



# Microbial Endophytes: A Hidden Plant Resident, Application and Their Role in Abiotic Stress Management in Plants

Touseef Fatima<sup>1,2\*</sup>, Swati Sharma<sup>2</sup>, Ambreen Bano<sup>2</sup>, Divya Srivastava<sup>3</sup>, Isha Verma<sup>1</sup> and Poonam C. Singh<sup>1\*</sup>

<sup>1</sup>Division of Microbial Technology, CSIR - National Botanical Research Institute, Rana Pratap Marg, Lucknow – 226001, Uttar Pradesh, India; pc.singh@nbri.res.in

<sup>2</sup>IIRC-3, Plant-Microbe Interaction and Molecular Immunology Laboratory, Department of Biosciences, Faculty of Sciences, Integral University, Lucknow – 226006, Uttar Pradesh, India

<sup>3</sup>School of Life Science and Biotechnology, Adamas University, Kolkata – 700126, West Bengal, India

## Abstract

Microbial communities in nature involve complex interactions with several biotic and abiotic components. An endo-symbiotic association is one in which one organism lives within the host plant for at least a part of its life. It is often obligate and does not create visible disease and has been reported to exist for at least 400 million years. Beneficial endophytes promote plant nutrient uptake, host plant growth, reduce disease severity, inhibit plant pathogens and improve tolerance to environmental stresses. Stresses like salinity, alkalinity, drought, global warming, temperature and pollution will increase in prominence and endophytes are predicted to play a significant role and offer eco-friendly techniques to increase productivity under such conditions. There also exists the potential for genetic modification of endophytes to impart additional stress tolerance traits in hosts. The present review discusses the beneficial effect of fungal and bacterial endophytes, emphasizing improving crop productivity under abiotic stress conditions. The review also discusses the various aspects of physiological and molecular mechanisms determining the interaction and stress tolerance, enhancing plant functions and productivity.

**Keywords:** Defense Management, Endophytes, Environmental Stress

## 1. Introduction

An endophyte is an endosymbiont, often a bacterium or fungus, that lives within a plant for at least part of its life cycle without causing apparent disease. Endophytes are defined as the microorganisms which live inside the host plant (endosymbiont) for the whole or a part of their life cycle without causing any apparent disease symptoms. The relationship between plants and microorganisms is an interesting subject and has been studied in different purviews. However, the term 'endophyte' integrates a broad diversity of largely uncharacterized microbe-plant interactions. Endophyte-host interaction is a symptomless microbial occupation of plant tissues that involves a balance between microbial aggression and host defense. This balance is dynamic and can be altered by changes in the physiological condition of either host or microbe, affecting the potential outcomes. For example, they do not cause any immediate

overt adverse effects but may become pathogenic through host senescence<sup>1,2</sup>. Thus, the interaction within an association is not necessarily stable but may change from one form to another across time and space<sup>3</sup>.

The alliance of endophytes with plants was probably associated back when plants colonized the land and played a sustained and crucial role in driving the evolution of terrestrial life<sup>1</sup>. About 400 million years old fossil records have shown plant association with endophytes and mycorrhiza fungi<sup>4</sup>. The first discovery of endophytes was reported as early as 1904; they received attention only after the discovery of their pharmacological and environmental importance<sup>5</sup>. Endophytic bacteria are phylogenetically related to saprophytic bacteria and plant diseases. Overall, abiotic and biotic variables, as well as the host, impact the dynamic patterns of bacterial endophytes, which in turn are controlled by the host plants. The unique ecological niche that a plant provides has made

\*Author for correspondence

endophytic bacteria an appealing and potentially successful tool for agricultural applications, particularly for those bacteria with commercial characteristics such as plant growth stimulation and activation of plant defense systems. It is now well known that these bacteria reside in several tissue types in a wide range of plant species, implying that they are harbors in almost all plants<sup>6,7</sup>.

Endophytes have significant potential as a major source of physiologically active chemicals with promising pharmaceutical or agricultural uses, as demonstrated by recent advancements in screening methods<sup>8</sup>. As a result, there is a huge possibility to find novel natural compounds such as alkaloids, phenolic acids, quinones, steroids, saponins, etc. from untapped endophytic microbes living in various niches and habitats<sup>9</sup>. One of the most significant aspects of endophytes has been in managing plant diseases and abiotic stresses by improving plant growth and its physiological status<sup>10,11</sup>. Endophyte colonization has been shown to assist in mitigating abiotic stress such as drought through increased water potential and improved osmotic adjustment, in addition to promoting the survival and development of infected plants<sup>12</sup>.

The increasing environmental stresses like global warming, temperature, air pollution and adverse soil condition such as salinity, metal toxicity, pesticides, drought and pH are affecting nearly all plant activities and are important limiting factors in crop output. There is considerable evidence that on the global scale, the climate is changing. It is predicted to increase temperature and decreasing precipitation will which uses a dynamical model to obtain the regional information, strongly depends on the horizontal resolution of the dynamical model. It provides the most reliable assessment of the regional climate, with the highest resolution. However, the computational expense of this high resolution limits the sample size. The third method (statistical downscaling eventually lead to extended duration and severity of summer droughts<sup>13</sup>. Various crops grown in arid and semi-arid environments are regularly subjected to a wide array of environmental stresses. Since these environmental conditions play a fundamental part in defining the significance and distribution of plants in natural ecosystems, as well as the amount and rate of climate change, will all have a significant impact on the extent to which plants in ecological systems can resist stress and adapt. Thus, considering endophytic associations as an essential stress management system, the present review focuses on how the response of plants to a stressed environment may depend on their ability to form endophytic relationships with microorganisms.

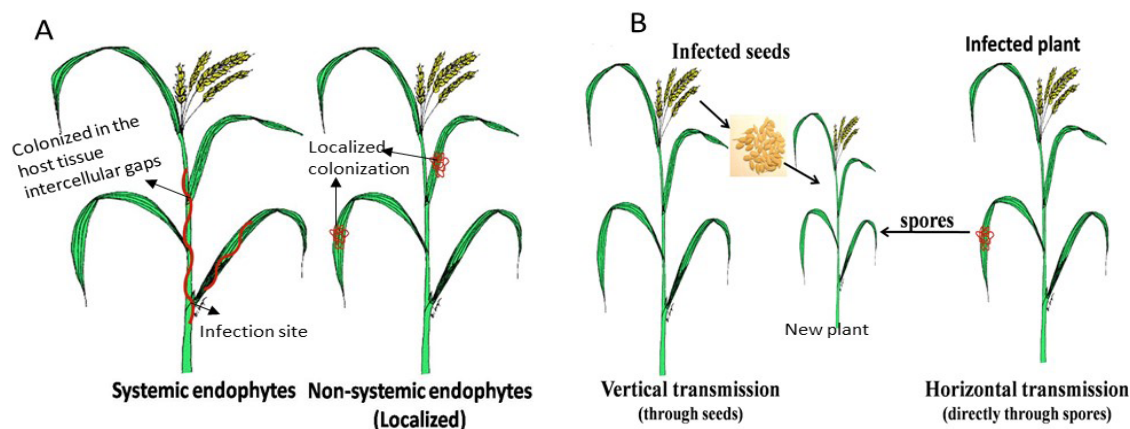
## 2. Endophytic Microbial Diversity

The term endophytes are used as a microbial domain, which includes fungi, bacteria, actinomycetes, etc. that occupy plant

eco-niches and enhance plant growth immunity. Endophytes show more diversity and abundance than the plant pathogens within the plant systems<sup>14</sup>. Recent molecular research on the variety of endophytic bacterial and fungal species has demonstrated the abundance of species<sup>15</sup>. Although the diversity of systemic endophytes in agronomic grasses has been thoroughly researched, the interactions between host plants and endophytes in wild populations and communities remain unknown. Recently, the role of endophytic microbial diversity in promoting the growth of wild medicinal plants has been well-reported<sup>16</sup>. Materatski<sup>17</sup> have disclosed temporal and spatial variation in richness and diversity of fungal endophytes associated with the phyllosphere of olive cultivars. The diversity and biological activities of culturable endophytic fungi isolated from *Catharanthus roseus* were also documented<sup>18</sup>. Apart from the endophytic diversity in the living plants, a methodology for analyzing endophytic diversity in herbarium specimens has been developed to understand the timeline and dynamics of the distribution of plant-associated microbial biodiversity to explore global change, phenology species distributions and functional traits<sup>19</sup>. A diverse group of endophytic microbes influenced the grain nutritional value in wheat under elevated CO<sub>2</sub> condition<sup>20</sup>. In halophytic ecosystem, the endophytic microorganism varied in richness and their colonization<sup>21</sup>. Thus, several reports of the diversity of culturable and non-culturable endophytic fungi and bacteria are now known in many plants, belonging to the phyla Pseudomonas, Bacilli, Proteobacteria, Firmicutes and Actinobacteria, with Enterobacter and Pseudomonas, etc. The potential of culturable halotolerant endophytic bacteria isolated from *Sporobolus specatus* (Vahr) Kunth and *Cyperus laevigatus* L. have been reported to have plant growth-promoting characteristics<sup>21</sup>. Colonization with non-mycorrhizal culturable endophytic fungi have been shown to enhance orchid growth and indole acetic acid production<sup>22</sup>. Non-culturable endophytic bacterial population has been shown to enhance plant's resistance to pathogens<sup>23</sup>.

