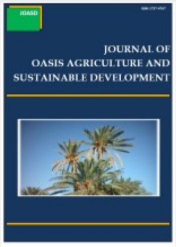

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Harnessing the potential of endophytes: Sustainable solutions for enhancing forage crop resilience and soil fertility

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Abstract

Environmental changes pose significant challenges to sustainable agriculture, adversely affecting crop production and soil fertility. Factors such as drought, salinity, pathogens, and soil type exert their influence on the behavior of fodder crops by altering their morphological, biochemical, and molecular mechanisms, ultimately leading to reduced yields and productivity. Consequently, there is a pressing need to develop mitigation strategies aimed at enhancing the tolerance of forage crops to both biotic and abiotic stresses, addressing a critical challenge in sustaining their growth.

In recent times, the use of biofertilizers has emerged as an environmentally friendly alternative to chemical fertilizers, holding promise for sustainable horticultural, agricultural, and forestry production systems. Notably, endophytic microorganisms play a pivotal role in promoting plant growth through direct or indirect mechanisms. Additionally, endophytic bacteria actively regulate gene expression responsible for the production of antioxidant enzymes, various phytohormones, siderophores, and ROS scavenging enzymes, all of which contribute to supporting the growth of host plants even in extreme environments. Consequently, there is a growing focus on understanding and validating the mechanisms through which beneficial plant endophytes interact to combat both biotic and abiotic stresses.

This review emphasizes the potential of endophytes as biofertilizers, biocontrol agents, and contributors to the mitigation of abiotic and biotic stresses, all of which play crucial roles in maintaining the development of forage crops and soil fertility.

1. INTRODUCTION

Forage crops, which encompass grasses and legumes like alfalfa, are vital for livestock feed, covering a substantial portion of agricultural land worldwide. These crops play a critical role in global agriculture, and their yield potential is influenced by genetics, environmental factors, and management practices. Genetic improvement is a key factor in increasing yield potential, as forage crops often face adverse environmental conditions like drought, floods, and nutrient deficiencies. These crops require robust protective mechanisms to withstand such challenges (FAO, 2020; Wang et al., 2021).

Endophytic bacteria, found within plant tissues, offer various benefits to host plants. They can originate from the rhizosphere, phylloplane, or endophyte-infested seeds. Previously considered weakly virulent plant pathogens, these bacteria have been recognized for their positive effects, such as promoting plant growth and enhancing resistance to pathogens and parasites. They inhabit different parts of the plant, including roots, stems, leaves, and seeds, impacting plant health and survival. The interaction between endophytic bacteria and plants can be influenced by environmental factors like temperature, humidity, and soil conditions. Environmental changes can also alter the richness and diversity of these endophytic communities, reflecting plants' adaptive strategies (Chiellini et al., 2014; Yang et al., 2017; Ou et al., 2019; Yarte et al., 2020).

Both climatic and soil conditions contribute to the nature and action of endophytes, which enhance plant growth through mechanisms like the production of growth-promoting hormones, nutrient cycling, and the synthesis of polyamines involved in root development and stress adaptation. These endophytes also exhibit phosphate solubilization, indole acetic acid production, siderophore production, and vitamin supplementation to plants. Moreover, they play a role in osmotic adjustment, stomata regulation, root morphology modification, enhanced mineral uptake, and alteration of nitrogen accumulation and metabolism. Additionally, endophytes can act as biocontrol agents by suppressing harmful pathogens and boosting plant immunity. Many of these beneficial traits have potential applications in agriculture, industry, and biotechnology, with the goal of improving crop yield, root development, germination rate, and plant stress resistance (Kandel et al., 2017a; Egamberdieva et al., 2017; Chaudhary and Sharma, 2019; Compant et al., 2005a, b; Khalil et al., 2021).

2. DEFINITION AND CARACTERIZATION OF ENDOPHYTES

Endophytes, which encompass a diverse group of microorganisms including fungi, bacteria, and actinomycetes, reside within plant tissues without causing harm (Larran et al., 2001). They are typically isolated from host plants after surface sterilization or exist within plant organs without inducing disease symptoms (Slama et al., 2019). Endophytes find applications in various fields, including agriculture, forestry, and biotechnology. In agriculture, these microorganisms influence host plants by promoting growth, increasing crop yield, nitrogen fixation, and phytohormone production. Moreover, they enhance plant tolerance to abiotic stresses like drought, salinity, and heavy metal toxicity (Rodriguez et al., 2009; Mei and Flinn, 2010). In forestry, endophytes facilitate faster tree growth, improved nutrient uptake, and resistance against pathogens.

