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REVIEW

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Fungi beyond limits: The agricultural promise of extremophiles

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Abstract

Global climate changes threaten food security, necessitating urgent measures to enhance agricultural productivity and expand it into areas less for agronomy. This challenge is crucial in achieving Sustainable Development Goal 2 (Zero Hunger). Plant growth-promoting microorganisms (PGPM), bacteria and fungi, emerge as a promising solution to mitigate the impact of climate extremes on agriculture. The concept of the plant holobiont, encompassing the plant host and its symbiotic microbiota, underscores the intricate relationships with a diverse microbial community. PGPM, residing in the rhizosphere, phyllosphere, and endosphere, play vital roles in nutrient solubilization, nitrogen fixation, and biocontrol of pathogens. Novel ecological functions, including epigenetic modifications and suppression of virulence genes, extend our understanding of PGPM strategies. The diverse roles of PGPM as biofertilizers, biocontrollers, biomodulators, and more contribute to sustainable agriculture and environmental resilience. Despite fungi's remarkable plant growth-promoting functions, their potential is often overshadowed compared to bacteria. Arbuscular mycorrhizal fungi (AMF) form a mutualistic symbiosis with many terrestrial plants, enhancing plant nutrition, growth, and stress resistance. Other fungi, including filamentous, yeasts, and polymorphic, from endophytic, to saprophytic, offer unique attributes such as ubiquity, morphology, and endurance in harsh environments, positioning them as exceptional plant growth-promoting fungi (PGPF). Crops frequently face abiotic stresses like salinity, drought, high UV doses and extreme temperatures. Some extremotolerant fungi, including strains from genera like *Trichoderma*, *Penicillium*, *Fusarium*, and others, have been studied for their

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beneficial interactions with plants. Presented examples of their capabilities in alleviating salinity, drought, and other stresses underscore their potential applications in agriculture. In this context, extremotolerant and extremophilic fungi populating extreme natural environments are muchless investigated. They represent both new challenges and opportunities. As the global climate evolves, understanding and harnessing the intricate mechanisms of fungal-plant interactions, especially in extreme environments, is paramount for developing effective and safe plant probiotics and using fungi as biocontrollers against phytopathogens. Thorough assessments, comprehensive methodologies, and a cautious approach are crucial for leveraging the benefits of extremophilic fungi in the changing landscape of global agriculture, ensuring food security in the face of climate challenges.

> Expect the best; prepare for the worst.
> Muhammad Ali Jinnah

INTRODUCTION

Humanity is approaching an unprecedented catastrophe. During the last decades, different regions of the planet have been severely impacted by exceptional weather and climate extremes, including heat waves, droughts, hurricanes, and heavy precipitation (Zhou et al., 2023). Data from the last year indicate that the consequences of the global warming process are much more significant than previously thought (IPCC, 2023). Climate extremes are expected to severely harm human society's welfare and ecosystem sustainability. The recognition by the Secretary General of the United Nations of the enormous difficulties in achieving the Sustainable Development Goals (SDGs) (UN Report, 2023) adds an additional layer of worry to the current universal perception of an uncertain future (Figure 1). Consequently, it is increasingly acknowledged that the effort required to meet the aspirations of a large part of humanity to achieve a better future for our planet and for all humankind will be of a colossal magnitude.

Among the SDGs, number two stands out: Zero Hunger. More than 820 million people are currently suffering from hunger, and another 250 million people will be on the brink of starvation by the end of the 2020s. According to estimates compiled by the Food and Agriculture Organization (FAO), to meet the future food demand of more than 9.3 billion people, food production should be increased by approximately 60 per cent by 2050 (FAO, 2017). Nevertheless, this will be out of reach if we do not introduce profound changes in the global agri-food system to increase agricultural production and food production sustainably since (i) the consequences of climate extremes impacting agricultural regions can be disastrous in terms of global food supply and global food security (Zhou et al., 2023); (ii) the amount of cropland is finite and has already been taken up, and marginal lands are too stressful for plants to grow well, due to harsh physical, chemical or agronomic factors (Pancaldi & Trindade, 2020); (iii) intensive farming systems cannot deliver food and crops sustainably, causing massive deforestation, water scarcities, soil depletion and degradation, and high levels of greenhouse gas emissions (FAO, 2017); and, (iv) the capacity of ecosystems to mitigate the impact caused by the excessive use of agrochemicals (fertilizers + pesticides) has been stretched to extreme limits. Failure in this area will sentence humanity to suffer from numerous crises: more hunger, more malnutrition, more wars, more forced migrations, and more inequity (Figure 1).

In the face of these threats, it has been suggested – based on a large body of evidence – that microbes may be part of the solution (Timmis et al., 2017). Indeed, scientists worldwide have insisted on considering microbes as ‘weapons for peace’ (Anand et al., 2023) and, among many other applications, using their abilities and ecological functions to promote plant growth for agricultural purposes (Bakker & Berendsen, 2022; Hu et al., 2022). The immediate consequence of taking advantage of beneficial microbes would be to increase food production sustainably and reduce hunger, with all the positive outcomes that derive from this.

Indeed, microorganisms have been used for agriculture intensification for decades (Mitter et al., 2021). In addition to participating in multiple processes related to the promotion of plant health and growth and being crucial for the restoration of degraded soils (Anand et al., 2023), microorganisms can be used to rationally design and produce different agricultural inputs (= ‘bioinoculants’ = ‘plant probiotics’) (see next section). These products date back to the end of the 19th century and have been gradually and steadily incorporated into the arsenal of tools that allow us to achieve higher levels of agricultural yields, with the advantage of not threatening the ecological balance of agricultural and natural ecosystems. In other

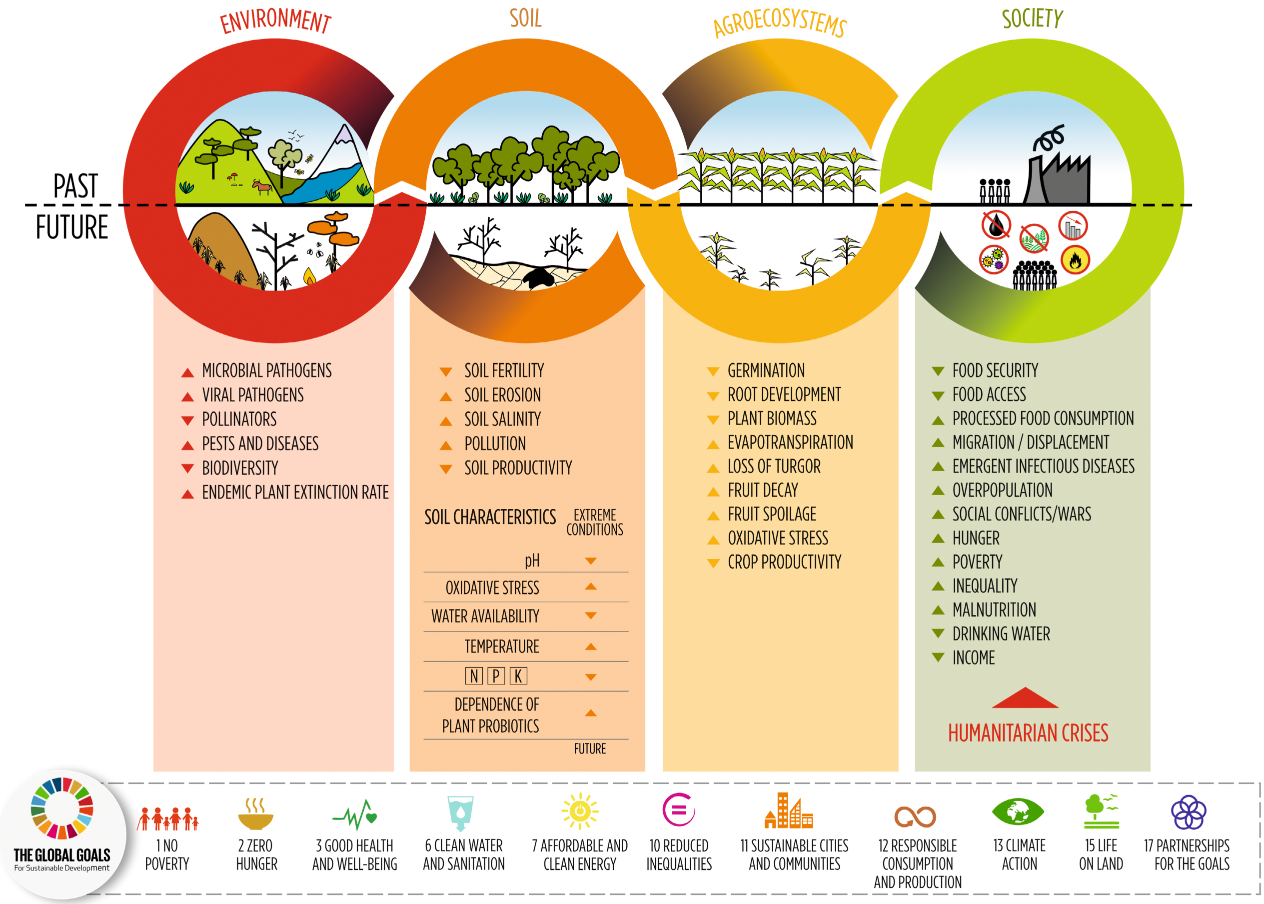

FIGURE 1 Some impacts of global warming and the threats posed on attaining the Sustainable Development Goals (SDGs). The sections, arranged sequentially from left to right, examine the principal projected future consequences of climate change on the environment, the interplay between plants, soil, and microbes (including anticipated soil properties under extreme conditions in the future), the productivity of agroecosystems, and the society, that could give rise to humanitarian crises in the near future. The SDGs that may be impacted due to the future extreme scenario are situated at the bottom.

words, adequately used plant probiotics allow the sustainable intensification of agriculture and, therefore, the production of more food.

