemotaxis to move towards plant roots, and subsequently enter root tissues either through cracks and crevices or by actively penetrating the root epidermis [55]. Once inside the roots, bacterial endophytes may spread systemically to other parts of the plant via the vascular system. (3) Seed transmission: Some bacterial endophytes can be vertically transmitted through seeds from one generation of plants to the next. These endophytes reside within the seeds or on the seed coat, allowing them to colonize the emerging seedling upon germination [52]. (4) Infection sites and wound entry: Certain bacterial endophytes use infection sites or wounds on plant surfaces to enter plant tissues. For example, pathogens may exploit natural openings or wounds caused by herbivores, pathogens, or mechanical damage to infect plants and establish endophytic colonization [54].

3.2.2. Reproduction and Transmission of Endophytes in Plant Parts

Bacterial endophytes undergo multiplication and reproduction within plant tissues, contributing to the establishment and maintenance of their populations. The processes of bacterial growth, replication, and dissemination within plant hosts are influenced by numerous factors, including nutrient availability, environmental conditions, and host–plant interactions. Understanding the mechanisms of multiplication and reproduction of bacterial endophytes within plants is essential for clarifying their roles in plant health, growth promotion, and adaptation to environmental stresses.

Multiplication and reproduction undergo multiple steps, including the following:

(1) Colonization and Establishment:

Bacterial endophytes initiate the colonization of plant tissues by adhering to and penetrating the surfaces of roots, stems, or leaves. Once inside the plant, they face the challenge of establishing themselves within the host environment. Endophytes may produce adhesins or exopolysaccharides to facilitate attachment to plant cells and evade the host's immune system [58].

(2) Growth and Multiplication:

Within plant tissues, bacterial endophytes multiply through processes such as binary fission or budding, depending on their specific growth characteristics. Nutrient availability within the plant, including sugars, amino acids, and other organic compounds, supports bacterial growth and proliferation [58]. Bacterial endophytes may also utilize plant-derived compounds or engage in metabolic interactions with the host to obtain essential nutrients [52].

(3) Biofilm Formation:

Bacterial endophytes can form biofilms within plant tissues, consisting of bacterial cells encased in a matrix of extracellular polymeric substances (EPS). Biofilm formation enhances bacterial colonization and persistence within the host, providing protection against environmental stresses and antimicrobial agents [59].

(4) Dissemination:

Bacterial endophytes can disseminate within the plant host via systemic movement through the vascular system or intercellular spaces. Systemic colonization allows endophytes to colonize various plant organs, including roots, stems, leaves, and reproductive structures. Endophytes may also spread locally within plant tissues, colonizing neighboring cells or moving from one tissue to another [58,59].

(5) Seed Transmission:

In cases of vertical transmission, bacterial endophytes can be passed from parent plants to offspring through seeds. Endophytes residing within seeds or on seed coats can colonize the emerging seedlings, ensuring the inheritance of bacterial populations across generations [60].

3.2.3. Mechanisms of Horizontal and Vertical Transmission of Bacterial Endophytes within Plants

Horizontal and vertical transmission are two primary modes through which bacterial endophytes are transmitted between plants (Figure 4). Understanding these transmission pathways is essential for understanding the dynamics of bacterial endophyte populations within plant communities and their persistence across generations.

Horizontal transmission refers to the transfer of bacterial endophytes between plants within the same generation. The evidence suggests that horizontal transmission is the predominant mode by which bacterial endophytes spread among plant populations, facilitated by their ability to adapt to and colonize various host plants in different environments [58,61–63].

