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Exploring the role of endophytic fungi in the amelioration of drought stress in plants

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Abstract: Drought is one of the environmental stresses that threaten food availability. It results in decreased crop yields and developments and diminishes overall plant health. Chemical solutions for alleviating drought stress may be harmful to the environment. Using an alternative, microorganisms help counter the effects of drought stress. Endophytes have a mutualistic relationship with the host as they provide protection and get nutrients. Fungal endophytes assist plants in countering the damaging results of drought stress by producing phytohormones and growth-promoting compounds that promote root and shoot growth and enhance crop productivity. Inoculating maize plants with endophytic fungi like *Fusarium oxysporum* and *Penicillium* sp. have a higher chance of surviving drought stress. These organisms can increase root length, allowing moisture to reach deeper into the soil. This review explores endophytic fungi's roles in alleviating drought stress's consequences on plants. More investigations should be carried out on the favourable effects of fungal endophytes in the mitigation of drought stress through pot and field inoculation.

Keywords: maize; plant protection; plant-growth promotion; endophytes

Endophytes are microbes that colonize plant tissues without injuring or damaging the plant (Omomowo & Babalola 2019). They exist in the roots, stem, leaves, flowers, fruits, seeds and pollen (Zhang et al. 2019). Endophytes are typically fungi or bacteria and, in most cases, are transmitted through seeds and begin to stimulate plant development and fitness as the seed germinates (White et al. 2019). Endophytes also enter the plants via naturally occurring wounds from growth or through the root hairs at epidermal conjunctions (Lata et al. 2019). Their diversity depends on factors such as plant age, plant parts, soil type, geography and climatic conditions (Ababutain et al. 2021). Endophytes are in most plants and are reported to be in crops, plants inhabiting harsh environments, forests, mangroves, pteridophytes, cone-bearing and flowering plants and wild plants (Burragoni & Jeon 2021). The interior of the plant host is a secured niche containing necessary nutrients for endophytic growth (Baron & Rigobelo 2022) as well as a balance between mutualistic, parasitic or commensal symbiosis, which is controlled by chemicals (Caruso et al. 2020). The relationship between plants and endophytes is suggested to be older than 400 mil. years old (Orozco-Mosqueda & Santoyo 2021), as the earliest evidence of the relationship was the discovery of fungal hyphae and spores in fossilized tissues in plant stems and leaves of over 460 mil. years ago (Yan et al. 2019). Since the host plant acts as the protected niche, the endophytic microorganisms produce me-

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tabolites that increase nutrient absorption, promoting healthy plant growth and biomass gain (Santos et al. 2018). This symbiotic relationship is a successful mechanism that enables plants to inhabit extreme environments and tolerate different environmental stresses (Hereme et al. 2020). Endophytes have plant-growth-promoting and biocontrol properties and abilities to shield plants from biological and environmental stresses (Burragoni & Jeon 2021). In promoting plant growth, endophytes have antimicrobial activity, synthesize bioactive compounds, cycle nutrients and tolerate stress (Fadiji & Babalola 2020). Laboratory experiments and greenhouse trials show the ability of endophytes to alleviate stresses in agriculturally important crops and increase productivity (Chitnis et al. 2020). Consequently, using endophytes will decrease the use of chemical fertilizers, thus reducing greenhouse gas emissions and runoff to aquatic ecosystems.

Endophytes have part or the whole of their life cycle inside the host plant, and most originate from the rhizosphere attracted by root exudates, and they colonize the root (Santos et al. 2018). These root exudates are rich in nutrients and water and attract other microorganisms like fungi (Khare et al. 2018). Endophytic fungi help in the secondary metabolism of the host, including phytohormone balance, improve the uptake of nutrients and solubilize minerals, resulting in defence against pathogens and stress tolerance (Taulé et al. 2021). Unfortunately, most studies on endophytes have widely explored endophytic bacteria in mitigating drought stress (Meenakshi et al. 2019; Tufail et al. 2022). Currently, limited information exists on endophytic fungi's beneficial roles, such as crop improvement, biotechnological potentials, and drought mitigation in sustainable agriculture (Vaishnav et al. 2019). This present mini-review explored the beneficial roles and potential drought mitigation mechanisms of endophytic fungi on plants with special concentration on maize plants. We also highlighted some of the limitations in their application and way forward for future applications.