However, when applied in the field, many plant probiotics are adversely affected by environmental factors that limit their universal and widespread use. Because they are alive, once introduced into agroecosystems, the microbes included in plant probiotics must reactivate and multiply actively to function efficiently (Sanjuán et al., 2023). Therefore, any biotic or abiotic factor that limits beneficial microbe's establishment and inhibits their active multiplication becomes a barrier to their utilization. At a time when soils in large regions of the planet are undergoing a process of aridification (Malpede & Percoco, 2023) and even desertification (Mirzabaev et al., 2019), factors such as high temperatures, salinization, and water scarcity – to mention a few – must be seriously considered when thinking about plant probiotics for the (near) future, because of the strong influence the former have on soil fertility, stability and biodiversity.

Since many agroecosystems worldwide experience already (or will experience soon) extreme conditions, the most apparent solution to intensify agriculture with plant probiotics would be to consider extremophilic microorganisms as the ones that offer the most promise for developing these bioinputs. Many microbes are not only capable of enduring extreme conditions (in which case they are considered 'extremotolerant') but often multiply and perform better when such conditions are met (the so-called 'extremophiles'). The group is as diverse as it is broad and includes bacteria, fungi, and microscopic algae (Coker, 2019).

Bacteria have been the most studied within the group of extremophiles able to promote plant growth. However, another group of extremophiles deserves to be considered in depth: extremophilic fungi. Beyond displaying plant-growth-promoting (PGP) traits, most of which resemble the ones exhibited by bacteria, fungi are fundamental components of all complex microbial communities such as the rhizosphere of plants (Pozo et al., 2021). It is there – but also in aerial and inner tissues – that they exert their promoting activity, providing nutrients, releasing plant hormone-like compounds, antagonizing (and even killing) plant pathogens, protecting plants from heavy metals, and providing many other ecological functions.

In the following pages, we will present the benefits that could result from using extremophilic fungi to develop future agriculture and prevent humanitarian crises. We will place extremotolerant and extremophilic fungi in the context of 'plant probiotics' and present illustrative examples of their use to mitigate the detrimental impacts caused by extreme environmental conditions on their plant hosts. Finally, we will discuss future perspectives, focusing on aspects that have not received sufficient attention from researchers and companies.

FROM 'PLANT GROWTH-PROMOTING MICROORGANISMS' AND 'BIOINOCULANTS' TO 'PLANT PROBIOTICS'

The plant holobiont concept

Microbes rarely multiply axenically under natural conditions; instead, they are members of complex communities (= natural microbiomes) in which many species act synergistically with others. Plants harbour a diverse, dynamic, complex, and interdependent community of microorganisms, interacting with each other through positive, neutral, or negative ecological relationships. Like every natural ecosystem, some microbial species depend on others to colonize a particular niche efficiently and must engage in mutually beneficial interactions (de Vries & Wallenstein, 2017; Ling et al., 2022).

This interdependency, usually seen to occur between microbial species and between these species and the host plant, resulted in the proposal of the 'plant holobiont' concept: an assemblage of species, closely interacting and inter-dependent, formed by the plant host and the resident symbiotic microbiota, which live inside and outside of its tissues and profoundly impact its growth, development, and survival (Vandenkoornhuyse et al., 2015).

Plant growth-promoting microorganisms

The soil surrounding the roots of plants is densely colonized by a heterogeneous community of microorganisms that benefit from the photosynthates released by roots as exudates, rich in many sugars and organic acids. In this environment, known as the rhizosphere, many plant-friendly microorganisms thrive compared to the bulk soil. Together, they form an assemblage that helps plants to grow better, faster, and stronger; for that reason, Kloepper and Schroth referred to these microbes as plant growth-promoting rhizobacteria (PGPR) (Kloepper & Schroth, 1981). The term was later modified to plant growth-promoting microorganisms (PGPM) to include other microorganisms, like fungi, participating in these promoting phenomena (Glick, 2012). The term also refers to microorganisms performing similar functions in the phyllosphere (i.e., the aerial part of plants, usually the surface of leaves) and the endosphere (i.e., the inner tissues of plants).

PGPM positively impacts the growth and development of plants through direct and indirect mechanisms that act in concert, sometimes in a redundant way, targeting different aspects of plant physiology. For instance, some microbial exo-metabolites contribute to solubilizing nutrients, like phosphorus, from sparingly soluble minerals such as hydroxyapatite or secondary P minerals like iron, calcium, and aluminium phosphates (Katiyar & Goel, 2004; Rodríguez & Fraga, 1999). Other, such as certain exo-enzymes, mineralize P from organic-P-containing compounds, like inositol phosphates and phosphonates, enabling plant access (Park et al., 2022). Other microbes fix nitrogen from the air into ammonia, making it available to plants (Dobbelaere et al., 2003). Certain fungi can even transport mineral nutrients from long distances and transfer them to plants, thanks to the extraordinary capacity of fungal hyphae to extend well beyond the rhizosphere (Bhattacharjee et al., 2022). Collectively, these microorganisms are known as **biofertilizers** (Figure 2).

On the other hand, certain microbes contribute indirectly to plant health (and, consequently, to improve their growth and development) by antagonizing plant pathogens. This is achieved, for instance, by producing diverse antimicrobial compounds, either soluble or volatile, such as siderophores and hydrogen cyanide, which kill specific pathogens and deter many others from the rhizospheric environment (O'Brien, 2017). This heterogeneous group of microorganisms includes viruses, bacteria, fungi, protists, and nematodes that act as predators that kill plant pathogens (for a review on this subject, see Vero et al. (2023)). Altogether, they are considered **biocontrollers**. The protective microorganisms are categorized as microbial pesticides when the defensive action targets plant pests or herbivores, like certain insects, arthropods, or nematodes (Ayilara et al., 2023; Estrada et al., 2013). A different function, i.e. induction of the expression of diverse defence mechanisms in their host plants, called Induced Systemic Resistance, is performed by **biomodulators** (Beneduzi et al., 2012).

Some microbes and micro-eukaryotes produce phytohormone-like molecules, like indole-3-acetic acid (IAA), directly stimulating plant growth (Berg, 2009). We refer to them as **phytostimulators**. Other PGPM releases volatile compounds, alter root morphology, produce high amounts of exopolysaccharides, and/or induces antioxidant defence mechanisms, all of which induce the plant resistance mechanisms against abiotic