Several mechanisms facilitate the horizontal transmission of bacterial endophytes. The soil, acting as a reservoir for microbial communities, plays a crucial role in the colonization of seeds and roots by endophytic bacteria. Soil serves as the primary source of inoculum for endophytes, with recent studies indicating that the epi- and endophytic bacteria associated with plants often share taxa with soil communities, suggesting a soil origin for both above- and belowground microbiota [64,65]. Bacterial endophytes can be transferred horizontally between plants via soil-mediated routes. For example, endophytes released from decomposing plant material or root exudates can colonize nearby plants [15] Endophytic colonization begins in the spermosphere, the zone surrounding germinating seeds, where seeds exudate compounds that shape the surrounding bacterial composition, potentially fostering beneficial interactions [66–68]. Subsequently, colonization progresses to the rhizosphere, the soil surrounding roots, which is rich in bacteria promoting plant growth, nutrient acquisition, and defense against pathogens and abiotic stresses [69,70]. Plants actively recruit and modulate rhizosphere communities through root exudates, influencing the selection of specific bacterial consortia [71,72]. The rhizosphere exerts a direct influence on bacterial colonization of the rhizoplane (root surface) and the interior as endophytes, with some bacteria showing specialized colonization patterns within different root structures [73]. This two-step model of endophytic entry via the rhizoplane is supported by microscopy studies demonstrating chronological colonization starting from root surfaces and progressing into internal tissues, ultimately colonizing various plant parts, though not all root bacteria colonize the entire plant [58,74].

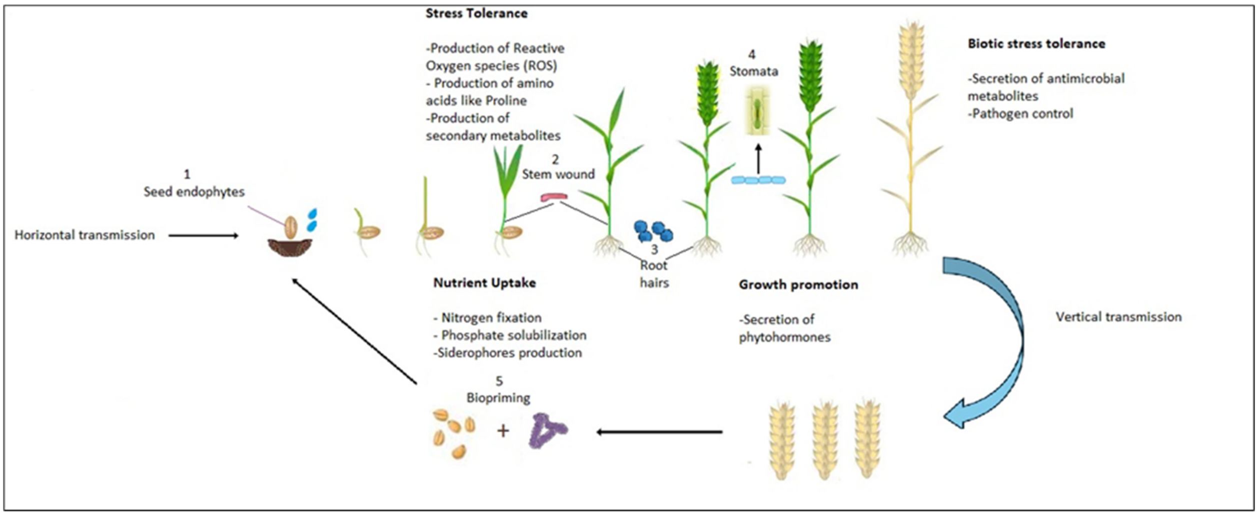

Figure 4. Endophyte–host interaction dynamics.

Horizontal Transmission

Endophytic bacteria, apart from infiltrating roots via soil, also traverse aerial tissues such as stems, leaves, flowers, and fruits. Potential bacterial sources encompass the atmosphere, rain, soil, and carriers like pollinators or other insects. While the stomatal route of entry into leaves and stems has been primarily studied for pathogens, evidence suggests it may also serve as an entry point for endophytes. The overlap in community composition between leaf surfaces and interiors indicates that leaves' exterior might represent the initial colonization site for certain foliar endophytes, underscoring the importance of understanding transmission and dispersal routes of plant surface-dwelling bacteria [75].