ENDOPHYTIC FUNGI

Fungal endophytes are a diverse group of asymptomatic fungi that intermittently colonize the plant tissue, resulting in saprophytic, commensalism or mutualistic interaction with their host plant (Galindo-Solís & Fernández 2022). Fungal endophytes have a close relationship with their host, and as a result, they face less competition for space and nutrients and receive protection against ultraviolet light and extreme temperatures (Gupta et al. 2020). The mutualistic relationship between plant host and endophytic fungi sees the plants giving necessary nutrients to the fungi, and the fungi, in turn, protect the host plant from both biotic and abiotic stresses (Sharaf et al. 2022). Fungal endophytes occupying plant tissues share mechanisms similar to those of host plants (Adeleke & Babalola 2021). Endophytic fungi increase the acquisition of plant hormones, thereby increasing biomass production, the expansion of the root system, plant development and crop yield (Baron & Rigobelo 2022). The endosymbiont synergy between fungal endophytes and plant hosts enhances the uptake of nutrients required for plants' metabolic activities relative to their function and growth (Adeleke & Babalola 2021). Endophytic fungi can break down the plant cell wall and change its structure by producing enzymes to degenerate the cell wall, allowing it to infiltrate and colonize the tissues (Lu et al. 2021). They live in a similar ecological niche to that of plant pathogens and control them by producing antagonistic substances through competition (Fontana et al. 2021). Plant roots have more diversity and an ample amount of endophytic fungi compared to shoots and seeds (Xia et al. 2019). The beneficial metabolites produced by endophytic fungi improve sustainable agriculture (Fadiji et al. 2020). One of the advantages of endophytic fungi is their ability to be grown in a laboratory setting and applied to plant hosts for research where their potential to be beneficial to the hosts is analysed (Morsy et al. 2020). Endophytic fungi with the capacity to synthesize plant hormones, acquire nutrients and secrete biocontrol agents are referred to as plant growth-promoting endophytes. Endophytic fungi promote plant growth directly through nutrient acquisition and phytohormone synthesis and indirectly by releasing enzymes that prevent injury to the plant (Adeleke et al. 2022). Therefore, endophytic fungi are prospective biotechnological tools in agricultural applications, mainly in harsh environmental conditions like arid and semi-arid areas (Moghaddam et al. 2021). Along with benefiting plant hosts, endophytic fungi have biological activities (El-Hawary et al. 2020). Endophytic fungi are divided into two

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major groups, namely the clavicipitaceous and non-clavicipitaceous. Clavicipitaceous endophytic fungi are common in grasses. Non-clavicipitaceous endophytic fungi are found in vascular and non-vascular plants. Non-clavicipitaceous endophytic fungi transfer systemically or horizontally and they occupy any part of the plant body (Rodriguez et al. 2009). Endophytic fungi can also be divided according to whether they are asexual or sexual, nutrition (biotrophic or necrotrophic) and the plant part they inhabit (foliar or roots) (Adeleke et al. 2022).

Organic farming practices increase the diversity of endophytic fungi. Fadiji et al. (2020), using shotgun metagenomic, identified two major endophytic fungi phyla, Ascomycota and Basidiomycota, in sites that had plants cultivated with organic fertilizers when compared to inorganic fertilizer sites and sites with no fertilizer. Various studies have revealed the capacity of endophytic fungi to mitigate abiotic stress in plants. Table 1 summarises recent studies using endophytic fungi in this regard.

IMPACT OF DROUGHT STRESS ON PLANTS

By meteorologists' definition, drought is the continued insufficiency of water with less than average rainfall (Zia et al. 2021). Drought stress happens when soil and atmospheric humidity are low and ambient air temperature is high (Lamaoui et al. 2018). Climate change, growing populations, and human activities result in drought becoming extreme and recurrent in arid and semi-arid regions, causing plant destruction (Zou et al. 2021) due to reduced water availability. The decrease in water availability for plants alters the concentrations of metabolites, which then limits plant growth and development (Ghabooli et al. 2020). Zhang et al. (2018) found that water stress decreases the photosynthetic rate with the lowest value observed on a 6-day drought treatment. Reacting to water stress, the stomata close, reducing leaf photosynthetic capacity, which leads to chloroplast dehydration and reduced carbon dioxide diffusion into the leaf

Table 1. Table showing some studies conducted on the stress mitigation potentials of endophytic fungi

Organisms	Plants	Effect	References
Pyrenophora, Chaetomium sp., *Phialocephala, Diarpothe* sp., *Fusarium* sp., *Acrocalymma* sp.	*Brassica oleraceae* var. *acephala* (Kale)	Cold tolerance	Poveda et al. 2020
Periconia macrospinosa, Neocamarosporium goegapense, N. chichasticinum	*Hordeum vulgare* L.	Salinity and drought tolerance	Hosseyni Moghaddam et al. 2022
Rhizopus oryzae	Sunflower and soybean	Heat stress tolerance	Ismail et al. 2020
Trichoderma harzianum, Glomus versiforme	Cowpea	*Cercospora* leaf spot disease mitigation	Omomowo et al. 2020
Penicillium minioluteum	*Glycine max* L. (Soybean)	Salt stress tolerance	Abdul Latif et al. 2011
Phomopsis liquidambaris	Peanuts	Increase in iron absorption	Du et al. 2022
Penicillium glabrum	Soybean and sunflower	Heat stress tolerance	Hamayun et al. 2021
Piriformospora indica	*Oryza sativa* L. (Rice)	Protection from arsenic	Mohd et al. 2017
Penicillium citrinum	Sunflower	Stem rot mitigation	Waqas et al. 2015
Porostereum spadiceum	Soybean	Salt stress mitigation	Hamayun et al. 2017
Fusarium verticillioides	Soybean	Salt stress mitigation	Radhakrishnan et al. 2013
Aspergillus japonicus	Sunflower and soybean	Heat stress mitigation	Hamayun et al. 2018
Bipolaris sp. CSL-1	Soybean	Salt stress mitigation	Lubna et al. 2022
Aspegillus tubingensis	Pepper	*Fusarium* wilt disease amelioration	Attia et al. 2022
Talaromyces versatilis, Aspergillus niger	Geranium	Cadmium stress amelioration	El-Shafey et al. 2021
Candida membranifaciens	Maize	Salt stress mitigation	Jan et al. 2022
Stemphylium lycopersici	Maize	Salt stress mitigation	Ali et al. 2022