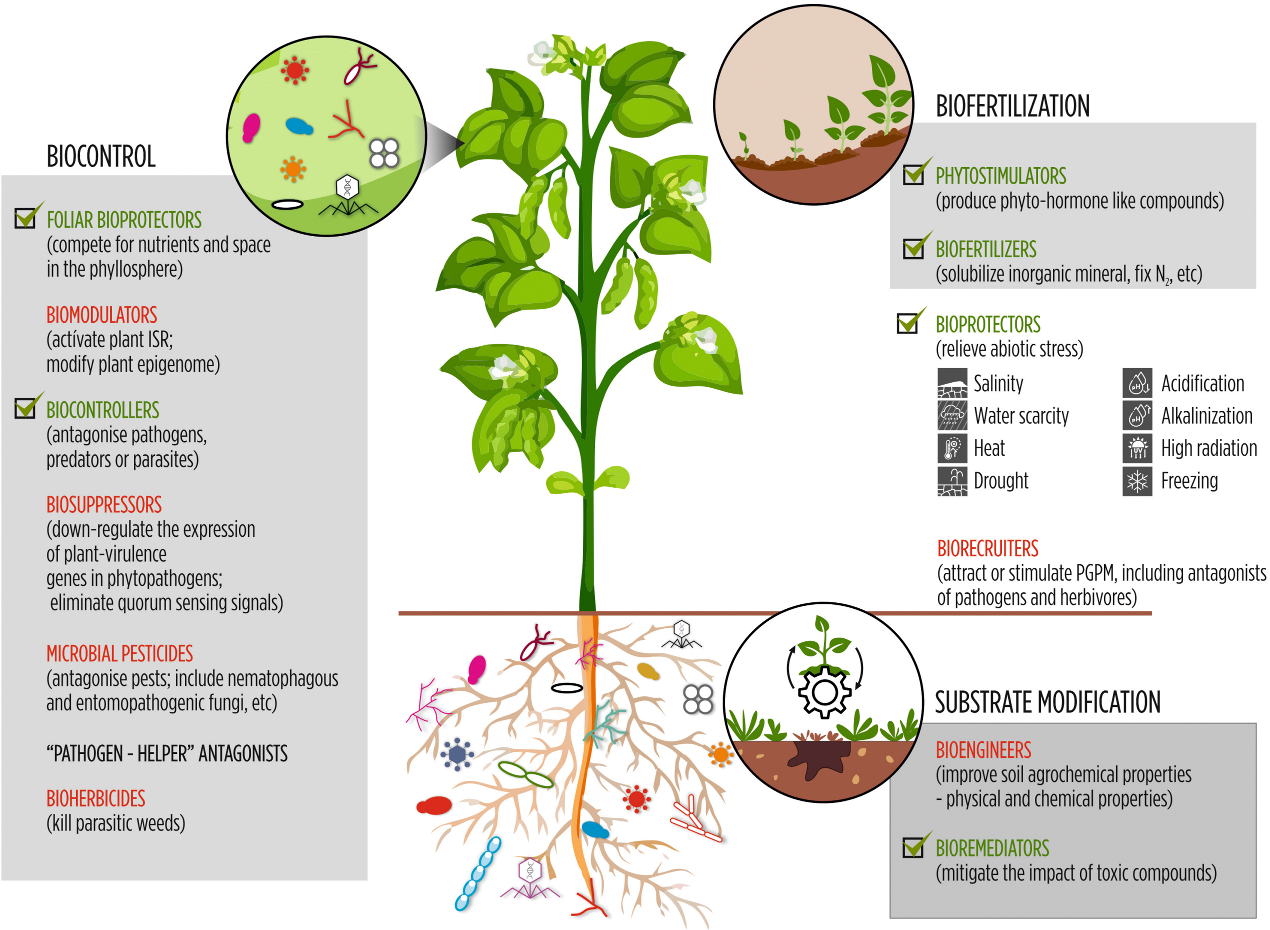

FIGURE 2 Diversity of ecological functions displayed by fungi to promote plant growth and development. Plant growth promoting (PGP) traits displayed by fungi can be grouped according to the impact they have on the growth and development of the plant holobiont through nutrient mobilization or hormone stimulation (Biofertilization), the positive modifications they introduce in the soil on which plants grow (Substrate modification), and the adverse effects they have on pathogens, pests, and herbivores that damages or kill their host plants (Biocontrol). We propose the term 'Bioengineers' to denote microorganisms that modify the soil's physical and chemical properties. A different group of PGP-fungi can also alleviate, in their host plants, the detrimental impact of abiotic stress factors such as drought, salinity, heat, and cold, among others. Finally, some fungi – that we tentatively named 'Biorecruiters' – can perform their PGP functions very indirectly, i.e., by stimulating or recruiting other microorganisms belonging to the groups mentioned above of PGP-organisms. The overall positive impacts of PGP-fungi on their plant hosts result in improved crop yields and quality. We have highlighted in green the PGP functions confirmed to be displayed by extremophilic/extremotolerant fungi (examples of this kind of fungi are presented in Table 1). We used red letters to distinguish ecological functions displayed by fungi not (yet) confirmed as extremotolerant/extremophiles. The function presented in black ('pathogen-helper' antagonism) has not yet been shown to be displayed by PGP-fungi.

stress (Dimkpa et al., 2009). These are categorized as **bioprotectors**.

On the other hand, **bioremediators** prevent plants from being impacted by the deleterious effect of xenobiotic soil pollutants by transforming them into less toxic forms through chemical modifications, bioaccumulation, chelation and/or acidification of the soil (Wang et al., 2022). Finally, even though it is not usually acknowledged as a PGP trait, some microbes can inhibit parasitic weeds, which infest certain crops and cause severe losses. These microbes are known as **bioherbicides** (Bailey, 2014).

Recently, previously unknown mechanisms of plant-growth promotion have been added to the microbial strategies displayed by PGPM to protect plants from biotic or abiotic stressors (Figure 2). For instance, the epigenome of plants can be modified in the presence of PGPM. These changes promote plant growth and remain functional even after the microbe–plant interaction ceases (Chen et al., 2022). We categorize this ecological function as **biomodulators**. Alternatively, some rhizosphere microorganisms indirectly promote plant growth by producing exo-metabolites that down-regulate – and even suppress – the expression of virulence genes in phytopathogens (Yin et al., 2022). We refer to them as **biosuppressors**.

Even though some bacterial species do not contribute directly to plant growth, they can attract fungal species that entrap and eliminate nematodes from the rhizosphere (Wang et al., 2014), while others stimulate resident bacteria and act synergistically to suppress phytopathogens and promote plant health (Hu

TABLE 1 Extremotolerant/extremophilic fungi displaying plant probiotic abilities under extreme environmental conditions. (A) Examples of confirmed extremophilic/extremotolerant fungi and (B) examples of putative extremotolerant/extremophilic species.

Fungal species	Type of extremophily	Source	Targeted plant species	Mode of life	Type of abiotic stress mitigated or beneficial traits displayed[a]	Reference
(A) Confirmed[b] extremophilic/extremotolerant fungi tested as plant probiotic under extreme conditions						
Alternaria alternata LQ1230	Xerotolerant	*Elymus dahuricus*	*Triticum aestivum* L.	Endophytic	Drought-stress tolerance	Qiang et al. (2019)
Aspergillus glaucus CCHA	Xerophilic	*Euphorbia indica* L.	*Glycine max* and *Helianthus* sp.	Endophytic	Heat-stress tolerance	Ismail et al. (2018)
Aspergillus japonicus EuR-26, *A. niger* NFCCI-2140, *Aspergillus niger* NFCCI-2141	Psychrotolerant	*Sanionia uncinata*, *Deschampsia alpina*, and *Dryas octopetala*	NR	Rizhospheric	Phosphate solubilization	Singh et al. (2011)
A. terreus BTK-1	Halotolerant	*Chenopodium album* L.	*Triticum aestivum*	Endophytic	Salt-stress tolerance	Khan et al. (2022)
Aureobasidium subglaciale	Psychrotolerant	Subglacial ice	Golden delicious apples *(Malus domestica)*	Carpospheric, Phyllospheric	Biocontrol against fruit decay pathogen's	Zajc et al. (2022)
A. pullulans, *A. melanogenum*, *A. subglaciale*	Psychrotolerant	Culture collection	Tomato and grapes	Carpospheric	Biocontrol against Botrytis cinerea	Di Francesco, Di Foggia, et al. (2020), Di Francesco, Zajc, et al. (2020)
Chaetomium sp. LAS-6	Thermotolerant	*Lasiurus scindicus*	*Oryza sativa* Genotype IR-64	Endophytic	Heat-stress tolerance	Sangamesh et al. (2018)
Cochliobolus lunatus MJ1	Halotolerant	*Mirabilis jalapa* L.	*Ablemoschus esculentus* L.	Endophytic	Salt-stress tolerance	Bibi et al. (2019)
Cunninghamella bertholletiae PGPF-F19	Halotolerant	*Solanum lycopersicum*	*Solanum lycopersicum*	Rhizospheric	Salt-, drought-, heavy-metals-stress tolerance	Kazerooni, Maharachchikumbura, Al-Sadi, Rashid, Kang, & Lee (2022), Kazerooni, Maharachchikumbura, Al-Sadi, Rashid, Kim, et al. (2022)
Curvularia crepinii G1-29	Moderate thermophilic	*Hedyotis diffusa*, *Trifolium repens*, *Digitaria ischaemum*, *Silene tenuis*, *Cynodon dactylon*, *and Alternanthera philoxeroides*	*Oryza sativa* L. ssp. indica	Endophytic	Heat-stress tolerance	Zhou et al. (2015)
C. brachyspora SCb	Halotolerant	*Oryza sativa* L.	*Oryza sativa* L.	Endophytic	Drought- and salt-stress tolerance	Redman et al. (2021)
C. protuberata	Thermophilic	*Dichanthelium lanuginosum*	*Solanum lycopersicum*	Endophytic	Heat-stress tolerance	Márquez et al. (2007)

TABLE 1 (Continued)

Fungal species	Type of extremophily	Source	Targeted plant species	Mode of life	Type of abiotic stress mitigated or beneficial traits displayed[a]	Reference
C. protuberata Cp4666D	Thermophilic	*Dichantelium lanuginosum*	*Oryza sativa*	Endophytic	Cold-stress tolerance and drought-stress tolerance	Redman et al. (2011)
C. protuberata	Thermophilic	*Dichanthelium lanuginosum*	*Leymus mollis*, *Dichanthelium lanuginosum*, *Solanum lycopersicum*, *Oryza sativa*	Endophytic	Heat-stress tolerance	Rodriguez & Redman (2008)
Fusarium sp. V-4J	Halotolerant	*Pokkali Rice* varieties IR-64 and JBT 36/14.	*Oryza sativa* (Pokkali)	Endophytic	Salt-stress tolerance	Sampangi-Ramaiah et al. (2020)
Fusarium oxysporum MH511104	Halophilic	*Ipomea pescaprae*	*Oryza sativa* L. variety-IR-64	Endophytic	Salt-stress tolerance	Manasa et al. (2020)
Glomus mosseae, *G. intraradices*, *G. etunicatum*	Halotolerant	*Acacia gerrardii*	*Cucumis sativus* L.	Arbuscular mycorrhizal fungi	Salt-stress tolerance	Hashem et al. (2018)
Mortierella antarctica MA DEM7, *Mortierella verticillata* MV DEM32	Psychrotolerant	Spitzbergen soils (Svalbard Archipelago)	*Triticum aestivum* L. cv Arkadia	Rhizospheric	Improved plant growth at low temperatures	Ozimek et al. (2018)
Paecilomyces formosus LHL10	Heavy-metal resistant	*Cucumus sativus* L. roots	*Glycine max*	Endophytic	Heavy-metals-stress	Bilal et al. (2017)
Paecilomyces formosus LHL10, *Penicillium funiculosum* LHL06	Heavy-metal resistant	*Cucumus sativus* L. and *Glycine max* roots	*Glycine max*	Endophytic	Heavy-metal, heat- and drought-stress tolerance	Bilal et al. (2020)
Penicillium funiculosum P1	Saline-alkali tolerant	NR	*Chenopodium quinoa* cv. Longli 1	NR	Saline-alkali stress tolerance; P-solubilization	Jin et al. (2022)
Penicillium chrysogenum 34-P	Halotolerant	*Axonopus purpusii*	*Zea mays*	Endophytic	Salt-stress tolerance	Galeano et al. (2023)
Penicillium olsonii A3	Halotolerant	^{EE}*Aleuropus littoralis*	*Nicotiana tabacum*	Rizhospheric	Salt-stress tolerance	Tarroum et al. (2022)
Penicillium sp. NAUSF2	Halotolerant	^{EE}Coastal rhizospheric soil (South Gujarat, India)	*Vigna radiata* L. cv. Co-4	Rizhospheric	Salt-stress tolerance; P-solubilization	Patel et al. (2021)
Periconia mascrospinosa, *Neocamarosporium goegapense*, *N. chichastianum*	Desert-adapted	*Seidlitzia rosmarinus (Boiss.)*, *Zygophyllum eichwaldii (C. A. Mey.)*, *Haloxylon ammodendron (C. A. Mey.)*	*Cucumis sativus* L.	Endophytic	Salt- and drought-stress tolerance	Hosseyni Moghaddam et al. (2021)