Aerial surfaces of plants constitute the phyllosphere, one of the most widespread microbial habitats, where bacteria can originate from within the plant or be deposited via bioaerosols [76]. Bioaerosols, comprising bacteria, fungi, viruses, or pollen, contribute significantly to bacterial dispersal over regional and even continental scales [77,78]. While studies have focused on their role in spreading plant and animal pathogens, their potential for dispersing beneficial plant microbiomes remains underexplored. Plants' canopies serve as significant sources of airborne bacteria, and while the exact fraction of the endophytic microbiome dispersed via the atmosphere is uncertain, shared bacterial communities between endophytes and airborne bacteria suggest a potential avenue for aerial transmission [79].

Endophytes can also enter aerial tissues through floral organs, potentially facilitated by insects, wind, or rain [80]. Flowers act as hotspots for microbial diversity and may provide predictable transmission routes for the aerial tissue microbiome [79]. Notably, pollen grains, released in vast quantities, may serve as efficient vectors for both vertical and horizontal transmission of endophytes between plants. Sap-feeding insects, such as leafhoppers and psyllids, also play a role in transmitting endophytes between plants, highlighting their potential as vectors of beneficial or commensal plant microbiomes within and across plant species. Further research is needed to elucidate the significance of these transmission routes in shaping plant-associated microbial communities.

Vertical Transmission

Vertical transmission involves the transfer of bacterial endophytes from one generation of plants to the next, typically via seeds or pollens [79]. The seed microbiome has brought increasing attention [81,82], with bacteria detected in the seeds of various plant species, including both crop plants [83–89] and wild plants [90–92]. Bacteria have been found in different parts of the seed, such as the coat, endosperm, and embryonic tissues. Endophytes residing within seeds or on seed coats can colonize the emerging seedlings upon germination, establishing early associations with the developing plants [60]. Some seed endophytes, particularly *Bacillus* and *Pseudomonas* species, have been associated with beneficial effects on host plants, including releasing seed dormancy, promoting plant growth under harsh conditions, and providing protection against fungal pathogens or heavy metal toxicity. While most seed endophytes are likely acquired from the environment horizontally, some evidence suggests intermittent vertical transmission [80]. Potential vertical transmission routes involve transfer through the shoot apical meristem or vascular connections to the endosperm [93]. High-throughput sequencing studies have provided insights into the assembly and diversity of seed-associated bacterial communities, suggesting both neutral processes and plant selection shape these communities [94]. However, definitive evidence of vertical transmission requires further investigation at the strain level, considering the complexities of seed-associated microbial dynamics and their implications for plant health and adaptation.

Endophytes may enter seeds via male gametes, as bacteria have been found inside and on the surface of pollen grains of various plant species [89,95]. Pollen, exposed to the external environment, can be colonized horizontally from the atmosphere, through pollinators, or other animals. Studies isolating endophytic bacteria like Enterobacter cloacae from surface-sterilized pollen of Mediterranean pines suggest an origin within the parent plant, with subsequent isolation from fertilized pine ovules supporting vertical transfer via pollen [80]. The abundance, diversity, and colonization pattern of bacteria associated with wind-pollinated and insect-pollinated plant species differ significantly, potentially influenced by species-specific pollen characteristics [95,96]. Insect-pollinated species exhibit more similarity in bacterial communities, hinting at a possible pollinator influence on pollen bacterial composition [79].

The symbiotic relationship between endophytes and host plants primarily enables the hosts to tolerate various biotic and abiotic stresses, particularly drought and salinity [43,97]. Table 1 shows the physiological role of bacterial endophytes in wheat (*Triticum* spp.) as a host plant.

Environmental conditions such as pH, temperature, and nutrient sources significantly influence the production of bacterial secondary metabolites. Numerous bacterial strains, including *Pseudomonas* spp. [45,98] and *Bacillus* spp. [20,43,45,99,100], have been identified to assist plants in resisting various environmental challenges, including drought and salinity [101,102]. The stress-reducing and growth-enhancing effects of bacterial endophytes are driven by complex mechanisms across multiple pathways. For instance, nitrogen fixation in Azotobacter chroococcum [103] and phosphate solubilization in *Pseudomonas* spp. [98] contribute to overall plant growth. Additionally, phytohormone synthesis, particularly by bacterial endophytes characterized by their ability to produce 1-aminocyclopropane-1-carboxylate (ACC) deaminase [102,104], leads to reduced ethylene levels in plants, especially beneficial in challenging environmental conditions like drought. These microorganisms can break down ACC into α-ketobutyrate and ammonia, resulting in reduced ethylene levels in plants [10].