Plant growth-promoting bacteria (PGPB) offer a sustainable approach to crop production by protecting plants from stress conditions and promoting their health (Timmusk et al., 2017). They serve as biofertilizers, stimulate plant growth, repair rhizomes, and control phytopathogens (Bambharolia et al., 2020).

The identification of endophytic bacteria involves gene amplification, sequencing, and phylogenetic analysis to determine their identity. Gene amplification, particularly the 16S rRNA gene, has become a valuable tool for accurate and rapid microbial identification (Clarridge, 2004; Drancourt et al., 2004). Endophytic bacteria exhibit the ability to produce plant growth-promoting substances like auxins, cytokinins, gibberellins, and can fix nitrogen, solubilize phosphate, and generate secondary metabolites with agricultural applications (Rodríguez et al., 1999; Glick, 2012; Li et al., 2019).

3. IMPROVEMENT OF TOLERANCE AND PRODUCTIVITY OF FORAGE PLANTS BY USING ENDOPHYTES

The interaction between endophytes and host forage plants is mutually beneficial (Fig. 1). Endophytes play a vital role in enhancing host forage plants by improving nutrient uptake, promoting growth, increasing tolerance to abiotic stress, preventing plant pathogen infections, and ultimately leading to higher plant biomass yield. In ecosystems with harsh climatic conditions and low soil fertility, certain forage species may struggle to establish and perform optimally, resulting in reduced vegetative growth, forage yield, and herbage nutritive content (Croce et al., 2001; Hodge, 2004). However, as plants engage in mutualistic or symbiotic relationships with other organisms, such as fungi or bacteria, they can enhance their performance under unfavorable conditions. Fungal endophytes, in particular, are capable of residing inside host plant tissues throughout their life cycle without causing disease symptoms (Rodriguez et al., 2009).

3.1. Drought stress

Endophytic microbes play a significant role in enhancing drought tolerance in forage plants through various mechanisms. Drought stress can have a substantial impact on crop yield, particularly during the reproductive stage

(Tiwari et al., 2017; Venuprasad et al., 2007). Despite advancements in breeding drought-tolerant crops, global food security remains a challenge due to factors like climate change and water scarcity (Nanzad et al., 2019). Endophytes contribute to plant survival in water-limited environments by forming protective barriers, improving electrolyte leakage, accumulating osmolytes, and synthesizing exopolysaccharides (Vurukonda et al., 2016).

Under water-deficient conditions, endophytic microorganisms colonize the plant's rhizosphere and promote growth and development through various mechanisms, including the production of plant hormones (Kang et al., 2014). Some studies, such as Hahn et al., (2008), have demonstrated positive effects of endophytes like *Epichloe lolii* on drought resistance in plants like perennial ryegrass (*Lolium perenne*). However, conflicting findings have been reported by Hall et al., (2014) and Tian et al., (2015), indicating that the influence of endophytes on drought tolerance may vary among different plant genotypes, as observed by Assuero et al., (2000).

Umapathi et al., (2021) found that specific endophytes significantly improved drought tolerance in sorghum seedlings by enhancing germination rates and speeding up the germination process. Maqbool et al., (2021) reported that the EPS-producing endophyte *Enterobacter cloacae* 2WC2 had both positive and negative effects on water content, antioxidant activity, chlorophyll, and proline content in maize under drought stress. Similar mechanisms of endophyte-mediated drought tolerance have been observed in fenugreek inoculated with arbuscular mycorrhizal fungi (AMF) (Irankhah et al., 2021) and in maize (Vardharajula et al., 2011; Naseem et al., 2014). Additionally, Nagabhyru et al., (2013) showed that symbiotic *Neotyphodium coenophialum* aids in the survival and recovery of tall fescue plants from water deficit by inducing the rapid accumulation of compatible solutes. Tyagi et al., (2017) reported that inoculation with both *Rhizophagus intraradices* and *Piriformospora indica* fungi improved drought tolerance in finger millet by enhancing antioxidant defenses, chlorophyll content, and osmoregulation. These findings highlight the diverse mechanisms through which endophytes enhance drought tolerance in forage plants, offering potential benefits for sustainable agriculture.