(Continues)

TABLE 1 (Continued)

Fungal species	Type of extremophily	Source	Targeted plant species	Mode of life	Type of abiotic stress mitigated or beneficial traits displayed[a]	Reference
Piriformospora indica	Desert-adapted	*Prosopis juliflora* (Swartz) DC. and *Zizyphus nummularia* (Burm. fil.)	*Arabidopsis thaliana*	Arbuscular mycorrhizal fungi	Drought-stress tolerance	Sherameti et al. (2008)
Porostereum spadiceum AGH786	Drought-resistant and Cu-resistant	*Glycine max* roots cv. Hwangkeumkong	*Solanum lycopersicum*	Endophytic	Drought-, heavy-metal-stress tolerance	Naz et al. (2022)
Thermomyces lanuginosus CpE	Thermophilic	*Cullen plicata*	*Cucumis sativus* L.	Endophytic	Heat-stress tolerance	Ali et al. (2018)
T. harzianum ThSM3a (three strain consortium)	Fungicide resistant	*Annual grasses* (arid región CA, USA)	*Corn and cotton*	Endophytic	Drought- and temperature extremes	Redman et al. (2021)
T. harzianum 81Y1 *and F. solani* 19K3	Drought-tolerant	[EE]Roots of desert trees (Iran)	*Zea mays* L. cv. Simon	Endophytic	Drought-stress tolerance	Bakhshi et al. (2023)
T. longibrachiatum HL167	Halotolerant	Saline-alkali soil	*Vigna unguiculata*	Rhizospheric	Salt-stress tolerance and antifungal biocontrol	Liu et al. (2023)
Trichoderma longibrachiatum T6	Halotolerant	*Triticum aestivum* roots	*Triticum aestivum*	Rhizospheric	Salt-stress tolerance	Zhang et al. (2016)
(B) Putative[c] extremotolerant/extremophilic fungi tested as plant probiotic under extreme conditions						
Ampelomyces sp. and *Penicillium chrysogenum*	NR	*Phyrrhopappus caroliniatus*	*Solanum lycopersicum* var. Better Boy	Endophytic	Drought- and salt- stress tolerance	Morsy et al. (2020)
Candida orthopsilosis MAK1 and *Rhodotorula mucilaginosa* MAK2	NR	[EE]Red Sea, Hurghada, Egypt	*Triticum aestivum*	Endophytic	Antifungal control, and plant growth promotion	Abdel-Kareem et al. (2021)
Epichloë sp.	NR	NR	*Festuca sinensis*	Endophytic	Cold-stress tolerance	Zhou et al. (2021)
Funneliformis mosseae	NR	*Incarvillea younghusbandii*	*Poncirus trifoliata* L. Raf.	Arbuscular mycorrhizal fungi	Drought-stress tolerance	Huang et al. (2017)
F. asiaticum Sfa	NR	Weedy rice plants	Weedy rice	Endophytic	Salt-stress tolerance	Redman et al. (2021)
F. culmorum FcRed1	NR	*Leymus mollis* (coastal beach)	*Oryza sativa*	Endophytic	Salt-stress tolerance and drought-stress tolerance	Redman et al. (2011)
Glomus etunicatum	NR	Soil	*Zea mays* L.	Arbuscular mycorrhizal fungi	High- and low-temperature stress.	Zhu et al. (2010a, 2010b)
Glomus mosseae and *Glomus intraradices*	NR	*Medicago scutellata* L.	*Pelargonium graveolens* L.	Endophytic arbuscular mycorrhizal fungi	Drought-stress tolerance	Amiri et al. (2015

TABLE 1 (Continued)

Fungal species	Type of extremophily	Source	Targeted plant species	Mode of life	Type of abiotic stress mitigated or beneficial traits displayed[a]	Reference
Mortieriella spp.	NR	^{EE}Coastal seashore soil (Jiangsu province, China)	*Kostelelzkya virginica*	Rhizospheric	Salt-stress tolerance	Zhang et al. (2011)
Penicillium resedanum LK6	NR	^{EE}*Capsicum annuum* L.	*Capsicum annuum* L.	Endophytic	Salt-, drought- and heat-stress tolerance	Khan et al. (2015)
Penicillium spp. RDA01, NICS01, DFC01	NR	*Arachis hypogaea*	*Sesamum indicum* L.	Rhizospheric	Salt-stress tolerance and biocontrol agent	Radhakrishnan et al. (2014)
Phoma spp., *Alternaria* spp., *Rhinocladiella* spp., *Cadophora* spp., *Penicillium* spp., *Bartalinia* spp., *Coniochaeta* spp., *Neonectria* spp., *Fusarium* spp., *Sarocladium* spp., and *Plectosphaerella* spp.	NR	*Chenopodium quinoa*	NR	Endophytic	NR	González-Teuber et al. (2017)
Piriformospora indica	NR	*Prosopis juliflora* and *Zizyphus nummularia* rhizosphere	*Hordeum vulgare* L. cv. Ingrid	Endophytic	Salt-stress tolerance	Johnson et al. (2014)
P. indica	NR	NR	*Hordeum vulgare* L. cv. Golden Promise	Endophytic	Drought-stress tolerance	Ghaffari et al. (2019)
P. indica	NR	*Prosopis juliflora* and *Zizyphus nummularia* rhizosphere (Thar Desert in Rajasthan, India)	*Oryza sativa*	Endophytic arbuscular mycorrhizal fungi	Drought-stress tolerance	Mohseni Fard et al. (2017)
P. spadiceum AGH786	NR	*Glycine max* roots cv.Hwangkeumkong	*Triticum aestivum*	Endophytic	Salt-stress tolerance	Gul et al. (2022)
T. harzianum Rifai (TH)	NR	^{EE}*Solanum lycopersicum*	*Solanum lycopersicum* L. var, Rio Grande	Endophytic	Drought-stress tolerance	Mona et al. (2017)
T. harzianum T22	NR	Culture Collection	*Brassica juncea* L.	Endophytic	Salt-stress tolerance	Ahmad et al. (2015)
T. harzianum Th-6	NR	Culture Collection	*Zea mays* L. var. NT6621, and *Oryza sativa* L. var. kernel	Endophytic	Salt-stress tolerance	Yasmeen and Siddiqui (2018)

Abbreviations: EE, extreme environment; NR, non-reported.

[a] Benefit: the fungal species have been reported with one of the following features: hydrolytic enzyme production, indole acid acetic production, phosphate solubilization, siderophore synthesis, ammonia production, and plant-growth promoting bioassay.

[b] Confirmed: refers to fungal strains whose extremotolerance/extremophily was verified experimentally.

[c] Putative: refers to fungal strains which, being isolated from samples collected in extreme environments, have not been experimentally characterized as extremotolerant or extremophilic.

et al., 2021; Sun et al., 2022). Finally, other microbes can assist plant health by stimulating indigenous beneficial bacteria, acting as cooperative partners (Hu et al., 2021; Sun et al., 2022). We categorize these microorganisms as **biorecruiters**.

A completely different PGP strategy is displayed by other rhizospheric microorganisms, which drastically modify their environment (including changes in soil particle aggregation, hydrology, and moisture), thus mitigating the threats imposed by certain soils to plants (Philippot et al., 2023). It is tempting to refer to these microorganisms as **bioengineers**. Additionally, some microbial species displace pathogens from the phyllosphere by competing for nutrients or space or producing toxic compounds (Esitken & Karlidag, 2002; Esitken et al., 2006; Hernández-Fernández et al., 2021). We named these microorganisms **foliar bioprotectors**. Finally, since some members of the rhizosphere microbiome 'collaborate' with pathogens in accelerating disease progression by strengthening their chemotaxis (Jung et al., 2018; Yin et al., 2022), any antagonist to these 'helper' microbes will indirectly favour the health of their plant hosts. We refer to them as **pathogen-helper antagonists**.

Even though we present these ecological services or functions separately (see Figure 2), many PGPM exert their beneficial action by expressing a combination of them.

Plant growth-promoting endophytes

Mutualistic plant-microbe interactions do not solely concern the below-ground, external milieu (i.e. the rhizosphere or the phyllosphere); indeed, the presence of beneficial microorganisms within plant tissues (endophytes) is a well-documented scientific fact (Partida-Martínez & Heil, 2011). This includes – but is not limited to – mutualistic fungal endophytes, mycorrhizal fungi, nodulating, and other plant-associated N-fixing bacteria. As can be deduced from this list, beyond pathogens, which are a minority, many endophytes perform as PGPM, influencing the phenotype of their hosts and, particularly, their epigenomes (Gilbert et al., 2010).

In recent years, several groups around the world contributed relevant data emphasizing the role of endophytes as PGPM (Beltran-Garcia et al., 2014, 2021; Dini-Andreote, 2020; Jayakumar et al., 2020; Macedo-Raygoza et al., 2019; Mastan et al., 2020; Reva et al., 2019). Some endophytes also colonize plants' roots, where they act as biofertilizers, phytostimulators, and, as bioprotectors (Vandana et al., 2021).