## 3. Endophytic Behavior in Colonization

Endophytes occupy both above ground and below ground parts of plants. Except for the rhizobacteria and endomycorrhiza that enter the plant through the root rhizosphere, endophytes often inhabit above-ground plant tissue such as stem, leaves and flowers of the host plants<sup>24</sup>. The growth form of the endophytes may be systemic or non-systemic (Figure 1A). Non-systemic endophytes induce single spore origin infections, with each spore colonizing a small proportion of the host whereas systemic endophytes grow in host tissue intercellular gaps,



**Figure 1(A).** Represents the growth pattern of endophytes, systemic and non-systemic and (B) represents the mode of transmission, vertical and horizontal.

infecting both vegetative and reproductive plant tissues<sup>25</sup>. Endophytes can spread horizontally *via* spores or vertically by seeds and clonal development of the host plant<sup>26</sup>. (Figure 1B). Systemic or vertically transmitted plant endophytes have only been identified in 20-30% of all the grass species, but non-systemic, horizontally transmitted endophytes have been found in all major plant families<sup>27</sup>. In cultivated crops, the systemic endophytes may be either very high or very low which may be due to selective breeding of the cultivars harboring endophytes which improve the agronomic characteristics of the host<sup>26</sup>. Horizontally transmitted endophytes as compared to systemic preferably result in an antagonistic or neutral relationship with the host plant which may be because of the less dependency of the horizontally transmitted endophytes on survival of host and less tight relationship as compared to the seed-borne endophytes<sup>28</sup>. The horizontal transmission is affected by external factors such as the surrounding vegetation, growing season, weather conditions and tree density<sup>26</sup>. Besides, the means of transmission,<sup>29</sup> have classified endophytes based on the source of nutrition, mode of reproduction, expression of symptoms and colonization of host plant part. In Citrus plant, *Beauveria bassiana* and *Metarhizium anisopliae* can successfully colonize and improved the seedling age (seedling height and leaf no.)<sup>30</sup>.

## 4. Endophytes in Plant's Abiotic Stress Tolerance

Abiotic stresses, such as salinity, drought, heavy metal toxicity, harsh temperatures and oxidative stress pose significant challenges to agriculture and are the leading cause of crop loss globally, decreasing average yields of key agricultural plants by more than 50%<sup>30</sup>. These abiotic stresses are manifested primarily in the form of osmotic stress, ion distribution in the cell, disruption of homeostasis and loss of membrane integrity<sup>30,31</sup>.

A series of physiological, morphological, molecular and biochemical changes occur in response to abiotic stress that leads to negative impact on plant growth and productivity<sup>31,32</sup>. A detailed description of such endophytes and plants are discussed comprehensively in the subsequent sections.

### 4.1 Role of Fungal Endophyte in Stress Management

Various research has elucidated the role of fungal endophytes in combating these stresses. Waller<sup>34</sup> analyzed the potential of *Piriformospora indica* to protect *Hordeum vulgare* from salt stress. The toxic effect of moderate salt stress like leaf chlorosis, reduced growth and biotic stress was overcome entirely by *P. indica* by reprogramming the metabolic state of the plants. The endophytes were reported to enhance antioxidant capacity and activate the glutathione ascorbate cycle. Khan<sup>33</sup> a gibberellin-producing strain, was investigated to assess its effects on cucumber plant growth and heat (40°C has reported that the endophytic association of *Exophiala* sp. with cucumber host plant modulated heat stress by physiological and biochemical components, under high temperature. However, the role of endophytes in cold stress is inconclusive. Endophytic fungi producing phytohormones such as auxins, gibberellins, abscisic acid etc. are reported to thrive in harsh environments and produce several secondary metabolites such as flavonoids to assist the plant in tolerating or avoiding stress<sup>34,35</sup>.

Heavy metals like Cd (Cadmium), Cu (Copper) and Ni (Nickel) added through agro-chemicals, sludge-based manure in agricultural lands and arsenic from ground-water irrigation pose abiotic stress on plants. Similarly, inorganic arsenic species directly interact with the cellular compartments in plants to disrupt physiological processes required for cell function and plant metabolism, while arsenate generates ROS in the plant tissue and induces lipid peroxidation and oxidative stress<sup>36</sup>. The contribution of Arbuscular mycorrhizal fungi, *Glomus*

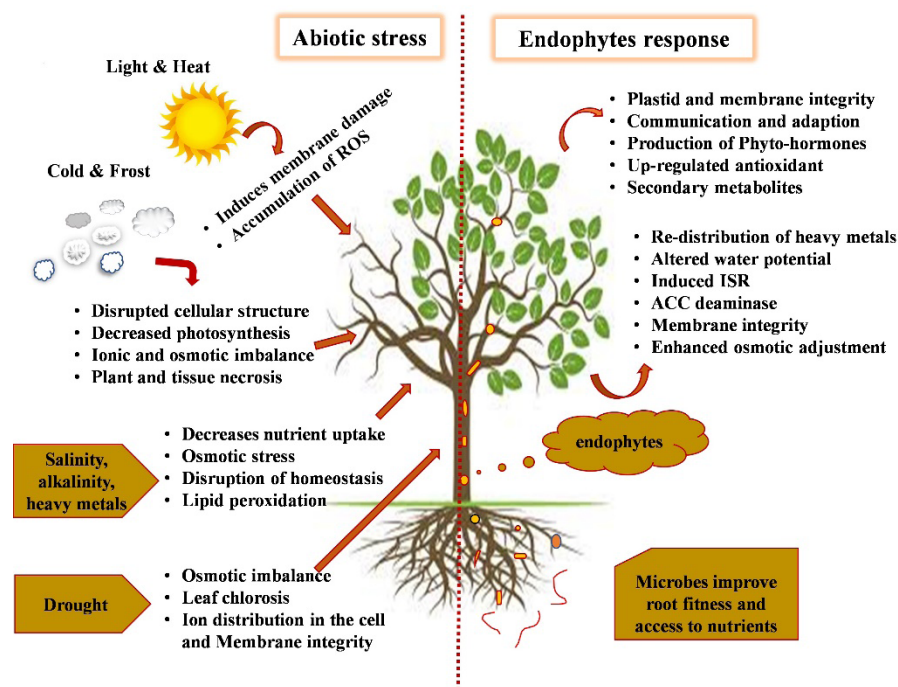
*claroideum* and *G. deserticola* to arsenic tolerance of *Eucalyptus globules* have been discussed<sup>37</sup>. Arbuscular mycorrhiza fungi redistributed some heavy metals inside the plant, decreasing the physiological damage caused to the plant. A thermophilic endophyte *Thermomyces lanuginosus* isolated from a hot desert-adapted plant *Cullen plicata*, can enhance heat and water stress tolerance in desert plants and improve the growth of its host plants through eco-physiological mechanisms<sup>38</sup>.

The rise of global atmospheric concentrations of Greenhouse Gases (GHGs) in recent times is increasing rapidly. Changes in plant phenology due to climate change in the commercially grown cereal varieties and many species have been wide across taxonomic groups<sup>39</sup>. Tolerance to such stress has been exhibited to be dependent on association with fungal endophytes in rice<sup>40</sup>. Redman<sup>40</sup> tested the effect of three endophytes on rice's tolerance to high salinity, low temperatures and desiccation, as well as the possibility of employing symbiotic technology to reduce the effects of climate change. Establishment of the symbiotic relationship between Endophytic fungi, Arbuscular mycorrhizal and the host species enhanced peanut drought resistant<sup>41</sup>.

## 4.2 Role of Bacterial Endophytes in Stress Management

Endophytic bacterial strains and rhizospheric bacterial community both help plant growth; however, it is unclear which of these two bacteria benefits the plant more. Endophytic bacteria have a lower density inside plant tissue than rhizospheric bacteria and bacterial pathogens<sup>14</sup>. Endophytic bacteria originated in the rhizosphere and phylloplane from the epiphytic bacterial populations. Several of these endophytes have the potential to be biocontrol agents, improving and promoting plant health<sup>3,11,42</sup>. Endophytic bacteria *Bacillus subtilis* NBRIW9, isolated from wild betelvine has been reported to impart biological control against *Fusarium oxysporum* in the cultivated betelvine varieties under conditions of high temperature and humidity<sup>43</sup>. The bacterium was reported to directly confront the *Fusarium* in the plants and degraded the fungal cell wall. Haroim<sup>44</sup> has shown under greenhouse conditions that biotic and abiotic factors both influenced the endophytic bacterial community structure. Rice plants planted in neutral-pH soil promoted the growth of seed-borne *Rhizobium radiobacter* and *Pseudomonas oryzihabitans*, whereas plants grown in low-pH soil supported the growth of *Enterobacter* such as *Dyella ginsengisoli*. The only dominating bacterial endophyte detected in plants grown in both soils was the seed-borne *Stenotrophomonas maltophilia*. Sgroy<sup>45</sup> grouped according to similarity, and identified by amplification and partial sequences of 16S DNAr. Isolates were grown until exponential growth phase to evaluate the atmospheric