3.2. Salt stress

The application of salt-tolerant plant growth-

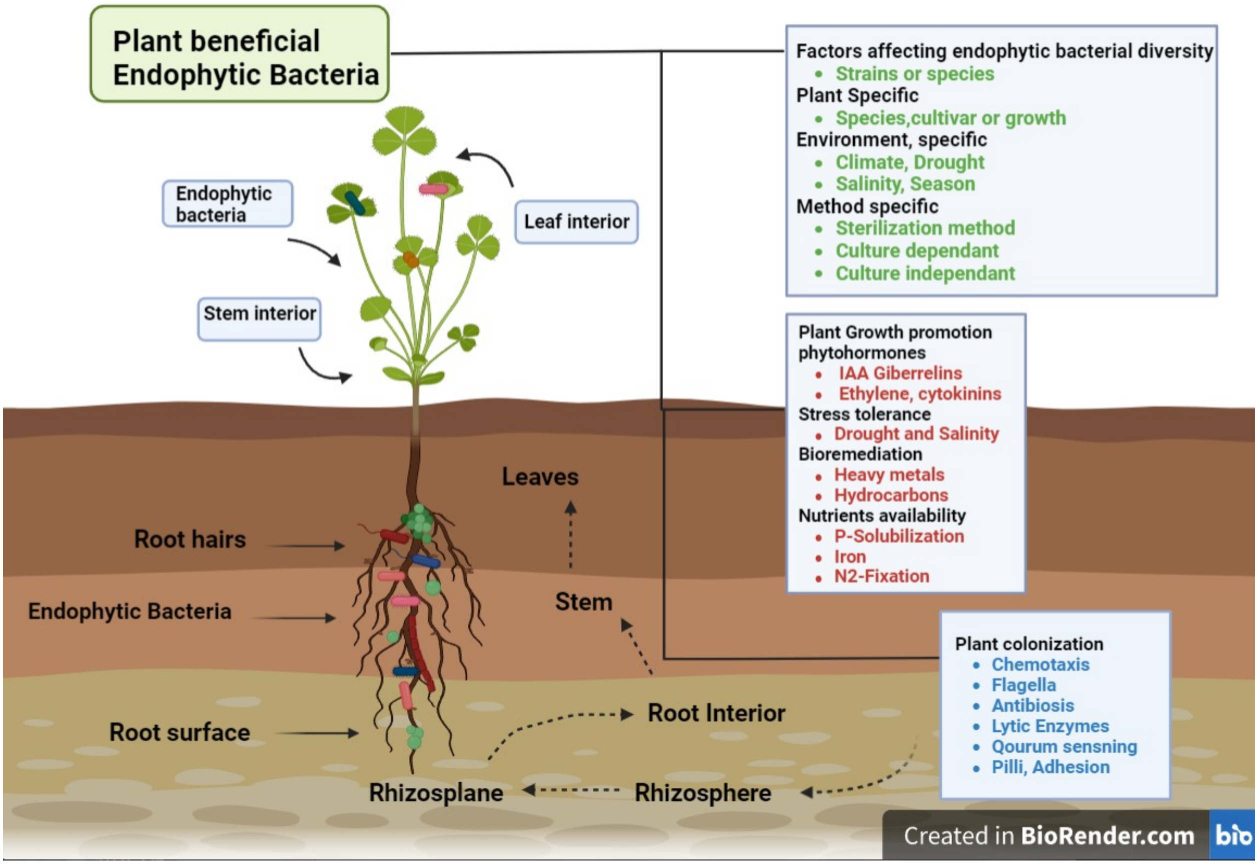

Fig.1. Factors affecting diversity of endophytes and plant-endophytes interaction (From Baber et al., 2022). This figure is created with BioRender.com.

promoting rhizobia (HT-PGPR) can mitigate salt stress in plants through various physiological and molecular mechanisms, including root system alterations, induction of antioxidant defenses, generation of exopolysaccharides (EPS) and siderophores, regulation of plant hormones, osmolyte synthesis, enhanced mineral uptake, and control of plant pathogens (Fig. 2). Several salt-tolerant soil bacteria species, such as *Arthrobacter*, *Azospirillum*, *Alcaligenes*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Flavobacterium*, *Pseudomonas*, and *Rhizobium*, have been identified as contributors to salt stress reduction in crops. For instance, the endophyte *Penicillium funiculosum* LHL06 was shown to enhance soybean growth under salt stress by promoting isoflavone biosynthesis (Khan et al., 2011). Additionally, studies by Waller et al., (2005) and Baltruschat et al., (2008) revealed that the root endophyte *Piriformospora indica* induced barley plant growth and mitigated NaCl-induced stress by activating the glutathione ascorbate cycle and increasing antioxidant enzyme activity. Furthermore, P. moraviensis was found to improve soil quality in saline sodic conditions by increasing nutrient content in maize (Enazy et al., 2018). Pereira et al., (2019) reported that fungal strains from *Festuca rubra* subsp. pruinosa roots significantly enhanced leaf biomass production in *Lolium perenne* under normal and saline conditions. In addition, Mahadik et al., (2020) suggested that fluorescent *Pseudomonas* strains SPF-33 and SPF-37 are strong candidates for alleviating salt stress in finger millet (Indaf-9) seeds. Moreover, Noori et al., (2018) demonstrated that alfalfa plants in saline regions harbor root nodules containing beneficial bacteria with various plant growth-promoting characteristics, contributing to salinity tolerance, even independently of the presence of the alfalfa plant's rhizobial symbiotic bacterium *Ensifer meliloti*.