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(Khan et al. 2018). Drought stress is a problem that adversely affects plant development, growth and yield and has a negative impact on the availability and movement of nutrients since they are transported by water (Ullah et al. 2019; Igiehon & Babalola 2021). Plants' physiological practices are disturbed by drought hence the decreased or slowed development. Poor germination rates can be caused by drought stress because of reduced water intake during the imbibition phase (Yang et al. 2020). Water is important for seed germination. Drought stress impedes the imbibition of seeds, thus hindering germination (Wahab et al. 2022). Seed germination is crucial for plant survival, and water deficit reduces water absorption by seeds, preventing seed germination (AL-Quraan et al. 2021). Plants increase osmotic potential at the cellular level to overcome harmful effects under drought stress, accumulating soluble carbohydrates, proteins, amino acids and proline (Ozturk et al. 2021). In stressful conditions, more reactive oxygen species are created and can lead to cell and tissue damage to macromolecules and nucleotide disruption, lipid peroxidation and eventually cell death due to the oxidative stress they cause (Khaleghi et al. 2019; Hanaka et al. 2021; Verma et al. 2021). Water deficiency in early plant development can inhibit cell expansion and turgor resulting in a reduced leaf area and if the water deficiency is later on in development, it can result in leaf senescence (Brito et al. 2019). Plants subjected to drought stress can display symptoms such as leaf wilting, leaf yellowing, leaf scorching and permanent wilting (Seleiman et al. 2021) Water deficit changes the structure and the synthesis of fatty acids, resulting in reduced oil yield in oilseed crops (El Sabagh et al. 2019). Figure 1 gives a summary of how plants are affected by drought stress.

RESPONSE OF PLANTS TO DROUGHT

Drought stress affects plant growth parameters and gene responses (Balkrishna et al. 2022). Plants have strategies to respond to drought: tolerance, avoidance, escape and recovery (Hanaka et al. 2021). Tolerance refers to the capability of a plant to withstand dehydration by using osmoprotectants. Plants avoid drought by reducing transpiration due to stomatal water loss control and water intake maintenance through a large and productive root system (Deka et al. 2018). Organic solutes accumulate in the cytoplasm, causing a decrease in osmotic potential below that of the soil to facilitate water uptake, maintaining cell membrane integrity and water potential equilibrium with the cells of drought-stressed plants (Mosupiemang et al. 2022). Plants avoid drought by retaining enough water by modifying root structure for effective water absorption or lowering transpiration through stomatal closure, leaf curling and shedding of aged leaves (Zia et al. 2021). Drought escape is characterized by the plant's capacity to avoid drought by completing life cycles before drought occurs to sustain some reproduction. This involves early flowering, maturity, and developmental plasticity (Begna 2020). Drought recovery is described as plants' potential to grow after drought injury (Khan et al. 2018). The plant can restart growth after undergoing drought stress (Ilyas et al. 2021).

MECHANISMS OF DROUGHT STRESS MITIGATION BY ENDOPHYTIC FUNGI

Endophytic fungi confer stress tolerance like drought stress by producing phytohormones and enzymes like 1-aminocyclopropane-1-carboxylate deaminase (ACCD), auxins, gibberellins, abscisic acid, siderophores and solubilization of soil nutrients (Bilal et al. 2020).

1-aminocyclopropane-1-carboxylate deaminase (ACCD). ACCD activity maintains ethylene below inhibitory levels. This allows for normal root development and delays senescence during drought (Dubey et al. 2021). Endophytic fungi aid in plants' survival under drought stress by reducing ethylene's inhibitory levels with the ACCD enzyme's help. The ACCD enzyme breaks down ethylene into ammonia and α-ketobutyrate (Devi et al. 2020). Ethylene is a plant hormone responsible for healthy growth and development under normal conditions. In stress conditions, ethylene levels increase and negatively impact plant growth by restricting root elongation and transport of auxin, so the production of ACCD by endophytic fungi reduces ethylene and root growth is promoted (Iqbal et al. 2017; Vandana et al. 2021). *Trichoderma gamsii, Fusarium proliferatum*, and their consortia, which produce the ACCD enzyme, have been shown to improve drought tolerance in *Moringa oleifera* L. cultivated under water deficit produced by PEG-8000 (Rehman