nitrogen fixation, phosphate solubilization, siderophores, and phytohormones, such as indole-3-acetic acid, zeatin, gibberellic acid and abscisic acid production, as well as antifungal, protease, and 1-aminocyclopropane-1-carboxylate (ACC) isolated and characterized endophytic bacteria from halophyte *Prosopis strombulifera*. Their study showed that bacterial processes were involved in the stimulation of plant growth or the regulation of stress homeostasis under in vitro conditions of extreme salinity. Regulation of plant homeostasis by micro-organisms with different PGP properties such as nitrogen fixation, phosphate solubilization, siderophores and phytohormones production, protease, antifungal and 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity has been shown in natural environmental conditions<sup>45</sup>. Lead (Pb) resistant endophytic bacteria isolated from metal-tolerant *Commelina communis* plants cultivated on Zinc (Zn) and lead mine tailing enhanced the dry weights of above-ground tissues (ranging from 39 to 71%) and roots (ranging from 35 to 123%) in rape plants compared to the uninoculated control<sup>46</sup>. The endophyte enhanced plant growth under sub-optimal conditions, increasing switch grass growth in marginal areas and greatly contributing to the development a low-input, sustainable feedstock production system. A review by Dudeja<sup>47</sup> nodules, leaves, flowers and sprouts of legumes, with numbers ranging from few to more than 150. Endophytes can accelerate seedling emergence, promote plant establishment under adverse conditions and enhance plant growth. Endophytic microbes promote plant growth by helping plants in acquiring nutrients, e.g. *via* nitrogen fixation, phosphate solubilization or iron chelation, by preventing pathogen infections *via* antifungal or antibacterial agents, by outcompeting pathogens for nutrients by siderophore production, or by establishing the plant's systemic resistance. Further growth promotion is affected by producing phytohormones such as auxin or cytokinin, or by producing the enzyme 1-aminocyclopropane-1-carboxylate (ACC has given details of endophytes occurring in different tissues, interactions and their benefits in legumes. Figure 2 summarizes the impact of salinity, alkalinity and drought stress on plants. Drought stress is mainly manifested in the form of osmotic imbalance, leaf chlorosis, membrane integrity and ion distribution in the cell. Salinity, alkalinity and heavy metal have overlapping impacts as the plants reduced nutrient uptake, lipid peroxidation, etc. while light and heat usually cause accumulation of Reactive Oxygen Species (ROS), decrease photosynthesis rate and cause membrane damage. The endophytes help in overcoming these stress markers and improve plant growth by producing phytohormones and secondary metabolites and upregulating the antioxidant enzymes. Endophytes, which live in host plants, have been shown to promote plant growth by improving overall plant hardiness, development and nutrients (nitrogen and



**Figure 2.** A diametric representation of mechanisms employed by the endophytes to reduce the abiotic stress in plants.

phosphorus) uptake into plants<sup>12,48</sup>. Bacterial endophyte provided drought tolerance against changing agro-climatic conditions in *Ananas cosmosus* by expressing plant beneficial mechanisms including  $N_2$  fixation and production of indole-3-acetic acid (IAA) and ACC deaminase<sup>49</sup>. In water stress responsive clones of Eucalyptus leaves endophyte abundance and many taxonomic markers were reported to differentiate the water stress tolerant groups and overcome water stress<sup>50</sup>. Similarly, variability in endophyte population was associated with the stress tolerant variety rather than applied stress in wheat<sup>51</sup>. In barley plants it was shown that under stress conditions the soil microbiota was disturbed affecting the colonization of root endophytes and was dominated by seed borne endophytes associated with plant disease development<sup>52</sup>. These kinds of reports show that the microbial communities present in the stress tolerant or wild varieties of plants are the most potential sources of microbe's selection and development of endophyte-based inoculums for stress tolerance in susceptible crops.

## 5. Endophyte Mediated Mechanisms for Stress Tolerance

Although there are many examples of endophyte-mediated tolerance to abiotic stresses in the literature, however they mostly focus on assessing the plant growth promoting effects. Mechanisms of plant–rhizobacteria interactions in alleviating abiotic stresses have been reviewed<sup>48,53</sup>.

Changes in root morphology, which are modulated by phytohormones is a primary adaptation of plants that are exposed to environmental stresses, and are also known to be induced by endophytes<sup>54</sup>. Root growth promotion results in a higher root surface that increases the water acquisition and nutrient uptake. Waqas<sup>55</sup> have reported two endophytic fungi *Penicillium* sp. and *Phoma glomerata* to produce phytohormones such as gibberellins and indoleacetic acid and to reduce the effect of abiotic stressors such as salt and dehydration in cucumber. The production of IAA by the coryneform and actinomycetes bacteria that were isolated from the roots of winter rye as it boosted germination capacity and accelerated seedling growth has reported<sup>56</sup>. One of the key factors contributing to root morphology is ACC deaminase activity, which is frequently secreted by endophytic and rhizosphere bacteria<sup>57</sup>. It has been shown that ACC deaminase activity and its regulation is one of the principal mechanisms by which bacteria have a positive effect on plants growing under abiotic stress conditions<sup>29,57</sup>. Bacteria with this enzyme may hydrolyze the immediate ethylene precursor ACC to  $\alpha$ -keto-butyrate and ammonia, resulting in a reduction in plant ethylene levels and enhanced root growth<sup>12,29,58</sup>.

The endophytes are conferred to mitigate both abiotic and biotic stress symptoms by inducing Induced Systemic Resistance (ISR) and priming the physiological state of an inoculated plant<sup>59</sup>. Many abiotic stresses, including hot and cold temperatures, initiate a common biochemical reaction and similar root physiological processes but later branch off into unique pathways<sup>60</sup>. These branching off may be a result

**Table 1.** Endophytes mediated abiotic stress tolerance mechanisms

Endophytes mediated abiotic stress tolerance mechanisms reported in different plants.					
Stress	Endophyte	Isolation source	Host	Mechanism/Physiological response	Reference
Salinity	<i>Bacillus amyloliquefaciens</i>	Seeds	<i>Oryza sativa</i>	Ameliorates the effect of salinity stress by up-regulating the production of essential amino acids and modulating the endogenous abscisic acid and salicylic acid levels.	69
	<i>Penicillium brevicompactum</i> & <i>P. chrysogenum</i>	Roots	<i>Solanum lycopersicum</i> and <i>Lactuca sativa</i>	Enhance energy production and sequestration of Na <sup>+</sup>	70
	<i>Piriformospora indica</i>	Roots	<i>Medicago truncatula</i>	Overexpression of P5CS2, defense-related gene PR1 and PR10 and transcription factor <i>MtAlfin1-like</i> and <i>MtZfp-c2h2</i> to induce stress tolerance	71
Drought	<i>Pseudomonas azotoformans</i>	Leaves of <i>Alyssum serpyllifolium</i>	<i>Trifolium arvense</i>	Nullified the effect of abiotic stress by increasing the levels of proline, soluble sugar, and MDA	72
	<i>Pantoea alhagi</i>	Leaves of <i>Sparsifoliashap.</i>	<i>Triticum aestivum</i>		73
Drought and mechanical combined stress	<i>P. indica</i>	Roots	<i>Triticum aestivum</i>	Plant growth promotes due to a higher absorption site for water and nutrient and lower CAT activity	74
Drought and heat Combined stress	<i>Thermomyces lanuginosus</i>	Roots	<i>Cullen plicata</i>	Improved plant growth through increasing Eco physiological parameters such as photosynthesis rate, stomatal conductance, and transpiration rate, among others.	38
Heavy metals	<i>Penicillium ruqueforti</i> Thom.	Roots	<i>Triticum aestivum</i>	Secreting indole acetic acid	75
	<i>Exophiala pisciphila</i>	Roots	<i>A. thaliana</i>	Melatonin biosynthetic enzyme limiting the heavy metal accumulation	76
Nutrient	<i>Pseudomonas</i> sp. and <i>Pseudomonas mosselii</i>	Rhizosphere and root	<i>Triticum aestivum</i>	Increase biomass and micronutrient assimilation	77
Osmotic stress	<i>Piriformospora indica</i>	Roots	<i>Oryza sativa</i>	Increases the uptake of phosphorus and zinc, proline level, and antioxidant enzymes and up-regulates the synthesis of Pyrroline-5-carboxylate synthase (P5C5)	63

Heat stress	<i>Aspergillus japonicus</i> EuR-26	Plant <i>Euphorbia indica</i> L.	<i>Glycine max</i> and <i>Helianthus</i>	Improved nutritional quality and plant biomass by negotiating the activity of the ABA, catalase, and ascorbic acid.	78
Cold stress	<i>Pseudomonas</i> sp. and <i>Brevibacterium</i> sp.	Leaf apoplast of cold-adapted wild plants	<i>Phaseolus vulgaris</i> L.	It exhibited ACC deaminase activity and secretes extra-cellular proteins under cold conditions and Lowers the ROS level like H <sub>2</sub> O <sub>2</sub> and O <sub>2</sub> <sup>•-</sup> in the seedlings.	79
	<i>Epichloë</i>	seeds	<i>Festuca sinensis</i>	Increase sugar concentration and exogenous calcium nitrate	80

of the nature of the endophytic population of the plant. The up-regulation of antioxidant enzymes like Superoxide Dismutase (SODs), a broad response to various abiotic stress conditions has been reported to get modulated by endophyte *P. indica* and alter the plant metabolism to prevent the oxidative damage caused by stress<sup>61</sup>. Primarily during salt and drought stress, several antioxidative enzymes are induced for detoxification of ROS. During abiotic stress, the interaction of an antioxidative environment mediated by Ascorbate and osmolytes (polyamine, proline, etc.) results in the preservation of plastid integrity and an increase in photosynthetic efficiency in the colonized plant. Furthermore, *P. indica* stimulates salt and drought stress-responsive genes in the plant, which may play an essential role in agricultural plant abiotic stress tolerance<sup>62,63</sup>. Furthermore, a persistent up-regulation of the antioxidative system in NaCl-treated roots of a salt-tolerant barley cultivar, regardless of plant colonization by *P. indica*, suggests that antioxidants may play a role in both hereditary and endophyte-mediated plant tolerance to salinity<sup>64</sup>.