Endophytes accumulate osmolytes and antioxidant substances, which mitigate the negative effects of salt stress on plants [105]. These substances stabilize cellular components scavenge free radicals, and aid in osmotic adjustment [104]. Endophyte colonization is dependent on the compatibility of the host and microbe interaction [106]. Various compounds, including indole-3-acetic acid, gibberellin, cytokinin, siderophore, and exopolysaccharides, are produced by microbes to aid plant growth [107]. Roots also secrete exudates, such as amino acids e.g., proline [97,99], sars, and secondary metabolites, acting as attractants for microbes, particularly endophytes, to colonize.

Indole-3-acetic acid (IAA) regulates plant growth and stress response, with endogenous accumulation aiding plants in resisting external abiotic stressors [108,109]. Additionally, siderophores, including phytosiderophores secreted by plants, play pivotal roles in mitigating stress caused by abiotic and biotic factors [110,111]. These siderophores play a pivotal role in plants and organisms themselves, such as the mitigation of stress caused by abiotic and biotic factors [112].

Siderophores facilitate several plant functions such as respiration [113], photosynthesis [114], bioremediation [115], plant growth promotion [116–119], and the phytoremediation of heavy metals [118–120]. Certain bacterial species, like *Pseudomonas aeruginosa*, have the potential to produce hydroxamate siderophores, enhancing chlorophyll content, antioxidant enzyme production, and plant growth under limited iron conditions [121].

Iron plays crucial roles in several enzymatic activities and acts as a cofactor in the synthesis of plant hormones like ethylene and ACC deaminase [122]. Furthermore, iron is essential for chlorophyll biosynthesis and electron transport in the photosystem [123].

Table 1. Bacterial endophytes and their role in mitigating abiotic stresses.

Endophyte	Mechanism of Action	Wheat Genotype	Type of Abiotic Stress	References
Bacillus subtilis	Regulate proline production. Regulate malondialdehyde (MDA) production.	*T. aestivum*	Drought	[99]
Pantoea alhagi	Regulate the production of proline. Regulate malondialdehyde (MDA) production. Regulate the metabolism of chlorophyll pigment.	*T. turgidum* subsp. *durum*	Drought	[97]
Salicornia brachiate *Bacillus* spp.	The production of IAA. The production of siderophores. Produce lytic enzymes. Nitrogen fixation. Phosphate solubilization.	*Triticum* spp.	Salinity	[43]
Pseudomonas spp.	Phosphate solubilization.	*T. aestivum*	Salinity	[98]
Azotobacter chroococcum	Nitrogen fixation.	*T. turgidum* subsp. *durum*	Salinity	[103]
Kocuria rhizophila *Cronobacter sakazakii*	The production of (ACC) deaminase.	*T. turgidum* subsp. *durum*	Salinity	[124]
Bacillus spp. Proteobacteria Firmicutes Actinobacteria	The production of IAA. Phosphate solubilization. Zinc and potassium solubilization. The production of siderophores.	*T. aestivum*	Heat	[20]

Table 1. *Cont.*

Endophyte	Mechanism of Action	Wheat Genotype	Type of Abiotic Stress	References
Pseudomonas *Bacillus* spp. *Stenotrophomonas* *Methylobacterium* *Arthrobacter* *Pantoea* *Achromobacter* *Acinetobacter* *Exiguobacterium* *Staphylococcus* *Enterobacter* *Providencia*	The production of siderophores. The production of ammonia. The production of hydrogen cyanide. The production of (IAA), gibberellic acid (GA), and cytokinin. Nitrogen fixation. Phosphate solubilization. Zinc and potassium solubilization.	*T. aestivum*	Cold stress	[45]

3.3. Analysis of Wheat Growth Response to Endophyte Inoculation under Drought and Salinity

Figure 5 illustrates the analysis of the influence of endophytic bacteria on wheat growth parameters, revealing varied responses. Negative response may indicate challenges from specific bacterial strains, while positive results highlight their potential to alleviate drought- and salinity-induced stresses and promote sustainable plant growth [80]. These findings underscore the necessity for further research to capitalize on the advantageous traits of endophytic bacteria in addressing the complex challenges posed by drought and salinity [36].