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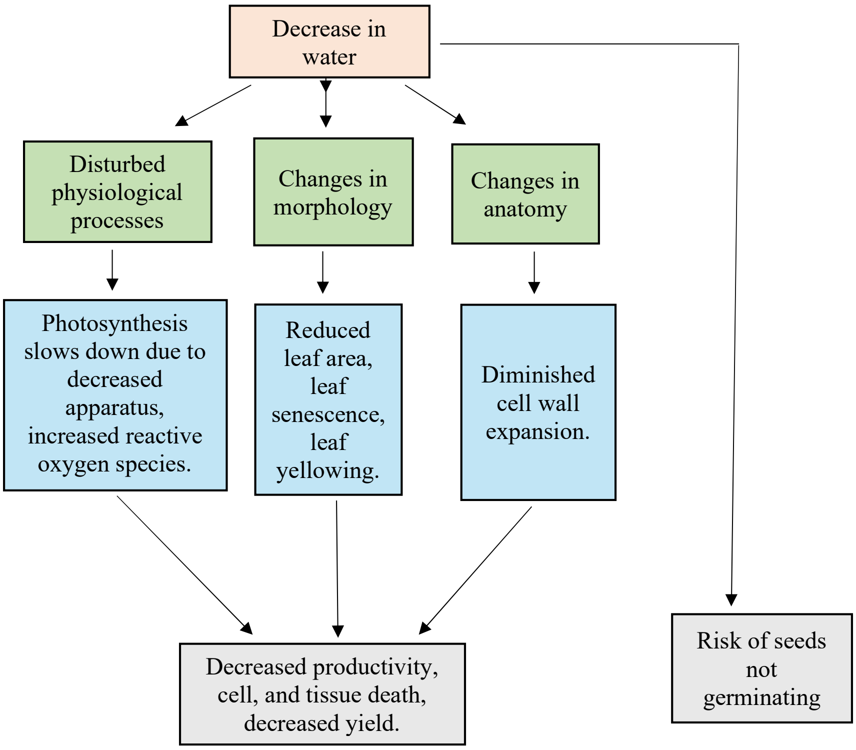

Figure 1. Diagram showing the effect of drought stress on plants. Drought stress means decreased water availability that has an impact in the plants' processes resulting in decreased yield and production

et al. 2022). However, investigations into the molecular and physiological processes by which drought tolerance in plants is improved by endophytic fungi that produce ACCD are still much needed. A better comprehension of these systems may result in more specifically focused applications.

Auxins. Auxin, a plant hormone, is important for growth and reaction to stress like drought and is mainly synthesized in the leaf primordial, young leaves and developing seeds (Ilyas et al. 2021). Auxins account for apical dominance and the direction of root and shoot growth (Fadiji et al. 2022b). Auxins mainly control plant growth, assisting in root development, cell elongation and division, vascular tissue differentiation and root formation (Baron & Rigobelo 2022).

Endophytic fungi work by triggering auxin production in their host, which changes the root architecture by increasing root length, quantity, volume, and biomass and enhances the host's capacity to extract water during droughts (Nataraja et al. 2022). The interaction between endophytes and host plants in the context of stress tolerance is a topic of rising interest despite the paucity of particular studies on auxin production by endophytic fungi for drought tolerance.

Abscisic acid. Abscisic acid regulates stomatal movement in the plant, which is important under drought stress to adjust the water status (Ali et al. 2020). Plants close the stomata early to conserve water inside the plant. This, however, can affect gas exchange, such as the intake of carbon dioxide and water vapour (Koza et al. 2022). Abscisic acid controls transpiration by controlling guard cell's ion fluxes of stomata (Ali et al. 2020). Abscisic acid can control stress-responsive genes to mediate the plant defence system against damage from drought (Gul Jan et al. 2019). Endophytic fungi, *Microdochium majus*, *Meyerozyma guilliermondi*, and *Aspergillus aculeatus*, were able to produce ABA, which enhances drought-tolerance in *Moringa oleifera*. (Javed et al. 2022) Although roots and shoots both synthesise ABA, a decrease in cellular turgor stimulates its greater accumulation (de Ollas & Dodd 2016). The molecular basis for the relationship between ABA accumulation and the perception of dryness is yet unknown despite the fact that ABA accumulation is closely connected with plant/tissue water status.

Future studies should explore using ABA-producing endophytic fungi as components of biofertilizers or soil amendments. These fungi could promote plant growth, nutrient uptake, and water use efficiency, ultimately contributing to improved soil health. Investigating the biotechnological approaches for introducing ABA-producing genes from endophytic fungi into crop plants to enhance their drought resistance is necessary because ge-

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netic engineering and synthetic biology techniques may play a role in this. Future studies should investigate the relationships between other plant microorganisms and endophytic fungus that produce ABA. Developing microbiome engineering techniques for better drought resistance by better understanding these interactions is possible. It is crucial to keep in mind that research in this field will probably continue to develop, and new findings can present new opportunities and difficulties. Researchers and decision-makers should also think about the moral, legal, and ethical implications of introducing modified species into natural habitats.

Indole-acetic acid (IAA). Endophytic microorganisms can produce indole-acetic acid, have an essential role in the mutualistic relationships between host plants and endophytes, and, therefore, control the growth of the plant (Fouda et al. 2021). Fungi produce indole-acetic acid that can promote plant growth and development by directly influencing physiological and biochemical processes in the plants (Qiang et al. 2019). Endophytic fungi produce indole-acetic acid, which encourages the growth of roots and root hairs, resulting in the effective assimilation of nutrients by corresponding plants (Ziaullah et al. 2020). The inoculation of wheat plants with an indole-acetic acid-producing endophytic fungus *Alternaria alternata* resulted in better growth and greener plants than uninoculated plants (Qiang et al. 2019). Research on endophytic fungi that produce IAA may result in the creation of crop types that are more drought-stress resilient. This can help boost agricultural production and food security, especially in areas prone to water shortage. Examining the use of endophytic fungi that produce IAA in various plant species, including both agricultural and non-agricultural plants, is very important. In locations that are prone to drought, this could have an impact on ecosystem restoration and biodiversity preservation. Future studies should investigate the potential application of IAA-producing endophytic fungus in sustainable agricultural methods. These fungi may decrease the demand for artificial fertilisers and growth regulators, resulting in more ecologically friendly farming.