Production of different osmolytes like proline, trehalose and polyamine contribute to osmolyte adjustment playing a significant role in imparting resistance to abiotic stress. *P. indica*, a root endophyte was reported to increase the level of osmolytes like proline and polyamine in response to drought and salinity stress in different crops<sup>62</sup>. Increased production of quaternary amines, like betaine, glycine enhances both tolerances to water deficiency and resistance to oxidative stress and protect plants against frost and salinity<sup>53</sup>. Physiological mechanisms like metabolic activity, lipid peroxidation, fatty acid composition, fatty acid desaturation metabolic heat efflux and ascorbate concentration underlie the *P. indica* mediated salt tolerance studies in salt-sensitive barley<sup>64</sup>. Using expression analysis of Expressed Sequence Tags (ESTs) in different tissues of cocoa, *Trichoderma hamatum* (DIS 219b) was reported to delay drought responses by inducing changes in the physiology<sup>65</sup>. The most basic reason offered was that DIS 219b colonization

increased root development, which resulted in improved water uptake and a rise in water content, net photosynthetic rate, Chlorophyll and carotenoids, transpiration rate and water use efficiency were found to play a considerable role in mitigating Pb stress in rice seedlings colonized with an endophytic fungus. The endophyte colonization increased the chlorophyll fluorescence parameters Fv/Fm and Fv/Fo and decreased the malondialdehyde accumulation under Pb stress<sup>66</sup>. Endophyte mediated adjustments in host cellular structures and anatomical features are observed in epidermal cell size and shape and wall thickening in cells proximal to hyphae<sup>66</sup>. Bacterial endophyte mediate drought tolerance by lowering the proline conc., electrolyte leakage and lipid peroxidation<sup>67</sup>. Synergistic association of endophyte provides abiotic as well as heavy metal tolerance<sup>68</sup>. Although considerable understanding of molecular, physiological and morphological mechanisms is available in the literature, however, the modes of action underlying endophyte mediated tolerance to biotic stresses remain majorly unsolved. A list of endophytes-mediated abiotic stress tolerance mechanisms in different crops/plants are enlisted in Table 1.

## 6. Use of Endophytes in Agriculture

Agriculture and its product are not only the ultimate sources of food and energy but also of livelihood worldwide. Basic needs of livelihood such as food, energy and refuge are received as a direct or indirect product of agriculture. However, due to decreasing agricultural land and increasing population, the present production levels will not be able to meet the future food demand. Due to the rising global temperatures, the prominence and persistence of salinity and drought are increasing throughout the world, posing enormous threats to sustainable agriculture. In fields, plants get confronted with both abiotic and biotic stress conditions, which reduce growth and productivity. To mitigate stress while not compromising

**Table 2.** Artificial inoculation methods used with different endophytes

Method of treatment	Endophytes,	Crop/plant	References
Seed treatment	<i>Beauveria bassiana</i>	<i>Cucurbitaceae</i>	89
	<i>Metarhizium robertsii</i>	<i>Zea mays</i>	90
	<i>Streptomyces thermocarboxydus</i>	<i>Solanum lycopersicum</i>	91
	<i>Bacillus amyloliquefaciens</i>	<i>Pennisetum glaucum</i>	88
Soil drenching	<i>B. bassiana</i>	<i>Capsicum annuum</i> <i>Cassava</i> <i>phaseolus vulgaris</i>	87,92
Foliar spraying	<i>B. bassiana</i>	<i>Solanum lycopersicum</i> , <i>Vitis</i>	93,94
	<i>B. brongniartii</i>	<i>V. Faba</i>	86
	<i>Bacillus subtilis</i>	<i>Betalvine</i>	44
Stem injection	<i>Bacillus venezensis</i>	<i>Nelumbo nucifera</i>	95
	<i>B. bassiana</i>	<i>Musa</i>	96
Root dipping	<i>B. bassiana</i>	<i>Nicotiana tabacum</i> , <i>Zea mays</i> , <i>Triticum</i> , <i>Capsicum annuum</i>	97 98
	<i>Trichoderma</i> sp.	<i>Alliumcepa</i>	99
	<i>Pseudomonas</i> spp.	<i>Solanum lycopersicum</i>	100
Treatment of leaf tissues	<i>B. bassiana</i>	<i>Vitis</i>	101
	<i>B. bassiana</i>	<i>Sorghum</i> , <i>Nicotiana tabacum</i> , <i>Triticum</i> , <i>Glycine max</i> , <i>Zea mays</i>	102 103

on plant growth as well as yield, the use of endophytes and rhizosphere microbes appear to be an ideal strategy<sup>81</sup>. Exploiting the positive characteristics of endophytes is critical at the applied level, whether to enhance agricultural yields, adapt the plant to optimal growing circumstances, manage plant diseases or pests or in reforestation efforts<sup>82</sup>. In spite of the extensive studies regarding the beneficial effects of endophytes and their metabolic products on various crops, their commercial use in agriculture is still in initial stages. To further the development of endophytes for agricultural applications, the discovery of novel strains will be a fruitful pursuit. This may result in the identification of new species that can be directly used in agriculture or at least provide with noteworthy new and additional information about mechanisms that endophytes can use to enhance plant growth<sup>83</sup>. Diverse strategies have been developed for implementation of endophyte for crop

management and agriculture productivity<sup>84</sup>. Seleno-bacteria used as a potential bio-inoculum for Se-biofortification and applicable as a novel approach for sustainable growth of soybean<sup>85</sup>.

It has been well documented that artificially inoculated endophytes established themselves in crop plants and improved the plant growth by improving plant biomass and other parameters<sup>86-88</sup>. There are different inoculation methods that may vary with plant variety as well as the type of endophyte. It is therefore important to understand the appropriate method of inoculating an endophyte depending on their preference to colonize the plant tissue followed by the mechanism of action. As there are different findings from different experiments, Table 2 summarizes the artificial inoculation methods preferred according to endophytes.



## 7. Endophytes as a Source of Biotechnological Tools

Though endophytes serve as the second genome of plants, they may be further genetically manipulated firstly as the source of genes and second as carriers of genes transformed in them for introducing desirable characteristics into host plants<sup>104</sup>. The genes obtained from the endophytes may be used for making transgenic plants or used for commercial production of many enzymes and secondary metabolites. Zang<sup>105</sup> has successfully cloned, expressed, purified and characterized Endo-1, 4- $\beta$ -mannanase, or  $\beta$ -mannanase (an endohydrolase used to hydrolyzemannans) from endophytic *Paenibacillus* sp. which is isolated from *Robinia pseudoacacia* (black locust) seeds. Their application as carriers of genes transformed in them for introducing desirable characteristics into host plants has been successfully shown in endophyte *Fusarium oxysporum* in which nitrate reductase *nia* genes from *Fusarium oxysporum* has been successfully transformed using plasmid pNH24 containing the *nia* genes and plasmid pNOM 102 carrying the *Escherichia coli*  $\beta$ -glucuronidase gus A gene<sup>106</sup>. Ellatif<sup>107</sup> successfully used fungus *Trichoderma harzianum* kj831197.1 to enhance the production of microbial xylanase and for the cloning of xylanase genes in *E. coli* DH5a using a pUC19 vector using restriction enzymes HindIII and EcoRI. It was shown that production of xylanase was increased up to 23.9-folds.

## 8. Conclusions

A plant is associated with endophytic microbial community comprising of diverse species of bacterial and fungal populations. Although much is not known about how these endophytes interact with the host tissues, however, they are not just passive inhabitants but are active colonizers. They manipulate plants' morphology and physiology and alter plant's immune system and metabolite profiles thereby increasing the potential fitness of plants by enhancing growth, development, biomass especially in stress conditions. The successful use of the endophytes in agriculture system will depend on the competence of the strains to establish in the already existing community of microorganisms grouped according to similarity, and identified by amplification and partial sequences of 16S DNAr. Isolates were grown until exponential growth phase to evaluate the atmospheric nitrogen fixation, phosphate solubilization, siderophores, and phytohormones, such as indole-3-acetic acid, zeatin, gibberellic acid and abscisic acid production, as well as antifungal, protease, and 1-aminocyclopropane-1-carboxylate (ACC With the increasing in-depth knowledge of the mechanisms of enhanced resistance to biotic and abiotic stresses and the phenomenon

of cross-protection and field application mechanisms effective technologies will be available very soon for field applications.

## 9. Conflicts of Interest

The authors declare no conflicts of interest.

## 10. Acknowledgments

The authors are grateful to Director, CSIR-NBRI, and Lucknow for providing all the facilities necessary for the research work under the project heads OLP-105 and BSC-204. The authors acknowledge Integral University for providing the MCN number IU/R&D/2022- MCN0001403 to the MS.