3.3. Mineral deficiency

Endophytes improve soil fertility and structure by increasing the activity of beneficial microorganisms and breaking down organic matter. They can also improve the efficiency of nutrient uptake by plants, reducing the need for fertilizer inputs.

Chen et al., (2020) elucidated the influence of the Epichloë endophyte on the growth, endurance, and elemental nutrient composition of perennial ryegrass (*Lolium perenne*) in conditions of limited fertility. The presence of the Epichloë endophyte exerted notable direct and indirect consequences on variables such as plant survival rate, potassium (K) content in leaves and roots, manganese (Mn) content in leaves, and the activity and dry weight of roots. These discoveries also underscored the time-dependent nature of the Epichloë endophyte's impact on plant growth. An essential determinant of whether endophytes yield positive or negative effects on their host lies in the availability of soil nutrients. When faced with inadequate nutrient availability, the detrimental effects of endophytes are amplified as plants grow, and nutrient resources become increasingly scarce.

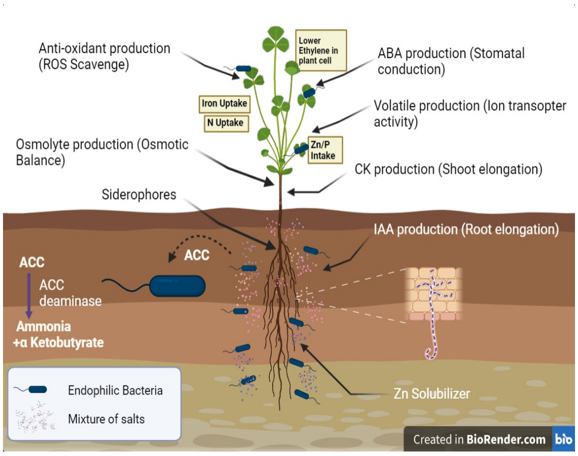

Fig. 2. The role of endophytic bacteria in induced drought and salinity tolerance by plants (from, Anukool et al., 2018). This figure is created with BioRender.com.

Garcia Latorre et al., (2021) demonstrated that endophytes could play a crucial role in influencing mineral acquisition by plants. For example, the presence of *S. intermedia* (E636) led to increased uptake of minerals such as calcium, copper, manganese, lead, thallium, and zinc, along with a rise in total ash content. This effect varied significantly depending on the specific interaction between the fungal strain and its host plant species, with different outcomes observed for *Trifolium subterraneum* and *Poa pratensis*.

In a study by Ren et al., (2007) conducted on ryegrass (*Lolium* spp.) plants; it was observed that variations in phosphorus levels significantly influenced phosphorus uptake and concentration in plants, regardless of endophyte status. Endophyte-infected roots exhibited increased total phosphorus content, possibly attributed to greater root dry weight in response to phosphorus deficiency. Furthermore, endophyte-infected plants demonstrated enhanced phosphorus utilization efficiency, with higher Acid phosphatase (ACP) activity, potentially facilitating efficient phosphorus recycling by ryegrass roots.

3.4. Heavy metals

Endophytes have potential use in bioremediation of contaminated soils (Chowdhary and Kaushik, 2015). They can be used in phytoremediation, which is the process of using plants to remove, detoxify, or stabilize contaminants from soil, air, and water. By colonizing the root systems, endophytes could improve the plants absorption of heavy metals such as lead, cadmium, and others, and reduce their concentrations in the environment. This approach is extremely useful in phytoremediation programs as a friendly technique with low coast and provides a more sustainable solution (Sharma et al., 2021; Khalaf et al., 2018).