The presentation of data from research articles via box and whisker charts highlights significant variations. Inoculation with endophytes notably enhanced growth parameters, as demonstrated in Figure 5. Furthermore, when examining the effects of endophytic bacteria under drought and salinity conditions on various growth parameters, it was observed that they exerted distinct effects on shoot length, root length, shoot fresh weight, root fresh weight, and shoot dry weight under salinity, in contrast to drought.

The inoculation treatment increased above-ground biomass under drought by enhancing nutrient uptake and increasing chlorophyll content, as indicated by Lubyanova et al. [125]. They reported a 10% increase in shoot length and a 15% increase in root length in response to inoculation with *Bacillus subtilis*.

Inoculation with *B. subtilis* on the growth parameters of wheat showed a range of responses from low to high values or high variation, as follows: shoot length (−1–8%), root length (−1–26%), shoot fresh weight (15–85%), root fresh weight (2–20%), shoot dry weight (3–17%), and root dry weight (6–16%). *B. subtilis* ameliorated the effect of drought on the linear size of treated wheat where bacterial-inoculated and drought-exposed wheat seedlings exhibited similar root length, plant height, and flag leaf area to non-stressed plants [125].

B. subtilis alleviated the impact of drought on the physical dimensions of treated wheat. Wheat seedlings inoculated with bacteria and exposed to drought displayed comparable root length, plant height, and flag leaf area to non-stressed plants [100].

In another study, the root weight of wheat seedlings increased by 34% when inoculated with *Acinetobacter* spp. and *Comamonas testosterone*, as reported by Khanghahi et al. [126]. Furthermore, *Pantoea alhagi* demonstrated notable improvements in shoot length (20%) and root length (30%), as well as in shoot fresh weight (130%) and root fresh weight (5%) [99]. Variations in endophytic bacterial species influence the growth of various plant parts of the same host plant differently. For instance, *Streptomyces* spp. exhibited enhancements ranging from 30 to 56% in shoot length, 54 to 186% in shoot fresh weight, 6 to 112% in root fresh weight, −20 to 80% in shoot dry weight, and 55 to 170% in root dry weight of wheat plants grown under intrinsic water stress [127].

Under salinity stress, bacterial endophytes exhibit varying effects depending on their halophytic or non-halophytic nature. For instance, wheat seed inoculation with *Comamonas* *testosterone* and *Acinetobacter* spp. decreased root fresh weight by (−2%) [126]. Meanwhile, *Pantoea agglomerans* increased shoot length (13–55%), root length (6–16%), shoot fresh weight (5–71%), root fresh weight (0–100%), shoot dry weight (2–90%), and root dry weight (30–100%) [41]. *Azotobacter chroococcum*, in contrast, increased root length (18–25%), shoot fresh weight (10–25%), and shoot dry weight (5–50%), with varied impacts on root fresh weight (−7–33%) and root dry weight (−7–55%) [103]. Another study by Aizaz et al. [128] examined the effects of halotolerant endophytic bacteria in wheat, revealing changes in shoot length (8–60%), root length (−9–80%), shoot fresh weight (9–76%), and shoot dry weight (−1–80%).

Analysis of plant growth parameters, particularly shoot length and shoot fresh weight, highlighted their significant sensitivity to salinity stress, as depicted in Figure 5b. Increased NaCl concentrations were found to adversely affect shoot dry weight. Nonetheless, the presence of endophytic bacteria ameliorated these effects, enhancing morphological traits and antioxidant activities while reducing Na+ contents across all treatments compared to uninoculated conditions [128]. For detailed statistical differences, please refer to Supplementary Table S1.