## 11. References

1. Rusty R, Regina Redman R. More than 400 million years of evolution and some plants still can't make it on their own: Plant stress tolerance via fungal symbiosis. *Journal of Experimental Botany*. 2008; 59(5):1109–14. PMID: 18267941. <https://doi.org/10.1093/jxb/erm342>
2. Chaturvedi H, Singh V, Gupta G. Potential of bacterial endophytes as plant growth promoting factors. *J Plant Pathol Microbiol*. 2016; 7(9):1–6.
3. Lata R, Chowdhury S, Gond SK, White JF. Induction of abiotic stress tolerance in plants by endophytic microbes. *Letters in Applied Microbiology*. 2018; 66(4):258–76. PMID: 29359344. <https://doi.org/10.1111/lam.12855>
4. Michael K, Taylor TN, Hass H, Kerp H, Dotzler N, Hermsen EJ. Fungal endophytes in a 400-million-yr-old land plant: Infection pathways, spatial distribution, and host responses. *New Phytologist*. 2007; 174(3):648–57. PMID: 17447919. <https://doi.org/10.1111/j.1469-8137.2007.02008.x>
5. Gunatilaka A, Leslie A. Natural products from plant-associated microorganisms: Distribution, structural diversity, bioactivity and implications of their occurrence. *Journal of Natural Products*. 2006; 69(3):509–26. PMID: 16562864 PMID: PMC3362121. <https://doi.org/10.1021/np058128n>
6. Gustavo S, Moreno-Hagelsieb G, Orozco-Mosqueda MDC, Glick BR. Plant growth-promoting bacterial endophytes. *Microbiological Research*. 2016; 183:92–9. PMID: 26805622. <https://doi.org/10.1016/j.micres.2015.11.008>
7. Khare E, Mishra J, Arora, NK. Multifaceted interactions between endophytes and plant: Developments and prospects. *Frontiers in Microbiology*. 2018; 9:2732.
8. Daniya E, Arthikala MK, Melappa G, Santoyo G. *Alternaria* Species: Endophytic fungi as alternative sources of bioactive compounds. *Italian Journal of Mycology*. 2018; 47(1):40–54. <https://doi.org/10.6092/issn.2531-7342/8468>
9. Fadji AE, Babalola OO. Elucidating mechanisms of endophytes used in plant protection and other bioactivities with multifunctional prospects. *Frontiers in Bioengineering and Biotechnology*.

- (2020). 8, 467. PMID: 32500068 PMCID: PMC7242734. <https://doi.org/10.3389/fbioe.2020.00467>
10. Dubey A, Malla MA, Kumar A, Dayanandan S, Khan ML. Plants endophytes: Unveiling hidden agenda for bioprospecting toward sustainable agriculture. *Critical Reviews in Biotechnology*. 2020; 40(8):1210–31. PMID: 32862700. <https://doi.org/10.1080/07388551.2020.1808584>
  11. Faegheh E, Harighi B. Isolation and identification of endophytic bacteria with plant growth promoting activity and biocontrol potential from wild pistachio trees. *Plant Pathology Journal*. 2018; 34(3):208–17. PMID: 29887777 PMCID: PMC5985647. <https://doi.org/10.5423/PPJ.OA.07.2017.0158>
  12. Brunetti C, Saleem AR, Della Rocca G, Emiliani G, De Carlo A, Balestrini R, Centritto, M. Effects of plant growth-promoting rhizobacteria strains producing ACC deaminase on photosynthesis, isoprene emission, ethylene formation and growth of *Mucuna pruriens* (L.) DC. in response to water deficit. *Journal of Biotechnology*. 2021; 331:53–62. PMID: 33727083. <https://doi.org/10.1016/j.jbiotec.2021.03.008>
  13. Zandalinas SI, Balfagón, Gómez-Cadenas A, Mittler, R. Responses of plants to climate change: Metabolic changes during abiotic stress combination in plants. *Journal of Experimental Botany*. 2022; 73(11):3339–54. PMID: 35192700. <https://doi.org/10.1093/jxb/erac073>
  14. Adeleke BS, Babalola OO. The plant endosphere-hidden treasures: A review of fungal endophytes. *Biotechnology and Genetic Engineering Reviews*. 2021; 37(2):154–77. PMID: 34666635. <https://doi.org/10.1080/02648725.2021.1991714>
  15. Chao Z, Wang J, Liu G, Song Z, Fang L. Impact of soil leachate on microbial biomass and diversity affected by plant diversity. *Plant and Soil*. 2019; 439(1-2):505–23. <https://doi.org/10.1007/s11104-019-04032-x>.
  16. Deyett E, Rolshausen PE. Endophytic microbial assemblage in grapevine. *FEMS Microbiology Ecology*. 2020; 96(5):fiae053.
  17. Materatski P, Varanda C, Carvalho T, Dias AB, Campos MD, Rei F, Félix MDR. Spatial and temporal variation of fungal endophytic richness and diversity associated to the phyllosphere of olive cultivars. *Fungal Biology*. 2019; 123(1):66–76. PMID: 30654959. <https://doi.org/10.1016/j.funbio.2018.11.004>.
  18. Dhayanithy G, Kamalraj S, Jayabaskaran C. Diversity and biological activities of endophytic fungi associated with *catharanthus roseus*. *BMC Microbiology*. 2019. PMID: 30665368 PMCID: PMC6341747. <https://doi.org/10.1186/s12866-019-1386-x>.
  19. Daru BH, Bowman EA, Pfister DH, A. Elizabeth Arnold AE. A novel proof of concept for capturing the diversity of endophytic fungi preserved in herbarium specimens. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 2019; 374. PMID: 30455213 PMCID: PMC6282087. <https://doi.org/10.1098/rstb.2017.0395>
  20. Jiang M, Wang Z, Li X, Liu S, Song F, Liu F. Relationship between endophytic microbial diversity and grain quality in wheat exposed to multi-generational CO<sub>2</sub> elevation. *Science of The Total Environment*. 2021; 776:146029. PMID: 33652312. <https://doi.org/10.1016/j.scitotenv.2021.146029>
  21. Enquahone S, van Marle G, Simachew A. Plant growth-promoting characteristics of halotolerant endophytic bacteria isolated from *Sporobolus spicatus* (Vahr) Kunth and *Cyperus laevigatus* L. of Ethiopian rift valley lakes. *Archives of Microbiology*. 2022; 204(7):1–15. PMID: 35723754. <https://doi.org/10.1007/s00203-022-03021-6>
  22. Shah S, Shah B, Sharma R, Rekadwad B, Shouche YS, Sharma J, Pant B. Colonization with non-mycorrhizal culturable endophytic fungi enhances orchid growth and indole acetic acid production. *BMC Microbiology*. 2022; 22(1):1–13. PMID: 35418028 PMCID: PMC9006483. <https://doi.org/10.1186/s12866-022-02507-z>
  23. Yavad U, Bano N, Bag S, Srivastava S, Singh PC. An insight into the endophytic bacterial community of tomato after spray application of Propiconazole and *Bacillus subtilis* Strain NBRI-W9. *Microbiology Spectrum*. Accepted. 2022.
  24. Li JL, Sun X, Zheng Y, Lü PP, Wang YL, Guo LD. Diversity and community of culturable endophytic fungi from stems and roots of desert halophytes in northwest China. *MycKeys*. 2020; 62:75. PMID: 32076383 PMCID: PMC7010840. <https://doi.org/10.3897/mycokeys.62.38923>
  25. Wolfe ER, Ballhorn DJ. Do foliar endophytes matter in litter decomposition? *Microorganisms*. 2020; 8(3):446. PMID: 32245270 PMCID: PMC7143956. <https://doi.org/10.3390/microorganisms8030446>
  26. Verma SK, Gond SK, Mishra A, Sharma VK, Kumar J, Singh DK, Kharwar RN. Fungal endophytes representing diverse habitats and their role in plant protection. In *Developments in Fungal Biology and Applied Mycology*. 2017; 135–57. Springer, Singapore.
  27. McCargo PD, Iannone LJ, Soria M, Novas MV. Diversity of foliar endophytes in a dioecious wild grass and their interaction with the systemic Epichloë. *Fungal Ecology*. 2020; 47:100945. <https://doi.org/10.1016/j.funeco.2020.100945>
  28. Mishra S, Bhattacharjee A, Sharma S. An ecological insight into the multifaceted world of plant-endophyte association. *Critical Reviews in Plant Sciences*. 2021; 40(2):127–46. <https://doi.org/10.1080/07352689.2021.1901044>
  29. Santangelo JS, Kotanen PM. Nonsystemic fungal endophytes increase survival but reduce tolerance to simulated herbivory in subarctic *Festuca rubra*. *Ecosphere*. 2016; 7(5):e01260.
  30. Bamisile BS, Senyo Akutse K, Dash CK, Qasim M, Ramos Aguila LC, Ashraf HJ, Wang L. Effects of seedling age on colonization patterns of Citrus limon plants by endophytic *Beauveria bassiana* and *Metarhizium anisopliae* and their influence on seedlings growth. *Journal of Fungi*. 2020; 6(1):29. PMID: 32106557 PMCID: PMC7151192. <https://doi.org/10.3390/jof6010029>
  31. Tiwari S, Gupta SC, Chauhan PS, Lata, C. An OsNAM gene plays important role in root rhizobacteria interaction in transgenic Arabidopsis through abiotic stress and phytohormone crosstalk. *Plant Cell Reports*. 2021; 40(1):143–55. PMID: 33084964. <https://doi.org/10.1007/s00299-020-02620-1>
  32. dos Santos TB, Ribas AF, de Souza SGH, Budzinski IGF, Domingues DS. Physiological responses to drought, salinity, and heat stress in plants: A review. *Stresses*. 2022; 2(1):113–35.