Gibberellins. Gibberellins stimulate growth in plants (El-Sayed et al. 2022). In promoting plant development, gibberellins promote seed germination, the emergence of seedlings, and growth of the leaf, the stem, flowers, early flowering, larger fruit size and floral induction, as well as delayed senescence (Rana et al. 2020). In addition, gibberellins increase water uptake and ion segregation in plants, resulting in improved growth and sustained metabolic rate under normal and stressed conditions (Ikram et al. 2020). Endophytic fungi *Phoma glomerata* LWL2 and *Penicillium* sp. LWL3 significantly promoted stress tolerance alongside shoot and allied growth attributes of GAs-deficient (Gibberellin) dwarf mutant Waito-C and Dongjin-beyo rice (Waqas et al. 2012). Future studies should investigate the potential of endophytic fungi-derived gibberellins to enhance drought tolerance in major crop species. This could lead to the development of drought-resistant crop varieties. Also, investigations of the molecular and physiological mechanisms by which gibberellins produced by endophytic fungi enhance drought tolerance in plants are needed as a deeper understanding of these mechanisms can lead to more targeted applications.

Siderophore production. Siderophore is responsible for the transport and storage of ferric ions. Fungi can produce a siderophore, an organic compound and a high-affinity ferric ion chelator (Ghosh et al. 2020). Iron is essential for plant growth (Ozimek & Hanaka 2021). The synthesis of siderophore increases the root's ability for iron uptake, resulting in plant growth. The endophytic fungi *Trichoderma koningii* ST-KKU1, *Macrophomina phaseolina* SS1L1O and *M. phaseolina* SS1R1O produce siderophores, so their inoculation into the sunchoke plant leads to the growth of the plant (Suebrasri et al. 2020). Future studies should investigate the potential of siderophore-producing endophytic fungi to enhance iron uptake in plants under drought conditions. Improved iron acquisition can mitigate the negative effects of drought stress on plant growth. Also, understanding the interactions between siderophore-producing endophytic fungi and other microorganisms in the plant microbiome is important. Optimizing these interactions may improve plant health and drought resilience.

Chlorophyll content and photosynthesis. The lack of water decreases chlorophyll content. Drought stress negatively affects photosynthesis as water deficiency inhibits carbon assimilation as well as causes harm to the photosynthetic apparatus (Wang et al. 2018). Inoculating sunflower with *F. proliferatum* increased chlorophyll *a* and *b* concentrations under drought stress (Seema et al. 2023). Drought stress negatively affects photosynthesis as water deficiency inhibits carbon assimila-

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tion as well as cause damage to the photosynthetic apparatus (Wang et al. 2018). Syamsia et al. 2020 inoculated aromatic rice with endophytic fungi and found that inoculation can improve chlorophyll content, which is important for harvesting light for photosynthesis. Wheat plants inoculated with *Zopfiella erostrata* had increased shoot and root dry weight, higher photosynthetic efficiency and increased stomatal conductance compared to the control (Miranda et al. 2023). Further studies on this will help provide a deeper understanding of how this interaction would improve drought resilience and plant health.

Malondialdehyde (MDA). Malondialdehyde is a final product of polyunsaturated fatty acid peroxidation in the cells and a marker for determining how much damage is caused to plants by drought stress. High MDA means more damage (Zhang et al. 2021). Sadeghi et al. (2020) reported decreased MDA content, O_2^- content and H_2O_2 concentration in drought-stressed mandarins inoculated with *Penicillium citrinum, Aurobassium pullunts* and *Dothideomycetes* sp. The colonization of *P. indica* results in lowered MDA levels in both water-stressed and well-watered conditions of *O. sativa* (Tsai et al. 2020). However, investigating whether certain endophytic fungi can regulate MDA levels in host plants by modulating the activity of antioxidant enzymes is necessary. This could potentially reduce oxidative stress and improve plant tolerance to drought. They also explore whether endophytic fungi produce secondary metabolites that can scavenge reactive oxygen species (ROS), indirectly leading to reduced MDA formation in plant tissues during drought stress. Studying the interactions between endophytic fungi and host plant metabolic pathways is important, especially those related to lipid peroxidation and MDA production. Understanding these interactions may reveal novel strategies for drought mitigation. Furthermore, they are developing and optimizing biochemical assays to detect MDA levels and oxidative stress markers in plants with endophytic fungi. This can facilitate the screening of fungal strains for their potential to mitigate drought-induced oxidative damage.