Bioinoculants and plant probiotics

Once isolated, characterized, and identified, PGPM can be used to develop bioinoculants (or microbial inoculants). These commercial products contain live microorganisms as the active principles, aimed at improving plant health, nutrition, or development when applied to seeds or soil (Sanjuán et al., 2023). Bioinoculants are produced worldwide and commercially exploited by many transnational corporations (like the company formerly known as Monsanto, today Bayer), and other national enterprises or local initiatives. Two aspects of bioinoculants are crucial: they must contain viable microbes in their composition and exert a beneficial effect on their target host plants. Therefore, as Sanjuán et al. (2023) noticed, they fall in the *probiotics* category.

According to the FAO/WHO definition probiotics are 'live microorganisms which when administered in adequate amounts confer a health benefit on the host' (FAO, 2001). Even though the term was initially proposed to be of use in human and animal health, it was borrowed by Haas and Keel to be applied in agronomy to refer to all kinds of rhizospheric microorganisms able to 'minimize a range of diseases caused by pathogens' (Haas & Keel, 2003). Even though at the beginning it was mainly applied to 'biocontrollers', nowadays the term 'plant probiotics' (PP) encompasses all types of PGPM without making any distinction on their mode of action (see, for instance, Menendez & Garcia-Fraile, 2017). Moreover, to profit from the ubiquity and good perception of many commercial products already in use to treat human gastrointestinal disorders, companies manufacturing 'bioinoculants' advertise them as 'probiotics', as a very effective marketing strategy. Nevertheless, as recently noticed by Sanjuán et al. (2023), inoculants must share at least three features to be considered probiotics: (i) they must contain viable (active or dormant cells), safe and identified cells; (ii) they must follow strict rules to be applied, in sufficient amounts, to their target plants; and, (iii) they must have a positive impact on the overall health of their plant hosts. These characteristics are paramount in distinguishing between 'probiotics' and other inoculants, like 'biostimulants'. Since the controversy on this subject has been addressed in depth by Sanjuán et al. (2023) and Yakhin et al. (2017), we will not discuss it further.

Incidentally, in a recent perspective review, Harutyunyan and co-workers emphasized conducting more research on 'One Health probiotics' (Harutyunyan et al., 2022). In brief, the concept refers to safe microorganisms displaying beneficial effects to all living beings taking part in the food chain of edible vegetables, i.e. helpful in any link of the soil–plant–animal-human chain. According to the authors, some lactobacilli would fulfil the features expected from any probiotic of this kind.

Plant probiotic consortia

When considering the promotion of plant growth, since not all the beneficial ecological functions are displayed by a single PGP species, it is often necessary to apply a consortium of species, to achieve an ecological complementarity through the simultaneous expression of multiple plant-beneficial functions by different members of the consortium (Assainar et al., 2018; Hu et al., 2017). This multifunctionality is driven mainly by the microbial diversity present in terrestrial ecosystems (Delgado-Baquerizo et al., 2016), which can be modified by the application of exogenous PP consortia (Castro-Sowinski et al., 2007; Hu et al., 2021; Xiong et al., 2017).

Many studies have shown that inoculation of plants with PP consortia benefits their health (for a review on this topic; see Menéndez and Paço, 2020; Suman et al., 2022). Abundant scientific evidence fostered an essential change of paradigm in bioinoculants: from probiotics containing single PGPM strains to consortia of species (Woo & Pepe, 2018). Many commercial PP consortia are currently available worldwide.

When consortia of PGPM are designed by making rational use of a combination of omic technologies – including genomics, metabolomics, culturomics, transcriptomics, etc. –, (= rationally 'engineered'), the resultant product resembles true microbial communities, however with reduced complexity. Therefore, the term 'Synthetic Community (SynCom)' has been introduced. SynComs can range from 3 to 190 microbial strains (Marín et al., 2021) and are currently studied with profound interest as new functional plant probiotics (de Souza et al., 2020; Ke et al., 2021; Suman et al., 2022).

FUNGI AS PLANT GROWTH-PROMOTING MICROORGANISMS

As we have seen, bacteria, archaea, protists, algae, fungi, and viruses thrive in the plant holobiont and contribute to its health. However, fungi are among the most relevant microbial partners in the plant holobiont. Fungi are an abundant and diverse group of eukaryotes whose PGP functions have been known for decades but, unfortunately, often neglected (Pozo et al., 2021; Suman et al., 2022). This is striking since, in certain aspects fungi surpass bacteria as PGP, mainly owing to their ubiquity, particular morphology, penetration abilities in solid substrates, broad ranges single colonies can cover in terrestrial environments, and a much higher capacity to tolerate harsh conditions (Bilal et al., 2017). Besides, fungi, either filamentous, endophytic, mycorrhizal, or yeasts display almost all the ecological functions already presented and characteristic of PGP bacteria (Hyde et al., 2019). Therefore, the plant mycobiome is considered an almost unexploited source of exceptional PGPF (Pozo et al., 2021).

AMF from the subphylum Glomeromycotina (phylum Mucoromycota) is one of the most relevant groups of PGPF. AMF are ubiquitous and form mutualistic symbiosis with roots of ≈72% of terrestrial plants (Brundrett & Tedersoo, 2018), enabling arbuscular mycorrhizae, a type of association that plays essential roles in plant nutrition, impacting positively plant growth, productivity, health and stress relief (Bothe et al., 2010; Helgason & Fitter, 2009; Nanjundappa et al., 2019).

Arbuscular mycorrhizae protect plants from challenging environmental conditions, such as augmented salinity (Landwehr et al., 2002), flood (Thomas, 2021), drought (Abdel-Salam et al., 2018; Matsunaga et al., 2001), the presence of heavy metals (Rivera-Becerril et al., 2005), the oxidative stress (Campagnac et al., 2010), heat stress (Maya & Matsubara, 2013), osmotic stress (Santander et al., 2017), abiotic stress (Begum et al., 2019), the presence of pathogens (Chen et al., 2021), and water stress (Hu & Chen, 2020). Additionally, AMF increases the P uptake by plants and enhances their water intake and mineral nutrition (Smith & Smith, 2012). As another facet of their ecological roles, AMF interacts with PGP bacteria (particularly P-solubilizing bacteria) and facilitates P availability (Nacoon et al., 2020; Nanjundappa et al., 2019). AMF can modulate also mycotoxin gene expression by other pathogenic fungi (acting thus as biosuppressors), mitigating their virulence and protecting the host plant (Ismail et al., 2011).

For all the above-mentioned reasons, AMF have been used to produce PP – as single species or as consortia with other AMF, ectomycorrhizal fungi, or PGP bacteria – and applied for several decades, mainly to improve horticulture and grain crop productivity (Basiru et al., 2021; Berdeja et al., 2023) while reducing environmental costs (Berruti et al., 2016).

Root-associated fungi can also modulate the composition of the rhizospheric microbiome by recruiting and facilitating the establishment of a 'probiotic community.' For example, a *Trichoderma guizhouense*-amended biofertilizer stimulated the colonization of plant roots by indigenous beneficial fungi (*Humicola* spp.), contributing to plant health (Tao et al., 2023).

In another example of their versatility, some rhizospheric fungal species control plant parasitic nematodes and herbivore insects. Nematophagous or entomopathogenic fungi control these pests, acting like 'bodyguards' of their respective hosts (Gange et al., 2019; Singh et al., 2013). For instance, inoculation of *Beauveria*, *Metarrhizium*, *Tolypocladium*, or *Pochonia* strains results in beneficial impacts on plant protection and growth (reviewed in Pozo et al., 2021; Tall & Meyling, 2018).

Endophytic fungi, colonizers of intercellular spaces in plant organs, have also been shown to behave as PGP. Endophytes perform diverse functions, among which facilitating nutrient acquisition by the host plants and protection from pathogens, herbivores, and pests are among the most relevant (for a review on this subject, please see Chitnis et al., 2020; Suryanarayanan et al., 2017). For example, some root endophytes favour and enhance N-uptake by their hosts when grown in nitrogen-depleted soil (Upson et al., 2009). Others upregulate the expression of phosphate transporters in their host plant, enhancing P uptake (Yadav et al., 2010), or producing toxic substances that detract herbivores from their hosts (Pozo et al., 2021). Finally, certain endophytic strains act as biocontrollers of parasite weeds by obstructing their xylem vessels (Marley & Shebayan, 2005) or inhibiting seed germination (Anteyi et al., 2022). This fascinating biocontrol ability allowed to develop mycoherbicides, efficient products for controlling parasitic weeds (Sands & Pilgeram, 2009). However, only a few commercial products take advantage of the panoply of ecological functions displayed by PGP endophytic fungi (Chitnis et al., 2020).

In addition to AMF, rhizospheric and endophytic fungi, many yeast species – collectively referred to as non-conventional yeasts – also behave as PGP, promoting plant growth through similar mechanisms as those described above [reviewed by Shruthi et al. (2022) and by Nimsi et al. (2023)]. For instance, *Wickerhamomyces anomalus* LBCM1105 and *Saccharomyces cerevisiae* strains LBCM1112 kill in vitro *Moniliophthora perniciosa*, the causative agent of cacao' severe fungal disease known as Witches' Broom Disease (Ferraz et al., 2021). Yeasts killed the pathogenic fungus and fed on their cells, an example of mycophagy or mycoparasitism.

As said before, from a commercial perspective, only a few fungal species have been included in many products promoting plant growth. *Trichoderma* spp. strains are, by far, the most frequently used. Well-known for their biocontrol abilities, *Trichoderma* spp. are particularly efficient as antagonists of several devastating phytopathogens like *Fusarium*, *Rhizoctonia*, or oomycete *Pythium* (Woo et al., 2023). Thus, *Trichoderma* spp. have been included in the formulation of several biocontrol products (= biopesticides or biocontrollers) as single strains or as part of consortia (Bradáčová et al., 2019; Chitnis et al., 2020).