33. Waller F, Beate A, Helmut B, József F, Katja B, Marina F, Tobias H, et al. The endophytic fungus *Piriformospora indica* reprograms barley to salt-stress tolerance, disease resistance, and higher yield. *Proceedings of the National Academy of Sciences of the United States of America*. 2005; 102(38):13386–91. PMID: 16174735 PMCID: PMC1224632. <https://doi.org/10.1073/pnas.0504423102>
34. Khan, Abdul Latif, Muhammad Hamayun, Muhammad Waqas, Sang Mo Kang, Yoon Ha Kim, Duk Hwan Kim, and In Jung Lee. “Exophiala Sp.LHL08 Association Gives Heat Stress Tolerance by Avoiding Oxidative Damage to Cucumber Plants.” *Biology and Fertility of Soils*. 2012.<https://doi.org/10.1007/s00374-011-0649-y>
35. Khan AL, Muhammad H, Yoon HK, Sang MK, In JLee. Ameliorative symbiosis of endophyte (*Penicillium funiculosum* LHL06) under salt stress elevated plant growth of glycine Max L. *Plant Physiology and Biochemistry*. 2011; 49(8):852–61. PMID: 21458283. <https://doi.org/10.1016/j.plaphy.2011.03.005>
36. Khan AL, Muhammad H, Yoon HK, Sang MK, Joon HL, In JLee. Gibberellins producing endophytic *Aspergillus fumigatus* Sp. LHO<sub>2</sub> influenced endogenous phytohormonal levels, isoflavonoids production and plant growth in salinity stress. *Process Biochemistry*. 2011; 46(2):440–7. <https://doi.org/10.1016/j.procbio.2010.09.013>
37. Tripathi RD, Srivastava S, Mishra S, Singh N, Tuli R, Gupta DK, Maathuis FJM. Arsenic hazards: Strategies for tolerance and remediation by plants. *Trends in Biotechnology*. 2007; 25(4):158–68. PMID: 17306392. <https://doi.org/10.1016/j.tibtech.2007.02.003>
38. Arriagada C, Aranda E, Sampedro I, Garcia-Romera I, Ocampo JA. Contribution of the saprobic fungi *trametes versicolor* and *Trichoderma harzianum* and the *Arbuscular mycorrhizal* fungi *Glomus deserticola* and *G. claroideum* to arsenic tolerance of *Eucalyptus globulus*. *Bioresource Technology*. 2009; 100(24):6250–7. PMID: 19648001. <https://doi.org/10.1016/j.biortech.2009.07.010>
39. Ali AH, Usama R, El-Zayat S, El-Sayed MA. The role of the endophytic fungus, *thermomycetes lanuginosus* on mitigation of heat stress to its host desert plant *Cullen plicata*. *Biologia Futura*. 2019; 70(1):1–7. PMID: 34554436. <https://doi.org/10.1556/019.70.2019.01>
40. Vita PD, Taranto F. Durum wheat (*Triticum turgidum* sp. durum) breeding to meet the challenge of climate change. In *Advances in plant breeding strategies: Cereals*. Springer, Cham. 2019; 471–524. [https://doi.org/10.1007/978-3-030-23108-8\\_13](https://doi.org/10.1007/978-3-030-23108-8_13)
41. Redman RS, Yong OK, Woodward CJDA, Greer C, Espino L, Doty SL, Rodriguez RJ. “Increased fitness of rice plants to abiotic stress via habitat adapted symbiosis: A strategy for mitigating impacts of climate change.” *PLoS ONE*. 2011; 6(7):e14823. PMID: 21750695 PMCID: PMC3130040. <https://doi.org/10.1371/journal.pone.0014823>
42. Xu FJ, Song SL, Ma CY, Zhang W, Sun K, Tang MJ, Xie XG, Fan KK, Dai CC. Endophytic fungus improves peanut drought resistance by reassembling the root-dwelling community of *Arbuscular mycorrhizal* fungi. *Fungal Ecology*. 2020; 48:100993. <https://doi.org/10.1016/j.funeco.2020.100993>
43. Vijayabharathi R, Arumugam S, Subramaniam G. A renaissance in plant growth-promoting and biocontrol agents by endophytes. In *Microbial Inoculants in Sustainable Agricultural Productivity: Vol. 1: Research Perspectives*. 2016. [https://doi.org/10.1007/978-81-322-2647-5\\_3](https://doi.org/10.1007/978-81-322-2647-5_3)
44. Singh PC, Shukla D, Touseef F, Nautiyal CS, Johri JK. Biological control of fusarium sp. NBRI-PMSF12 pathogenic to cultivated betelvine by *Bacillus* Sp. NBRI-W9, a Potential Biological Control Agent. *Journal of Plant Growth Regulation*. 2017; 36(1):106–17. <https://doi.org/10.1007/s00344-016-9623-0>
45. Hardoim, PR, Hardoim CCP, van Overbeek LS, van Elsas JD. Dynamics of seed-borne rice endophytes on early plant growth stages. *PLoS ONE*. 2012; 7(2):e30438. PMID: 22363438 PMCID: PMC3281832. <https://doi.org/10.1371/journal.pone.0030438>
46. Sgro V, Fabricio C, Masciarelli O, Del Papa MF, Lagares A, Luna V. Isolation and characterization of endophytic Plant Growth-Promoting (PGPB) or Stress Homeostasis-Regulating (PSHB) Bacteria associated to the halophyte *Prosopis strombulifera*. *Applied Microbiology and Biotechnology*. 2009; 85(2):371–81. PMID: 19655138. <https://doi.org/10.1007/s00253-009-2116-3>
47. Zhang YF, Lin YH, Zhao JC, Wen HZ, Qing YW, Meng Q, Xia FS. Characterization of lead-resistant and ACC deaminase-producing endophytic bacteria and their potential in promoting lead accumulation of rape. *Journal of Hazardous Materials*. 2011; 186(2-3):1720–5. PMID: 21227577. <https://doi.org/10.1016/j.jhazmat.2010.12.069>
48. Dudeja SS, Giri R, Saini R, Suneja-Madan P, Kothe E. Interaction of endophytic microbes with legumes. *Journal of Basic Microbiology*. 2012; 52(3):248–60. PMID: 21953403. <https://doi.org/10.1002/jobm.201100063>
49. Khan N, Ali S, Shahid M, Mustafa A, Sayyed RZ, Curá JA. Insights into the interactions among roots, rhizosphere and rhizobacteria for improving plant growth and tolerance to abiotic stresses: A review. *Cells*. 2021; 10(6):1551. PMID: 34205352 PMCID: PMC8234610. <https://doi.org/10.3390/cells10061551>
50. Jayakumar A, Padmakumar P, Nair IC, Radhakrishnan EK. Drought tolerant bacterial endophytes with potential plant probiotic effects from *Ananas comosus*. *Biologia*. 2020; 75(10):1769–78. <https://doi.org/10.2478/s11756-020-00483-1>
51. Dasgupta MG, Burragoni S, Amrutha S, Muthupandi M, Parveen ABM, Sivakumar V, Ulaganathan, K. Diversity of bacterial endophyte in *Eucalyptus* clones and their implications in water stress tolerance. *Microbiological Research*. 2020; 241:126579. PMID:32861101 <https://doi.org/10.1016/j.micres.2020.126579>
52. Ziarovská J, Medo J, Kysel M, Zamiešková L, Kačániová M. Endophytic bacterial microbiome diversity in early developmental stage plant tissues of wheat varieties. *Plants*. 2020; 9(2):266. PMID: 32085509 PMCID: PMC7076375. <https://doi.org/10.3390/plants9020266>
53. Yang L, Schroder P, Vestergaard G, Schloter M, Radl V. Response of barley plants to drought might be associated with the recruiting of soil-borne endophytes. *Microorganisms*. 2020; 8(9):1414. PMID: 32937884 PMCID: PMC7565417. <https://doi.org/10.3390/microorganisms8091414>