Proline content. Proline content can be used as a measure of environmental stress. Proline content increases if there is stress to maintaining osmotic potential (Prema Sundara Valli & Muthukumar 2018). Maintaining osmotic potential helps host plants sustain the photosynthetic apparatus (Chun et al. 2018). Proline can participate in the scavenging of ROS, which protects the cell membrane from oxidative damage from drought stress (Bayat & Moghadam 2019). Maize inoculated with *P. indica* accumulates more proline, which may be in control of increasing drought tolerance in *P. indica* colonized maize (Xu et al. 2017). Proline enhances the growth of plants by conserving cell membranes and proteins, decreasing the amount of free radicals and buffering cellular redox potential (Dubey et al. 2021). However, studying the interactions between proline-producing endophytic fungi and other microorganisms in the plant microbiome is important. Manipulating these interactions may optimize plant health and stress responses.

Phosphate solubilization. Phosphorus is a vital element in nucleic acids, phospholipids, phosphoproteins and metabolites, which are physiological aspects that promote plant growth and development (Emmanuel & Babalola 2020). Phosphorus does not exist in elemental form in the soil. Microorganisms solubilize phosphate by secreting organic acids that will lead to the acidification of microbial cells and the surrounding environment, which will release phosphate ions (Emmanuel & Babalola 2020). Microorganisms that can solubilize phosphate hydrolyze the organic and inorganic compounds from insoluble compounds to a soluble form of phosphorus that plants can efficiently assimilate (Kalayu 2019). The solubilization of inorganic phosphate salt by endophytic fungi is dependent on their ability to manufacture organic acids which reduce the soil pH, supplying the resources to exchange the metal portion of the insoluble phosphate for potassium or sodium, resulting in the formation of soluble phosphate salts (Adhikari & Pandey 2019).

Inoculating rice with *P. indica*, an endophytic fungus, enabled it to survive dehydration. This was evident in re-watering the uninoculated plants that wilted or died, and the inoculated ones survived (Tsai et al. 2020). Llorens et al. (2019) inoculated the fungal endophytes *Sarocladium implicatum* and *Acremonium sclerotigenum* into wheat plants for drought stress mitigation. They grew the wheat under optimal watering conditions, and then they stopped. The treated wheat plants showed improved growth parameters, retained the turgor, and the leaves remained green as opposed to the untreated wheat plants as they wilted. In addition, there was growth in the root network under drought stress. Inoculation of wheat with en-

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dophytic fungi increased biomass production and leaf area in salt-stressed plants compared to the uninoculated (Bouzouina et al. 2021). The potential of endophytic fungi to bring about tolerance to environmental stress calls for more research. The favourable plant-microbe collaboration for increased biomass yield can be linked to the diverse function of these microorganisms in the environment (Adeleke et al. 2022). Figure 2 summarises the mechanisms used by endophytic fungi to mitigate drought stress.

DROUGHT STRESS AMELIORATION IN MAIZE AND OTHER CROPS BY ENDOPHYTIC FUNGI

Maize is considered among the most valuable crops in the world as it provides a staple food and can contribute to people's livelihoods in many parts of the world (Ngoune Tandzi & Mutengwa 2020). It is used as animal feed and processed into other foodstuff like cornmeal, grits, starch, flour, tortillas, snacks and breakfast cereals (Rouf Shah et al. 2016). The powder of the maize cob is used as filler for explosives in manufacturing plastics, glues, adhesives, resin, vinegar and artificial leather (Sah et al. 2020). This means maize is important, and strategies to ensure it is secured and protected from harsh conditions that may destroy it. Drought threatens food security and crop production, such as maize, due to the loss of moisture from the soil surface and fewer water supplies to the soil, either from rain or other sources of precipitation (Sogoni et al. 2021). Drought stress disturbs enzymatic activity and causes the formation of free radicals, which leads to lipid peroxidation, ultimately resulting in membrane damage and cell desiccation (Yadav et al. 2021).

The strain *F. oxysporum* inoculated into maize seedlings enhanced shoot and root growth compared to controls (Mehmood et al. 2018). Root