FUNGAL PLANT PROBIOTICS AND EXTREME ENVIRONMENTS

Crops of agricultural interest often suffer from abiotic stress when environmental conditions (including temperature, moisture, radiation, and salinity, among others) become significantly harsher compared to optimal field growth conditions (Derbyshire et al., 2022). Fortunately, the scientific evidence shows that some plant probiotics can improve the tolerance of their hosts to diverse biotic and abiotic stresses (Sahay, 2022). For that reason, it is usual to monitor the potential of these plant probiotics under extreme environmental conditions – either in vitro, in the greenhouse, or the field –, similar to those imposed on plants by abiotic stress factors (Hang et al., 2022).

As we will present in continuation, fungi belonging to genera *Trichoderma*, *Penicillium*, *Fusarium*, *Curvularia*, *Morteriella*, *Glomus*, and *Piriformospora*, among others, can participate in beneficial interactions with plants. They reside in their host plants' rhizosphere and phyllosphere but mostly in their endosphere, as endophytes. Some have often been isolated from extreme ecosystems worldwide (Coleine et al., 2022). Thus it is not surprising that they can carry out their ecological functions under extreme environmental conditions. Table 1 presents the available information related to fungal species of this group studied in the past decade. Even though it indicates a sustained and increasing interest in this subject, the amount of information is scarce and fragmented, evidencing that the field is still in its infancy. In continuation we present some of the most emblematic examples of the PP abilities of these extremophilic/extremotolerant fungi.

Extremophilic/extremotolerant fungi and their ecological functions as plant probiotics

Salinity, drought, and temperature extremes are the main abiotic stress factors causing severe impacts on plant growth and development (Krasensky & Jonak, 2012). As mentioned previously, these are the kinds of challenging conditions agriculture will face in the near future. High salinity is usual in eroded soils and globally affects agricultural production (Oney-Birol, 2019), limiting water and nutrient availability and causing cellular damage, osmotic stress, and toxicity in plants. High salt concentrations inhibit the growth of shoots and roots and reduce seed germination (Yang et al., 2021). Halotolerant fungi can enhance plant growth and assist crops in saline areas. Besides, some strains can also be crucial in controlling plant diseases, making them useful not only as biofertilizers but also as biocontrollers and biopesticides (Boamah et al., 2021).

For instance, several extremophilic endophytic *Penicillium* spp. strains can alleviate plant salt stress (Leitão & Enguita, 2016) (Table 1). This is the case of *Penicillium funiculosum* P1, which improved the growth of quinoa plants under severe saline-alkali stress (Jin et al., 2022), or a halotolerant endophytic strain of *Penicillium chrysogenum* which, when inoculated to tomato plants, promoted their growth even though they were irrigated with a 300 mM saline solution for almost 10 weeks (Morsy et al., 2020). Similarly, inoculation of lettuce seedlings with two psychrotolerant root-fungal endophytes, *Penicillium brevicompactum* KJ881370 and *P. chrysogenum* KJ881371, isolated from Antarctic plants, enhanced their survival under saline conditions, and also increased drought tolerance and water use efficiency (Molina-Montenegro et al., 2016, 2020). Furthermore, when inoculated in consortium with two halotolerant plant growth-promoting rhizobacteria (*Arthrobacter* sp. and *Planocccocus* sp.), the fungal probiotics reduced the physiological impact of saline stress in salt-susceptible crops

(Acuña-Rodríguez et al., 2019). A rhizospheric halotolerant strain of *Penicillium* sp., NAUSF2 was able to mitigate abiotic stress in *Vigna radiata* when grown in P-deficient saline soil and to promote its growth by solubilizing P and producing phytohormones (Patel et al., 2021).

A similar protecting ability was attributed to *Fusarium culmorum* FcRed1, naturally colonizing all non-embryonic tissues of coastal dune grass (*Leymus mollis*). In this case, the symbiotic association of both organisms (plant and fungus) was necessary to sustain their ability to proliferate when exposed to high salinity levels (300–500 mM NaCl), similar to those present in their native habitat (Rodriguez et al., 2008). When inoculated into rice seeds (*Oryza sativa*), the same strain conferred salt-stress tolerance (Redman et al., 2011).

On the other hand, three halotolerant endophytic fungal species, namely *Periconia macrospinosa*, *Neocamarosporium goegapense*, and *N. chichastianum*, previously isolated from the roots of plants growing on the shore of a salt lake in the central desert of Iran, mitigated not only saline stress but also drought stress when inoculated into dicot plants (Hosseyni Moghaddam et al., 2021) and in barley (*Hordeum vulgare* L.) (Hosseyni Moghaddam et al., 2022). Similarly, *Trichoderma longibrachiatum* HL167, a halotolerant rhizospheric strain, alleviated damage caused by salt stress when inoculated into Cowpea plants (Liu et al., 2023). This strain also antagonized *Fusarium oxysporum*, a fungal phytopathogen.

Finally, some haloalkaliphilic fungi are also helpful in remediating the impact caused to soils by salinization and alkalinization processes. As Wei and Zhang (2019) reported, applying amendments supplemented for several years with *Aspergillus glaucus* CCHA in the Songnen Plain of northeastern China enabled a higher yield of rice compared to that achieved in the control plot.

Drought is another abiotic factor limiting robust plant growth, inhibiting their development and often causing wilting, resulting in reduced productivity or even zero fruit or seed yield (Yadav, 2017). Several PP extremotolerant fungi can alleviate these effects. For example, inoculation of maize seedlings with two xerotolerant endophytic fungi, *Trichoderma harzianum* 81Y1 and *Fusarium solani* 19K3, isolated from the roots of desert trees enhanced their tolerance to drought (Bakhshi et al., 2023). Another xerotolerant endophyte, *Alternaria alternata* LQ1230 alleviated drought stress when inoculated to wheat plants (Qiang et al., 2019). Finally, *Piriformospora indica* mitigated drought stress when inoculated into *Arabidopsis* plants (Kumar et al., 2015; Sherameti et al., 2008).

Heat causes dehydration in plants due to increased transpiration rates that lower the water available to crops, sometimes resulting in lethal effects. Heat also affects plant growth and development when it reaches extreme values because it can provoke oxidative stress, harming plant cells and impairing their growth by releasing reactive oxygen species (ROS) (Zhao et al., 2021). Again, plant colonization by extremophilic fungi can result in a tolerant phenotype to heat stress.

For example, *Thermomyces lanuginosus* CpE, a thermophilic fungal endophyte isolated from extremely desert-adapted plants in Egypt, promoted growth and also relieved heat stress in its natural host (*Cullen plicata*) (Ali et al., 2019). This protective effect was also recorded when tested on cucumber plants (Ali et al., 2018).

Curvularia protuberata, another thermophilic endophyte, colonizes the tissues of *Dichanthelium lanuginosum*, a species of grass from geothermal soils, allowing it to grow at high soil temperatures in Yellowstone National Park, while nonsymbiotic plants become shrivelled, chlorotic and die (Redman et al., 2002). When *C. protuberata* is inoculated in tomato plants (*S. tuberosum*), it confers tolerance to heat stress (Márquez et al., 2007). Surprisingly, the ability to protect plants from heat is related to the virus's presence in the endophytic fungus genome. Another related thermotolerant endophytic fungus, *Curvularia crepinii*, isolated from the roots of plants grown in geothermal ecosystems in Yunnan Province (Southwest China), also improved thermotolerance in its host plant (Zhou et al., 2015).

Besides alleviating drought stress, endophytes colonizing the inner tissues of desert plants can also protect their host plants from heat. This was observed when a combination of three endophytic strains of *T. harzianum*, isolated from grasses in arid habitats of the Western USA, were tested on corn and cotton (Redman et al., 2021).

Exposure of plants to low temperatures (= cold stress) also impacts them adversely in many physiological and biochemical cell functions, causing visible symptoms like wilting, chlorosis, or necrosis (Ruelland & Zachowski, 2010), resulting from cellular dysfunction, membrane modifications, and many ultrastructural changes (reviewed by Theocharis et al., 2012). When grown in the cold, plant nutrient management helps activate various mechanisms that effectively alleviate abiotic stresses and promote plant health and higher crop yields (Kumari et al., 2022).

C. protuberata Cp4666D, a thermotolerant endophyte isolated from *D. lanuginosum*, conferred tolerance to cold temperatures and drought stress when inoculated into rice seeds (Redman et al., 2011). *Rhodotorula* sp., *Mrakia* sp., and *Naganishia* sp., three psychrotolerant yeast strains isolated from rhizospheric soils collected at a volcano crater in Mexico, promoted *Solanum lycopersicum* (tomato) germination and plantlet growth at low temperatures (Tapia-Vázquez et al., 2020). Also, these yeasts inhibited the growth of various pathogenic fungi.

Even though plants can cope with UV-radiation through several protection mechanisms, when the doses are too high, they may cause DNA damage, protein polymerization, enzyme inactivation, and increased cell membrane permeability, among many other effects

(Vanhaelewyn et al., 2020). Certain extremophilic endophytic fungi allow *Colobanthus quitensis* (an Antarctic dicotyledonous perennial herb) to cope with UV stress. Indeed, colonization of native plants by *P. chrysogeunum*, *P. brevicompactum*, *Alternaria* sp., *Phaeosphaeria* sp., and *Eupenicillium osmophilum* improved the photosynthesis efficiency of *C. quitensis* minimized cell damage and boosted its physiology, thus increasing the tolerance to harmful doses of UV-B radiation (Ramos et al., 2018; Hereme et al., 2020; Barrera et al., 2020). Incidentally, the presence of endophytes also favoured tolerance to drought in *C. quitensis* (Hereme et al., 2020).