In this context, Lui et al. (2021) revealed a promising method of tailing non-soil cover phytoremediation by endophyte assisting *Trifolium repens* L. was established. Endophytic *Pseudomonas putida* strain RE02, with great heavy metal detoxification ability, could colonize in both rhizosphere and endosphere of roots.In the same way, Ignatova et al., (2021) showed that five strains endophytic microorganisms (*Beauveria bassiana* T7, *Beauveria bassiana* T15, *Rhodotorula mucilaginosa* MK1, *Rhodotorula mucilaginosa* RH2, *Metschnikowia pulcherrima* MP2) with the highest levels of Cd tolerance and removal ability were selected. These isolates act as strains promising for alleviation of Cd stress and decrease the accumulation of metals in soybean tissues. In addition, Hou et al., (2020) suggest that the dark septate endophytes DSE (*Acrocalymma vagum* and *Scytalidium lignicola*) inoculation improved the root growth and nutrient absorption of non-host plants (*Medicago sativa and Ammopiptanthus mongolicus*), altered the soil Cd concentration, and facilitated plant growth and survival under Cd stress.

In their study, Żurek et al., (2022) investigated the role of the Epichloë fungal endophyte in the tolerance of perennial ryegrass to elevated concentrations of heavy metal ions (Cd^{2+}, Pb^{2+}, and Cu^{2+}) in the soil. They found that the presence of the endophyte influenced the accumulation of heavy metal ions in the aboveground parts of the plants, sometimes enhancing the ryegrass's ability to accumulate these ions from the soil. Interestingly, exposure to higher levels of Cu^{2+} ions induced a hormesis effect in both endophyte-infected (E+) and non-infected (E-) plants, leading to improved growth and photosynthetic activity as measured by Chlorophyll a fluorescence.

3.5. Diseases

Endophytes play a crucial role in enhancing plant resistance to diseases. Forage plants are susceptible to various pathogenic diseases like rusts, leaf spot diseases, blights, blotches, molds, and wilts caused by pathogenic fungi, bacteria, or viruses. Endophytes help plants combat these diseases by competing for resources, producing antimicrobial compounds, and promoting plant defense mechanisms. Their positive impact on plants has elevated their significance in disease biocontrol.

In a study by Mercado-Blanco et al., (2004), the treatment of roots with the *Pseudomonas fluorescens* PICF7 strain in greenhouse conditions significantly delayed the onset of symptoms and reduced *Verticillium* wilt incidence and severity by 82% and 96%, respectively, highlighting how endophytes can mitigate disease impact.

Additionally, Mousa et al., (2016) found that finger millet possesses fungal endophytes capable of synthesizing previously unreported anti-fungal compounds effective against *F. graminearum*, demonstrating the potential of endophytes in developing bio-fungicides.

Moreover, Waller et al., (2005) revealed that *Piriformospora indica* could induce resistance against fungal diseases and enhance salt-induced stress tolerance in barley. This effect extends to leaves distant from the infection site, indicating the fungus's systemic ability to induce resistance as a root-endophyte. This enhanced "defense readiness" is associated with increased antioxidative capacity, attributed to the activation of the glutathione–ascorbate cycle, resulting in higher barley grain yields. Importantly, *Piriformospora indica* can be cultivated independently of a host plant, offering potential for enhancing disease resistance and crop yields.

In a study by Chen et al., (2020), endophytes were investigated as potential biocontrol agents to enhance agricultural productivity. The study isolated 362 endophytic strains, including fungi, bacteria, and actinomycetes, from alfalfa. Among these, three endophytic bacterial strains, NA NX51R-5, NA NX90R-8, and NA NM1S-1, exhibited robust biocontrol potential, with effectiveness exceeding 50%, particularly against the widespread alfalfa root rot pathogen *Fusarium oxysporum* F. sp. *medicaginis*.

4. CONCLUSIONS

Researchers are exploring innovative approaches to improve forage plant performance in sustainable agriculture by tapping into the beneficial interactions between forage plants and endophytic microorganisms. These endophytes, residing within plant tissues harmlessly, influence plant growth, stress tolerance, and disease resistance through intricate signaling networks. They enhance nutrient acquisition and utilization, particularly in nutrient-deficient soils, leading to increased biomass and nutrient-rich forage. Endophytes also bolster stress tolerance against drought, salinity, and extreme temperatures, ensuring higher survival rates and sustained growth, especially in regions with climate fluctuations. Additionally, they serve as natural protectors by inducing systemic acquired resistance, reducing the need for chemical interventions, and improving crop quality and yield. While challenges exist in harnessing endophytes, ongoing research indicates their potential to revolutionize forage production, contributing to sustainable and resilient agricultural systems that ensure a consistent supply of nutritious forage for livestock and global food security.

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