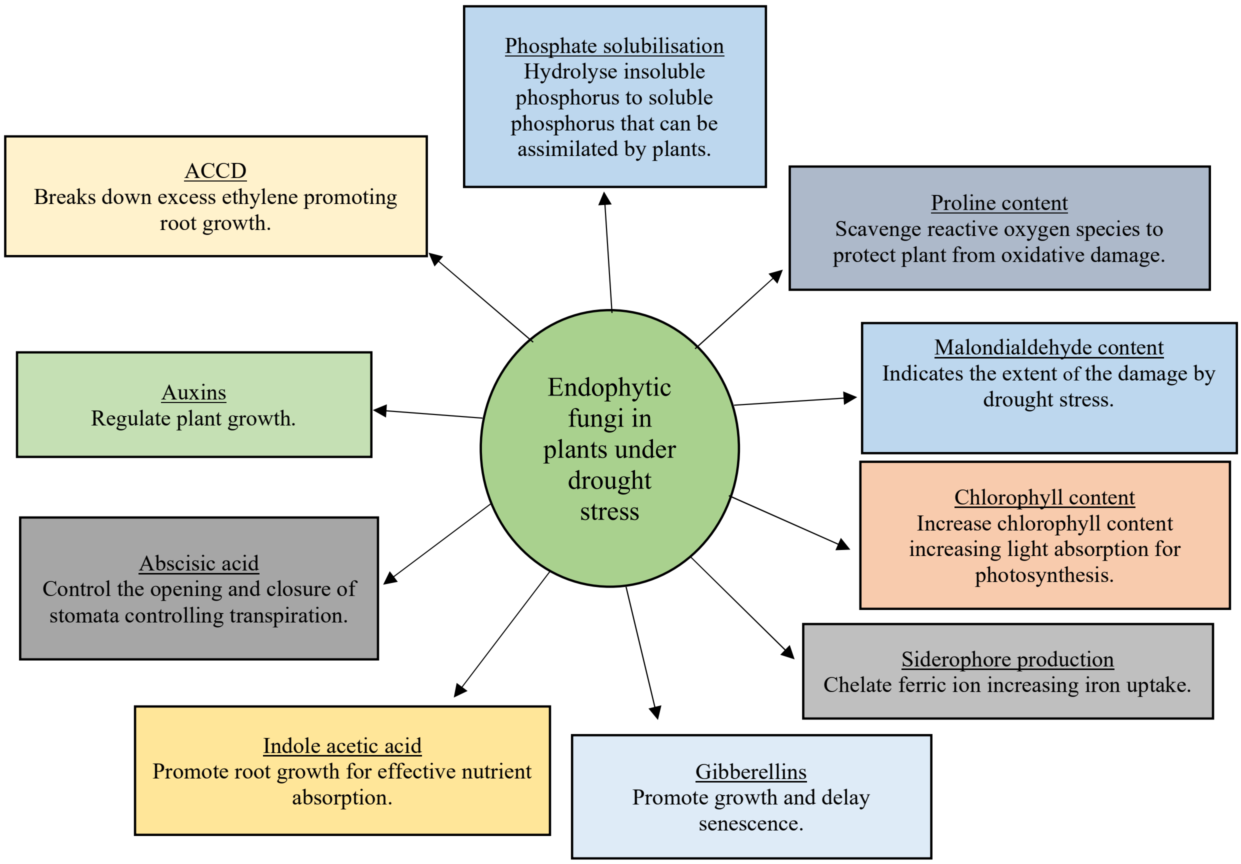

Figure 2. Diagram summarising the outcomes of the presence of fungal endophytes in mitigating drought stress. Endophytic fungi synthesize phytohormones as well as facilitate nutrient acquisition in order to boost plant growth under drought stress

ACCD – 1-aminocyclopropane-1-carboxylate deaminase

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and shoot length and dry weight are lower when the plant is under drought stress. Guler et al. (2016) inoculated maize seedlings with *Trichoderma atroviride* ID20G to alleviate drought stress, and it resulted in increased dry and fresh weights. Maize plants inoculated with *P. indica* under PEG-6000 induced drought conditions had more proline accumulation, and malondialdehyde was reduced, indicating reduced membrane damage. *P. indica* inoculation also increased enzyme activities (superoxide dismutase and catalase) under drought conditions (Xu et al. 2017). Maize seeds inoculated with *Colletotrichum tofieldiae* produce longer shoots, higher fresh weight and longer roots compared to the uninoculated under drought stress conditions (Díaz-González et al. 2020). Khalil et al. (2021) found *Penicillium crustosum* EP-2, *Penicillium caseifulvum* EP-11, and *Penicillium commune* EP-5 inoculated maize had increased root length and *P. crustosum* EP-2, *Penicillium chrysogenum* and *Aspergillus flavus* EP-14 were able to solubilize phosphate. The ability to solubilize phosphate can be beneficial in crop production and plant growth promotion by making phosphate available.

Plants require an ample amount of water and nutrients for survival and development. The water and nutrients are mainly obtained from the soil, and reduced moisture, like drought, harms healthy plant growth (Dastogeer et al. 2020). Maize is no exception. Reactive oxygen species and free radicles, including hydrogen peroxide and superoxide radicals, are released due to drought stress and endophytic fungi inoculation results in their decrease in promoting plant health and development under drought (Fadiji et al. 2022b).

Under drought stress, the chlorophyll pigments are affected in maize plants. The inoculation with *T. harzianum* and *Fusarium solani* increases the chlorophyll content compared to the uninoculated under drought stress (Bakhshi et al. 2023). *C. tofieldiae* Ct0861 inoculated maize had a higher yield – increased cob number, increased cob weight and higher kernel number compared to uninoculated maize under water stress (Díaz-González et al. 2020).

Drought stress impacts chlorophyll content, weight, height, and yield. Endophytic fungi (*Rhizopus* sp and *Curvularia* sp.) inoculated wheat showed increased growth under severe drought compared to uninoculated wheat plants. (Badr Eldin et al. 2022). Endophytic fungi increased rice growth under drought-stressed conditions compared to uninoculated ones (Pang et al. 2020). In their study, Pang et al. (2020) found that inoculating rice with endophytic fungi enabled the detoxification of reactive oxygen species in rice seedlings, therefore inducing osmotic stress. *Diaporthe atlantica* increased shoot biomass in tomato plants by 80% under drought stress, increased chlorophyll content under drought stress and prompted the assimilation and movement of both micronutrients and macronutrients to the plant shoot (Pereira et al. 2023). He et al. (2019) on their study found that dark septate *Acrocalymma vagum* inoculated licorice plants had increased root length, surface area, diameter, and branch number, increased photosynthetic rate, stomatal conductance and increased soluble protein compared to the uninoculated plants. They also used other dark septate endophytic fungi, namely *Paraboeremia putaminum* and *Fusarium acuminatum,* which work together to promote plant growth and drought tolerance in the licorice plant.