Accumulation of heavy metals in plant tissues can cause morphological abnormalities and metabolic disorders that reduce plant yield (Amari et al., 2017). Plant-associated microbes can help to alleviate this abiotic stress by reducing metal bioavailability in soil (Tiwari & Lata, 2018). *Porostereum spadiceum* AGH786 is a heavy-metal-resistant, Cu hyperaccumulator, and drought-stress tolerant fungus (Naz et al., 2022), which can remove Cu from the soil and trigger *S. lycopersicum* L. defence mechanisms to cope with Cu toxicity. Inoculation of tomato plants with this fungal strain induced enhanced metal chelation in roots and suppressed the Cu uptake and translocation machinery, avoiding its transport to upper vegetative parts; it also alleviated the effects of a simultaneous water deficit, acting as a drought-stress mitigator. This way, tomato plants were transformed into efficient phytoremediators.

Biocontrol abilities of extremophilic fungi

Pathogens – including fungi, bacteria, viruses, and nematodes – can cause severe diseases in plants, affecting the quality and quantity of their fruits, leading to significant losses and posing a substantial threat to global food production annually (Thambugala et al., 2020). Furthermore, they can persist in their host's organs and multiply during post-harvest storage, affecting the overall quality of the product and potentially impacting human health when consumed (Brimner & Boland, 2003).

Some extremophilic fungal species have been shown to efficiently protect plants and their fruits from diseases caused by phytopathogenic fungi and spoiling microorganisms, acting as biocontrollers. For instance, *Trichoderma longibrachiatum* HL167 is a halotolerant endophytic strain isolated from saline-alkali soils in China, which protected cowpea from Fusarium wilt (a disease caused by *Fusarium oxysporum*), when tested in the field (Liu et al., 2023). Strain HL167 also protected the plants against saline stress.

On the other hand, *Aureobasidium subglaciale*, a melanized yeast-like psychrophile, can significantly reduce apple rot caused by three low-temperature mould pathogens, thus holding great potential for preventing fruit rot during cold storage (Zajc et al., 2022). The closely related species, *Aureobasidium pullulans*, able to grow at 0°C and to tolerate salinity, exhibits vigorous biocontrol activity against post-harvest rot (Zajc et al., 2020). Similarly, *A. pullulans* and *A. subglaciale* control *Botrytis cinerea*, the causal agent of grey mould in tomatoes (Di Francesco, Di Foggia, et al., 2020; Di Francesco, Zajc, et al., 2020). However, as we will see later, substantial risks are linked to using fungi for the biocontrol of phytopathogens.

Current avenues explored by our team to test the suitability of extremophilic fungi as plant probiotics

We concisely illustrate our endeavours to develop novel plant probiotics for agricultural applications, emphasizing the role of extremophilic fungi (Figure 3A–D). The first one aims to test the agricultural efficacy of a collection of filamentous fungi and yeasts isolated from the Tehuacán Desert in Mexico. Numerous strains accelerated germination, supported root development, and stimulated leaf growth of basil (*Ocimum basilicum*) (Zenteno-Alegría et al., in preparation). Additionally, we are monitoring how these strains facilitate the mobilization of nutrients to enhance the mineral nutrition of this plant species and other spice plants such as tarragon, rosemary, and mint (Figure 3A).

The second path deals with the xerotolerant/halotolerant endophytic fungi of quinoa plants (*Chenopodium quinoa*) isolated from Salar de Uyuni, Bolivia. We are studying how these fungi colonize the roots of quinoa plants and whether they mitigate the stress caused by salinity (Zenteno-Alegría et al., 2024). Furthermore, we are assessing the contribution of these fungi to the biogeochemical cycles in these ecosystems and their contribution to soil fertility (Figure 3B).

We are also engaged in gaining insight on the protection of crops from sudden frost damage by psychrophilic- or psychrotolerant fungi. The primary objective of this research endeavour is to determine whether fungal strains isolated from periglacial formations on Mexican volcanoes can mitigate cold-stress in tomato (*S. lycopersicum*) plants (Zenteno-Alegría et al., 2024). Similarly, we are investigating if extremotolerant fungi from the Chichonal volcano in Mexico can protect tomato plants from heat shocks (Figure 3C) (Martirena-Ramírez et al., 2024).

Finally, our focus extends to postharvest biocontrol by utilizing extremophilic black yeasts of the genus *Aureobasidium* (Zajc et al., 2019). The primary outcomes of our research relate to the management of pathogenic fungal infections in apples and tomatoes (Figure 3D).

FUTURE PERSPECTIVES

Given the current state of global change, the rational design of forthcoming biofertilizers will face significant

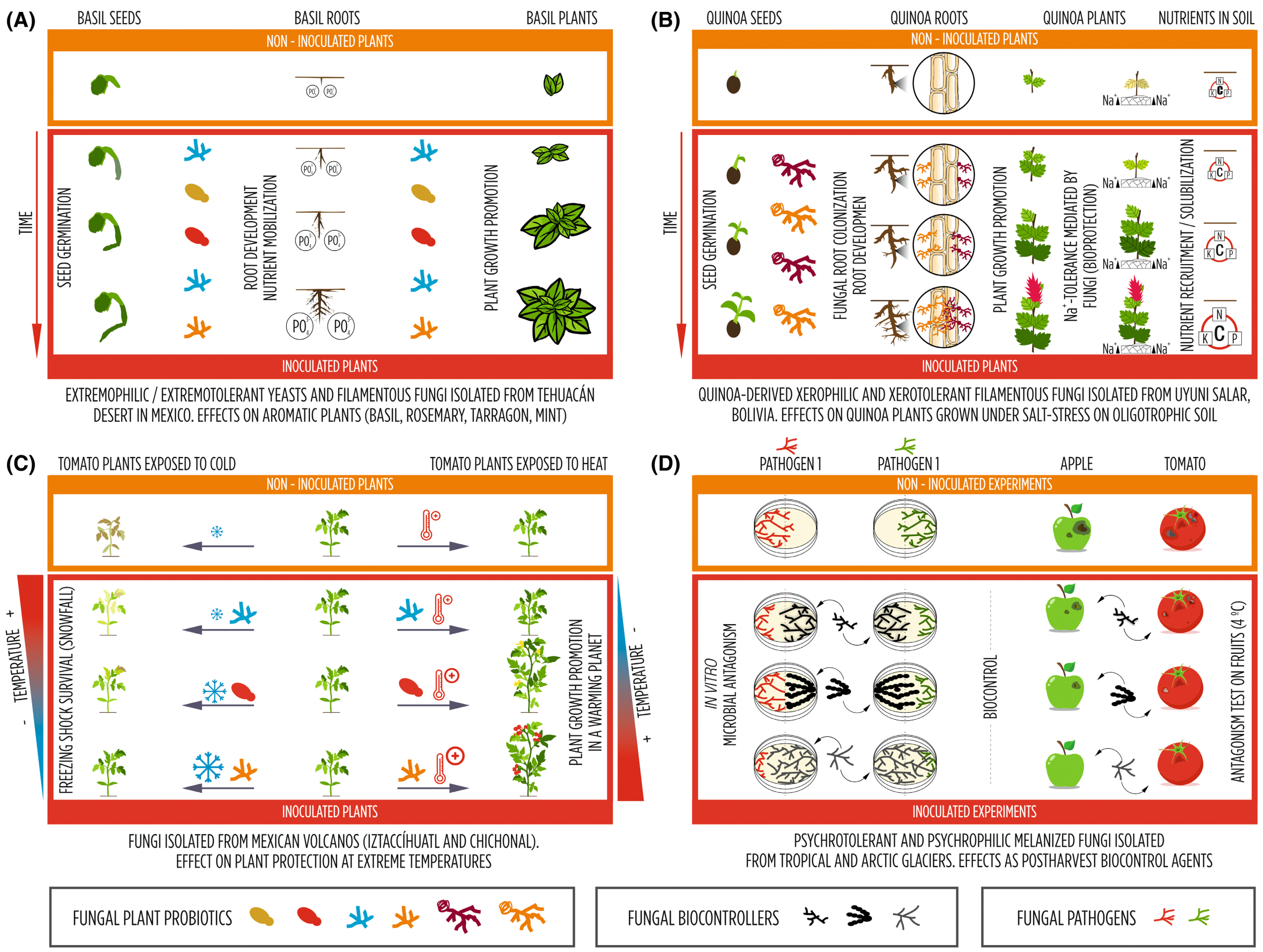

FIGURE 3 Projects in progress related to the use of extremophilic fungi to develop new bioinputs for agriculture. (A) Use of extremophilic and extremotolerant fungi isolated from the Tehuacán Desert in Mexico to formulate biofertilizers for aromatic plants such as basil, rosemary, mint, and tarragon. (B) Use of fungi associated with quinoa plants for the rational design of biofertilizers based on xerophilic and halophilic fungi to induce protection against salinity and promote plant growth. (C) Use of fungal strains isolated from Mexican volcanoes to protect tomato plants when exposed to extreme temperatures. (D) Use of black yeasts for postharvest control of pathogenic fungi that affect fruits such as apples and tomatoes.

obstacles. Current biofertilizers/plant probiotics are not viable solutions for upcoming scenarios. It is almost certain that the most frequently used bioinputs, derived from *Trichoderma* species, are inadequate for the biofertilization of crops that are of critical food importance to humanity in extreme soils. Future agroecosystems are expected to exhibit distinct stressors, including extreme temperatures, extreme acidity or alkalinity, significant depletion of organic matter content (as a result of intense erosion processes), heightened salinization, extended periods of drought accompanied by limited water availability for farming, and the presence of exceptionally hazardous substances, including heavy metals and emerging contaminants. This situation could compromise the efficient functioning of *Trichoderma*-containing plant probiotics.