54. Goswami M, Suresh DEKA. Plant growth-promoting rhizobacteria-alleviators of abiotic stresses in soil: A review. *Pedosphere*. 2020; 30(1):40–61.
55. Potters G, Pasternak TP, Guisez Y, Palme KJ, Jansen MAK. Stress-induced morphogenic responses: growing out of trouble? *Trends in Plant Science*. 2007; 12(3):98–105. PMID: 17287141. <https://doi.org/10.1016/j.tplants.2007.01.004>
56. Waqas, M, Khan AL, Kamran M, Hamayun M, Kang SM, Kim YH, Lee IJ. Endophytic fungi produce gibberellins and indoleacetic acid and promotes host-plant growth during stress. *Molecules*. 2012; 17(9):10753–73. PMID: 22960869 PMCID: PMC6268353. <https://doi.org/10.3390/molecules170910754>
57. Merzaeva OV, Shirokikh IG. The production of auxins by the endophytic bacteria of winter rye. *Applied Biochemistry and Microbiology*. 2010. <https://doi.org/10.1134/S0003683810010072>
58. Chandra D, Srivastava R, Glick BR, Sharma AK. Rhizobacteria producing ACC deaminase mitigate water-stress response in finger millet (*Eleusine coracana* (L.) Gaertn.). *Biotech*, 2020; 10(2):1–15. PMID: 32030334 PMCID: PMC6979641. <https://doi.org/10.1007/s13205-019-2046-4>
59. Soni R, Sarita K. Yadav SK, Rajput AS. ACC-deaminase Producing Rhizobacteria: Prospects and application as stress busters for stressed agriculture. 2018; 161–75. [https://doi.org/10.1007/978-981-10-7146-1\\_9](https://doi.org/10.1007/978-981-10-7146-1_9)
60. Jung SC, Martinez-Medina A, Lopez-Raez JA, Pozo MJ. Mycorrhiza-induced resistance and priming of plant defenses. *Journal of Chemical Ecology*. 2012; 38:651–64. PMID: 22623151. <https://doi.org/10.1007/s10886-012-0134-6>
61. Smirnov N, Smallwood MF, Calvert CM, Bowles DJ, Eds. 1999. Plant responses to environmental stress. 224 Pp. Oxford: Bios Scientific Publishers. 2000£70 (Hardback). <https://doi.org/10.1006/anbo.2000.1110>
62. Torres, MS, White JF, Zhang X, Hinton DM, Bacon CW. Endophyte-mediated adjustments in host morphology and physiology and effects on host fitness traits in grasses. *Fungal Ecology*. 2012; 5(3):322–30. <https://doi.org/10.1016/j.funeco.2011.05.006>
63. Kumar M, Sharma R, Jogawat A, Singh P, Dua M, Johri AK, Gill SS, et al. Piriformospora indica, a root endophytic fungus, enhances abiotic stress tolerance of the host plant. In *Improving Crop Resistance to Abiotic Stress*. 2012. <https://doi.org/10.1002/9783527632930.ch24>
64. Saddique, MAB, Ali Z, Khan AS, Rana IA, Shamsi IH. Inoculation with the endophyte piriformospora indica significantly affects mechanisms involved in osmotic stress in rice. *Rice*. 2018; 11:34. PMID: 29799607 PMCID: PMC5968016. <https://doi.org/10.1186/s12284-018-0226-1>
65. Helmut B, Fodor J, Harrach BD, Niemczyk E, Barna B, Gullner G, Janeczko A, et al. Salt tolerance of barley induced by the root endophyte *Piriformospora indica* is associated with a strong increase in antioxidants. *New Phytologist*. 2008; 180(2):501–10. PMID: 18681935, <https://doi.org/10.1111/j.1469-8137.2008.02583.x>
66. Hanhong B, Sicher RC, Kim MS, Kim SH, Strem MD, Melnick RL, Bailey BA. The beneficial endophyte *Trichoderma hamatum* isolate DIS 219b promotes growth and delays the onset of the drought response in theobroma cacao. *Journal of Experimental Botany*. 2009; 60(11):3279–95. PMID: 19564160 PMCID: PMC2718224. <https://doi.org/10.1093/jxb/erp165>
67. Xuemei L, Bu N, Li Y, Ma L, Xin S, Zhang L. Growth, photosynthesis and antioxidant responses of endophyte infected and non-infected rice under lead stress conditions. *Journal of Hazardous Materials*. 2012; 213-214:55–61. PMID: 22356744. <https://doi.org/10.1016/j.jhazmat.2012.01.052>
68. Lastochkin O, Garshina D, Ivanov S, Yuldashev R, Khafizova R, Allagulova C, Fedorova K, Avalbaev A, Maslennikova D, Bosacchi M. Seed priming with endophytic *Bacillus subtilis* modulates physiological responses of two different *Triticum aestivum* L. Cultivars under drought stress. *Plants*. 2020; 9(12):1810. PMID: 33371269 PMCID: PMC7766295. <https://doi.org/10.3390/plants9121810>
69. Bilal S, Shahzad R, Imran M, Jan R, Ki, KM, Lee IJ. Synergistic association of endophytic fungi enhances *Glycine max* L. resilience to combined abiotic stresses: Heavy metals, high temperature and drought stress. *Industrial Crops and Products*. 2020; 143:111931.
70. Raheem S, Khan AL, Bilal S, Asaf S, Lee IN. What is there in seeds? Vertically transmitted endophytic resources for sustainable improvement in plant growth. *Frontiers in Plant Science*. 2018. PMID: 29410675 PMCID: PMC5787091. <https://doi.org/10.3389/fpls.2018.00024>
71. Molina-Montenegro MA, Acuna-Rodríguez I.S., Torres-Díaz C, Gundel PE, Dreye, I. Antarctic root endophytes improve physiological performance and yield in crops under salt stress by enhanced energy production and Na<sup>+</sup> sequestration. *Scientific Reports*. 2020; 10(1):1-10. PMID: 32242034 PMCID: PMC7118072. <https://doi.org/10.1038/s41598-020-62544-4>
72. Liang L, Li L, Wang X, Zhu P, Wu H, Qi S. Plant growth-promoting endophyte *Piriformospora indica* alleviates salinity stress in *Medicago truncatula*. *Plant Physiology and Biochemistry*. 2017; 119:211–23. PMID: 28898746. <https://doi.org/10.1016/j.plaphy.2017.08.029>
73. Ying M, Rajkumar M, Moreno A, Zhang C, Freitas H. Serpentine endophytic bacterium *Pseudomonas azotoformans* ASS1 accelerates phytoremediation of soil metals under drought stress. *Chemosphere*. 2017; 185:75–85. PMID: 28686889. <https://doi.org/10.1016/j.chemosphere.2017.06.135>
74. Chen C, Kaiyun X, Hao L, Juanli C, Xihui S, Yao W, Lei Z. Pantoea Alhagi, a novel endophytic bacterium with ability to improve growth and drought tolerance in wheat. *Scientific Reports*. 2017; 7:41564. PMID: 28128318 PMCID: PMC5269684. <https://doi.org/10.1038/srep41564>
75. Fatemeh H, Mosaddeghi MR, Dexter AR. Effect of the fungus *Piriformospora indica* on physiological characteristics and root morphology of wheat under combined drought and mechanical stresses. *Plant Physiology and Biochemistry*. 2017; 118:107–20. PMID: 28624682. <https://doi.org/10.1016/j.plaphy.2017.06.005>
76. Muhammad I, Ali N, Jan G, Jan FG, Ur Rahman I, Iqbal A, Hamayun M. IAA producing fungal endophyte *Penicillium roqueforti* thom., enhances stress tolerance and nutrients uptake in wheat plants grown on heavy metal contaminated soils.