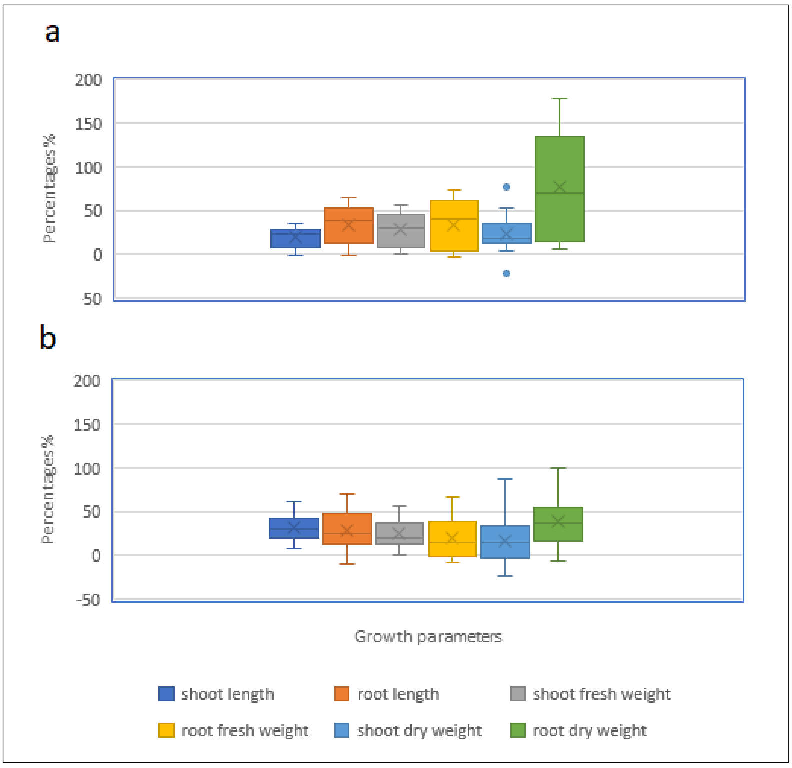

Figure 5. The percentage improvement in wheat growth parameters with presence of various endophytic bacteria under drought and salinity stresses. (**a**) Drought stress [42,97,99,125]; (**b**) salinity [42,43,103,128]. Outlier values are denoted by circles.

4. Conclusions

Drought and salinity pose significant challenges to agricultural productivity, particularly for staple food crops like wheat, due to their detrimental effects on growth and yield. In response to these challenges, there has been an increasing focus on the utilization of endophytic bacteria as an emerging tool to mitigate these stresses. This review highlights the pivotal role of endophytic bacteria in supporting host plant development by stimulating the production of plant growth regulators (PGRs) to alleviate stress. Phosphate-solubilizing endophytes have shown efficacy in enhancing plant growth even under nutrient limitations, suggesting their potential to improve nutrient availability to seedlings. Additionally, wheat endophytes demonstrate promise in alleviating both drought and salinity stresses.

Endophytes emerge as promising tools for enhancing plant stress tolerance, promoting growth, and acting as biocontrol agents, thereby safeguarding plants and boosting crop yields. However, research gaps include a scarcity of studies examining endophyte anatomy and their interactions with host plants, as well as inadequate exploration of how endophytes influence key growth parameters. These parameters include those related to osmotic adjustments, such as proline, soluble sugars, and polyamines, chlorophyll content, and grain yield under field conditions rather than controlled-conditions studies.

In conclusion, this systematic review underscores the necessity for further research to address existing gaps and thoroughly explore the benefits of bacterial endophytes for sustainable farming practices, particularly under field conditions. Prioritizing the filling of these knowledge gaps is essential to fully harness the effectiveness of endophytic bacteria in agricultural systems.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agriculture14050769/s1. Table S1: Analysis of variance (ANOVA) results for selected growth parameters [129].

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