Limitations. Agriculture flourishes when the soil is of good quality, the crops receive enough water, and the weather conditions are stable. It becomes vulnerable, however, due to climate change as soil quality and weather conditions change for the worst (Fadiji et al. 2022a). The problem with using microbes is the inconsistency in their performance in various environments (Dastogeer et al. 2020). In a natural setting, the research is not efficient enough to be commercialized worldwide (Fadiji et al. 2022b). The results obtained in the laboratory setting may not necessarily be the same in the field. Endophytes are screened for one type of stress *in vitro*, though the field may face multiple and must compete with other microorganisms in the field for entry (Verma et al. 2021). Endophytic fungi yield secondary metabolites. It is, therefore, important to assess these metabolites when introduced to crop plants, mainly if they can reach edible parts of the plants (Chitnis et al. 2020). Introducing fungal endophytes should not disturb the original microbiome, which could negatively impact plant performance. Endophytic fungi can produce and accumulate alkaloids in plant tissues and can be poisonous to some invertebrates and a few vertebrates, like livestock, though few studies have been done (Baron & Rigobelo 2022).

Furthermore, the effectiveness of endophytic fungi in drought mitigation can vary significantly depending on the specific fungal strain used. Identifying and optimizing the right strain for a particular

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plant or environment can be challenging (Pozo et al. 2021). Endophytic fungi may not perform consistently across different environmental conditions. Temperature, soil type, and humidity levels can affect their activity and effectiveness. Also, native endophytic fungi exist in many plant species, and introducing non-native strains may lead to resource competition. This competition could reduce the effectiveness of the introduced fungi. Some endophytic fungi have a limited range of host plants they can colonize effectively. This limits their applicability in agriculture and ecosystem restoration efforts. Using genetically modified endophytic fungi or introducing non-native strains may face regulatory hurdles and concerns about potential ecological impacts (Agarwal & Singh 2021). Also, the long-term stability of endophytic fungi in the host plants and the surrounding environment is not always guaranteed. Changes in environmental conditions or host plant health may affect their persistence.

Consequently, the effectiveness of endophytic fungi in drought mitigation can vary from one application to another. Factors like the timing of inoculation, the health of the host plant, and the severity of drought can influence outcomes (Compant et al. 2010). Likewise, much research is still needed to fully understand the mechanisms of action and optimal application methods for endophytic fungi in drought mitigation. This lack of comprehensive knowledge can limit their practical use. Developing and applying endophytic fungi for drought mitigation may require specialized expertise and resources, making it less accessible to small-scale farmers and resource-limited regions. Also, the deliberate introduction of non-native organisms into ecosystems may raise ethical and ecological concerns about unintended consequences, such as disruptions to native species or ecosystems.

CONCLUSION AND FUTURE PROSPECTS

Focus on ensuring safety while consuming endophytic fungi-inoculated crops should be prioritized. The majority of the work done on endophytic research is on bacteria. Fortunately, endophytic fungi studies are growing, and the use of endophytes is important as fungi are proving important in stress mitigation. In the isolation of fungi, various environments should be considered to obtain fungal isolates that survive different environments in addition to drought. This may help ensure plants survive all the inconveniences of drought.

This review showcased how endophytic fungi contribute to ensuring plants' survival in drought. Drought stress creates an unfavourable environment for plants. The plants' processes are then disturbed, resulting in compromised growth and development. Plants host endophytic microorganisms with the potential to protect them against drought stress. Plants have a mutualistic relationship with these microorganisms. Endophytes are an alternative to harmful substances that promote plant growth and health. Endophytes do not harm plants, though pathogenic, harmful microbes inhabit plants and can be defeated by endophytes. Endophytic fungi secrete substances to ensure plants' survival in harsh conditions like drought, which is a need in this ever-changing climate. Plants may be able to tolerate, escape or avoid drought. However, it could be to the detriment of normal growth, while endophytic fungi ensure normal growth and development of the plant without distressing the host plant. Using endophytic fungi enhances crops like maize and will help ensure food security for the future. Endophytic research is growing, though attention is mostly on bacteria.

Furthermore, genetic modification of endophytic fungi will enhance the drought tolerance capabilities of plants. Ongoing research will likely provide deeper insights into how endophytic fungi help plants withstand drought. This knowledge can inform more targeted and effective applications. Researchers may explore combinations of endophytic fungi with other drought mitigation strategies, such as crop breeding for drought resistance or soil amendments. Synergistic approaches could offer even greater benefits. Beyond agriculture, endophytic fungi may find applications in ecosystem restoration efforts, helping to revive drought-affected ecosystems and promote biodiversity. Future research may focus on the sustainability of using endophytic fungi, including assessing their long-term effects on soil health, biodiversity, and ecosystem stability.

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