- PLoS ONE. 2018; 13(11): e0208150. PMID: 30496253 PMCID: PMC6264496. <https://doi.org/10.1371/journal.pone.0208150>
77. Yu Y, Teng Z, Mou Z, Lv Y, Li T, Chen S, Zhao D, Zhao Z. Melatonin confers heavy metal-induced tolerance by alleviating oxidative stress and reducing the heavy metal accumulation in *Exophiala pisciphila*, a Dark Septate Endophyte (DSE). *BMC Microbiology*. 2021; 21(1):1–11.
  78. Somayeh E, Alikhani HA, Pourbabaei AA, Etesami H, Zadeh BM, Sarmadian F. Improved growth and nutrient acquisition of wheat genotypes in phosphorus deficient soils by plant growth-promoting rhizospheric and endophytic bacteria. *Soil Science and Plant Nutrition*. 2018; 64(6):719–27. <https://doi.org/10.1080/00380768.2018.1510284>
  79. Hamayun IM, Hussain A, Iqbal A, Khan SA, Lee IJ. Endophytic fungus *Aspergillus japonicus* mediates host plant growth under normal and heat stress conditions. *BioMed Research International*. 2018; 2018: 7696831. PMID: 30627568 PMCID: PMC6304497. <https://doi.org/10.1155/2018/7696831>
  80. Tiryaki D, İhsan A, Okkeş A. Psychrotolerant bacteria isolated from the leaf apoplast of cold-adapted wild plants improve the cold resistance of bean (*Phaseolus vulgaris* L.) under low temperature. *Cryobiology*. 2019; 86:111–9. PMID: 30419217. <https://doi.org/10.1016/j.cryobiol.2018.11.001>.
  81. Mohamad OAA, Liu YH, Li L, Ma JB, Huang Y, Gao L, Fang BZ, Wang S, El-Baz AF, Jiang HC, Li, WJ. Synergistic plant-microbe interactions between endophytic actinobacteria and their role in plant growth promotion and biological control of cotton under salt stress. *Microorganisms*. 2022; 10(5):867. PMID: 35630312 PMCID: PMC9143301. <https://doi.org/10.3390/microorganisms10050867>
  82. Zhou L, Li C, White JF, Johnson RD. Synergism between calcium nitrate applications and fungal endophytes to increase sugar concentration in *Festuca sinensis* under cold stress. *Peer J*. 2021; 9:e10568. PMID: 35070512 PMCID: PMC8759379. <https://doi.org/10.7717/peerj.10568>
  83. Maclá-Vicente JG, Rosso LC, Ciancio A, Jansson HB, Lopez-Llorca LV. Colonisation of barley roots by Endophytic *Fusarium equiseti* and *Pochonia chlamydosporia*: Effects on plant growth and disease. *Annals of Applied Biology*. 2009; 155(3):391–401. <https://doi.org/10.1111/j.1744-7348.2009.00352.x>.
  84. Morales-Cedeño LR, del Carmen Orozco-Mosqueda M, Loez-Lara PD, Parra-Cota FI, de Los Santos-Villalobos S, Santoyo G. Plant growth-promoting bacterial endophytes as biocontrol agents of pre-and post-harvest diseases: Fundamentals, methods of application and future perspectives. *Microbiological Research*. 2020; 242:126612. PMID: 33059112. <https://doi.org/10.1016/j.micres.2020.126612>
  85. Trivedi G, Patel P, Saraf M. Synergistic effect of endophytic selenium bacteria on biofortification and growth of Glycine max under drought stress. *South African Journal of Botany*. 2020; 134:27–35. <https://doi.org/10.1016/j.sajb.2019.10.001>
  86. Jaber LR, Enkerli J. Fungal entomopathogens as endophytes: Can they promote plant growth? *Biocontrol Science and Technology*. 2017; 27(1):28–41. <https://doi.org/10.1080/09583157.2016.1243227>
  87. Jaber LR, Araj SE. Interactions among endophytic fungal entomopathogens (Ascomycota:Hypocreales), the green peach aphid myzus persicae sulzer (Homoptera:Aphididae) and the Aphid Endoparasitoid *Aphidius Colemani* Viereck (Hymenoptera: Braconidae). *Biological Control*. 2018; 116:53–61. <https://doi.org/10.1016/j.biocontrol.2017.04.005>
  88. Kushwaha P, Kashyap PL, Kuppasamy P, Srivastava AK, Tiwari RK. Functional characterization of endophytic bacilli from pearl millet (*Pennisetum glaucum*) and their possible role in multiple stress tolerance. *Plant Biosystems*. 2019; 154(4):503–14. <https://doi.org/10.1080/11263504.2019.1651773>
  89. Jaber LR, Salem NM. Endophytic colonisation of squash by the fungal entomopathogen *Beauveria bassiana* (Ascomycota:Hypocreales) for managing zucchini yellow mosaic virus in cucurbits. *Biocontrol Science and Technology*. 2014; 224(10):1096–109. <https://doi.org/10.1080/09583157.2014.923379>
  90. Flonc B, Barberchec, M, Ahmad, I. Observations on the Relationships between Endophytic *Metarhizium robertsii*, *Spodoptera frugiperda* (Lepidoptera:Noctuidae) and Maize. *Pathogens*. 2021; 10(6):713. PMID: 34200234 PMCID: PMC8230249. <https://doi.org/10.3390/pathogens10060713>
  91. Passari AK, Upadhyaya K, Singh G, Abdel-Azeem AM, Thankappan S, Uthandi S, Singh BP. Enhancement of disease resistance, growth potential and photosynthesis in tomato (*Solanum lycopersicum*) by inoculation with an endophytic actinobacterium, *Streptomyces thermocarboxydus* strain BPSAC147. *PloS one*. 2019; 14(7):e0219014. PMID: 31269087 PMCID: PMC6608948. <https://doi.org/10.1371/journal.pone.0219014>
  92. Greenfield M, Gómez-Jiménez MI, Ortiz V, Vega FE, Kramer M, Parsa S. *Beauveria bassiana* and metarhizium anisopliae endophytically colonize cassava roots following soil drench inoculation. *Biological Control*. 2016; 95:40–8. PMID: 27103778 PMCID: PMC4825668. <https://doi.org/10.1016/j.biocontrol.2016.01.002>
  93. Wei QY, Li YY, Xu C, Wu YX, Zhang YR, Liu H. Endophytic colonization by *Beauveria bassiana* increases the resistance of tomatoes against *Bemisia tabaci*. *Arthropod-Plant Interactions*. 2020; 14(3):289–300. <https://doi.org/10.1007/s11829-020-09746-9>
  94. Rondot Y, Reineke A. Endophytic *Beauveria bassiana* in grapevine vitis vinifera (L.) reduces infestation with piercing-sucking insects. *Biological Control*. 2018; 116:82–9. <https://doi.org/10.1016/j.biocontrol.2016.10.006>
  95. Wang GF, Meng JF, Tian T, Xiao XQ, Zhang B, Xiao YN. Endophytic *Bacillus velezensis* strain B-36 is a potential biocontrol agent against lotus rot caused by *Fusarium oxysporum*. *Journal of Applied Microbiology*. 2020; 128(4):1153–62. PMID: 31808212 PMCID: PMC7079251. <https://doi.org/10.1111/jam.14542>
  96. Akello J, Thomas D, Clifford SG, Coyne D, Nakavuma J, Paparu P. *Beauveria bassiana* (Balsamo) Vuillemin as an Endophyte in tissue culture banana (*Musa Spp.*). *Journal of Invertebrate Pathology*. 2007; 96(1):34–42. PMID: 17391694. <https://doi.org/10.1016/j.jip.2007.02.004>

97. Qayyum MA, Waqas W, Muhammad JA, Shahbaz TS, Dunlap CA. Infection of *Helicoverpa armigera* by endophytic *Beauveria bassiana* colonizing tomato plants. *Biological Control*. 2015; 90:200–7. <https://doi.org/10.1016/j.biocontrol.2015.04.005>
98. Allegrucci N, Velazquez M., Russo ML, Vianna MF, Abarca C, Scorsetti AC. Establishment of the entomopathogenic fungus *Beauveria bassiana* as an endophyte in *Capsicum annuum* and its effects on the aphid pest *Myzus persicae* (Homoptera:Aphididae). *Revista de Biología Tropical*. 2020; 68(4):1084–94. <https://doi.org/10.15517/rbt.v68i4.41218>
99. Muvea AM, Meyhofer R, Subramanian S, Poehling HM, Ekesi S, Maniania NK. Colonization of onions by endophytic fungi and their impacts on the biology of *Thrips tabaci*. *PLoS ONE*. 2014; 9(9):e108242. PMID: 25254657 PMCID: PMC4177896. <https://doi.org/10.1371/journal.pone.0108242>
100. Win KT, Fukuyo T, Keiki O, Yoshinari Ohwaki Y. The ACC deaminase expressing endophyte *Pseudomonas* spp. enhances NaCl stress tolerance by reducing stress-related ethylene production, resulting in improved growth, photosynthetic performance and ionic balance in tomato plants. *Plant Physiology and Biochemistry*. 2018; 127:599–607. PMID: 29730579. <https://doi.org/10.1016/j.plaphy.2018.04.038>
101. Jaber LR. Grapevine leaf tissue colonization by the fungal entomopathogen *Beauveria bassiana* L. and its effect against downy mildew. *BioControl*. 2015; 60(1):103–12. <https://doi.org/10.1007/s10526-014-9618-3>
102. Tefera T, Vidal S. Effect of inoculation method and plant growth medium on endophytic colonization of sorghum by the entomopathogenic fungus *Beauveria bassiana*. *BioControl*. 2009; 54:663–9. <https://doi.org/10.1007/s10526-009-9216-y>
103. Russo ML, Pelizza SA, Cabello MN, Stenglein SA, Scorsetti AC. Endophytic colonisation of tobacco, corn, wheat and soybeans by the fungal entomopathogen *Beauveria bassiana* (Ascomycota, Hypocreales). *Biocontrol Science and Technology*. 2015; 25(4):475–80. <https://doi.org/10.1080/09583157.2014.982511>
104. Jin M, Yang C, Wei L, Cui L, Osei R, Cai F, Ma T, Wang Y. Transcriptome analysis of *Stipa purpurea* interacted with endophytic *Bacillus subtilis* in response to temperature and ultraviolet stress. *Plant Growth Regulation*. 2022 Jun; 22:1–4. <https://doi.org/10.1007/s10725-022-00849-2>
105. Zhang JX, Chen ZT, Meng XL, Mu GY, Hu WB, Zhao J, Nie GX. Gene cloning, expression, and characterization of a novel  $\beta$ -Mannanase from the Endophyte *Paenibacillus* Sp. CH-3. *Biotechnology and Applied Biochemistry*. 2017; 64(4):471–81. PMID: 27222362. <https://doi.org/10.1002/bab.1510>
106. Pamphile JA, da Rocha CLMSC, Azevedo JL. Co-transformation of a tropical maize endophytic isolate of *Fusarium verticillioides* (Synonym F. Moniliforme) with GusA and Nia Genes. *Genetics and Molecular Biology*. 2004; 27:253–8. <https://doi.org/10.1590/S1415-47572004000200021>
107. Sawsan Abd E, Abdel Razik ES, Al-Surhane AA, Al-Sarraj F, Daigham GE, Mahfouz AY. Enhanced Production, Cloning, and Expression of a Xylanase Gene from Endophytic Fungal Strain *Trichoderma harzianum* kj831197.1: Unveiling the In Vitro Anti-Fungal Activity against Phytopathogenic Fungi. *Journal of Fungi*. 2022; 8(5):447.