Furthermore, considering the anticipated substantial increase in the concentration of chaotropic compounds in soils, the future of current plant probiotics becomes considerably more precarious and susceptible. As a result, the development of novel probiotics for plants through the selection of adequate fungal species from extremophilic mycobiomes seems like a practical resolution; however, this path is also fraught with challenges and knowledge gaps, mainly concerning the complex interactions established between plants and extremophilic fungi in extreme environments. For instance, the study of cellular and molecular mechanisms that explain the interaction between fungi and plants under extreme conditions is a field in his infancy. To gain more profound knowledge about these mechanisms, it is critical and urgent to employ a variety of experimental methods, including microscopy, microbial and plant physiology, genomics, transcriptomics, proteomics, metabolomics, phenomics, and phenotype microarray techniques for characterizing plant and fungal metabolism, among other. Combining all these experimental approaches will facilitate the rational design of novel agricultural bioproducts, among which fungal plant probiotics, to ensure the sustenance of an expanding global population and prevent the outbreak of humanitarian emergencies caused by food scarcity.

When discussing future plant probiotics, we should think beyond food production for human consumption; we must also consider developing fungal plant probiotics that stimulate growth and increase the productivity of forage species intended for animal feed. Also, there are additional situations where extremophilic mycobiomes could have great application potential. For instance, extremotolerant and extremophilic fungi may also be used to develop probiotics that are beneficial to improving the quality of soils devastated by high-impact wildfires and reforesting those areas. This emerging field demands immediate attention due to the critical nature of ecological restoration in such ecosystems. In addition, using mycobiomes colonizing arid or hyperarid regions may also find utility in the design of probiotics to enhance root development of cacti, thereby improving their ability to establish themselves in desert soils after being transferred from greenhouses. In countries with a high rate of cactus endemism and significant deforestation of their cactus reserves, such as Mexico, this issue is particularly alarming, such as in the Tehuacán Desert.

An additional highly advantageous application of extremotolerant fungi is the development of probiotics intended to reforest arid regions, such as those found in the Andean Altiplano. Indeed, native populations in the Altiplano of the Bolivian Andes, for instance, cultivate quinoa as a primary food source. The Altiplano is a polyextremophilic ecosystem characterized by hypersaline and extremely oligotrophic soils with a high chaotropic salt concentration, including lithium, magnesium, and sodium. Also, the Altiplano shows exceptionally high soil erosion rates, a relative humidity of less than 3%, and a very low annual rainfall regime. In addition to contributing to soil fertilization through quinoa cultivation, the reforestation of Altiplano's soils with native grasses is an urgent and critical matter for several indigenous communities. These communities utilize the grasses as living barriers to safeguard soils dedicated to seasonal quinoa culture, for instance, against wind erosion. Utilizing fungi originating from arid regions and salty environments presents a compelling alternative to pursuing distinctive extremophilic ecotypes that may facilitate the growth of plants, specifically grasses.

In addition, probiotics derived from extremotolerant and extremophilic fungi could also be utilized to promote the development of bryophytes. The potential biotechnological significance of the positive interactions between bryophytes and fungi remains largely unexplored, even though certain bryophytes, such as *Marchantia polymorpha*, exhibit remarkable bioremediation capabilities in highly polluted environments containing environmental toxic compounds. However, comprehending these interactions also holds significant ecological and evolutionary significance because mosses colonize the rocks of extinct tropical glaciers and contribute extraordinarily to soil formation in polyextreme environments such as the deserts of Antarctica. In conjunction with mosses, fungi may be significant biocatalysts, playing essential roles in these ecological transition processes. In summary, the instances above unequivocally demonstrate that the interplay between plants and fungi adapted to extreme conditions is a matter that necessitates immediate attention and comprehension. In other words, fungal plant probiotics are needed not only to boost agriculture in extreme soils but also for their ecological and evolutionary significance.

Finally, to gain more insight into understanding the mechanisms driving the interaction between extremophilic fungi and plants, it is critical to devise experiments at the laboratory level, in greenhouses, and in the field. Additionally, it is imperative to address comprehensive and cross-cutting inquiries to consider the interplay between probiotic fungi, viruses, and all the plant's microbiome components, including endophytic and epiphytic microorganisms. We also need to refine our understanding of the temporal and spatial processes governing plant colonization by extremophilic fungi, how they trigger differential transcriptional responses in plants, and how this response modifies the physiology of plants in terms not only of their growth but also of their tolerance to different biotic and abiotic stresses. Further inquiries warrant consideration regarding how extremophilic fungi might enhance soil health and, consequently, the implications for plant nutrition and phytopathogen biocontrol. All these questions remain unanswered to date.

However, plant probiotics derived from extremophilic fungi will perish without well-defined policies for the isolation and preservation of such mycobiomes. Therefore, establishing biological banks to safeguard the fungal biodiversity of extreme ecosystems must be mycologists' and biotechnologists' top priority. As a sad illustration of this urgency, the native mycobiomes of numerous Latin American tropical glaciers, including those that recently vanished from Humboldt and Bolivar peaks in the Venezuelan Andes, have ceased to exist due to the impacts of climate change.

CONCLUDING REMARKS – HARNESSING EXTREMOTOLERANT FUNGI FOR SUSTAINABLE AGRICULTURE IN A CHANGING CLIMATE

Facing the challenges of global climate change

Global climate changes increasingly expose agronomical land to drought, salinity, and extreme temperatures, threatening traditional agronomic practices. In this context, sustainable agricultural practices and innovative solutions cannot be overstated.

Plant growth-promoting microorganisms (PGPM): A green paradigm for agriculture

Within the intricate web of the plant holobiont, the role of PGPM emerges as a promising green paradigm. These microorganisms exhibit multifaceted contributions to plant well-being and present a holistic approach to sustainable agriculture and environmental resilience.

Bacteria versus fungi: Commercialization disparity

While bacteria have garnered significant attention and commercial success in the realm of PGPM, fungi, with their remarkable plant growth-promoting (PGP) functions, remain comparatively understudied and underutilized. The unique attributes of fungi, encompassing their ubiquity, morphology, and ability to endure harsh environments, position them as exceptional plant growth-promoting fungi (PGPF).

Fungi's comparative advantages and the need for more synergistic consortia

Fungi, with their diverse forms, including filamentous, yeasts, and polymorphic fungi, bring distinctive advantages compared to bacteria as PGPM. The ubiquity and endurance of fungi make them exceptional contributors to sustainable agriculture. Furthermore, the call to transition from single-strain probiotics to synergistic, multi-functional consortia aligns with the versatility exhibited by fungi in controlling plant-parasitic nematodes, herbivore insects, and pathogens. This shift opens avenues for the emergence of synthetic communities (SynComs) as promising functional plant probiotics.

Unlocking the potential of extremotolerant fungi

In the face of escalating challenges, extremotolerant fungi stand out in relation to potential new solutions. Their beneficial properties, ranging from extreme salinity and drought tolerance to biocontrol abilities, position them as indispensable components of future agricultural strategies. Certain genera of fungi, including *Trichoderma*, *Penicillium*, *Fusarium*, and others, have already shown their capabilities in mitigating a spectrum of stresses. Research on their interactions with plants opened a new frontier for harnessing the benefits of extremotolerant and extremophilic fungi, populating diverse extreme environments.

Fungal probiotics: Unveiling the potential

Within the diverse realm of plant probiotics, fungi emerge as potent contributors with almost untapped potential. The notion of fungal probiotics challenges the prevailing emphasis on bacterial counterparts, introducing a paradigm shift in harnessing the benefits of microorganisms for plant health. Despite the commercial utilization of bacterial plant probiotics, the inclusion of fungal counterparts remains limited, opening the way for innovative applications. Research endeavours focusing on isolating and characterizing these fungal probiotics present a new way for expanding our understanding of plant-microbe interactions and, in turn, enriching sustainable agricultural practices.

Changing agricultural strategies through advanced technologies

Agricultural research is marked nowadays by new technological innovations, also featuring advanced ‘omics’ technologies. The integration of genomics, transcriptomics, proteomics, and metabolomics into the study of plant-microbe interactions offers new insights into the intricate mechanisms governing these relationships. Harnessing the power of these omics technologies will allows researchers to decipher the genomic blueprint of extremotolerant fungi, unravelling the genetic basis of their resilience to extreme conditions. Furthermore, the application of metagenomics facilitates a comprehensive understanding of microbial communities in diverse environments, aiding in the identification of novel extremotolerant fungi. The emergence of synthetic communities (SynComs), designed also by applying omics technologies, represents a pioneering approach to developing functional plant probiotics. These consortia, comprising carefully selected microorganisms, highlight the potential for precision agriculture, where the microbiome is strategically tailored to enhance plant health and productivity.

Further research and caution

Understanding the intricate mechanisms of fungal–plant interactions, especially in stressed environments, is important for leveraging the benefits of extremotolerant fungi. Increased research, especially on the synergies between plants and extremotolerant fungi, is urgently needed. In this way we can increase sustainable agriculture and help to ensure food security in the face of unprecedented climate challenges. Fungi, with their potential, can significantly contribute to a more sustainable future.

AUTHOR CONTRIBUTIONS

Claribel Orquídea Zenteno-Alegría: Investigation. **Luis Andrés Yarzábal Rodríguez:** Conceptualization; investigation; writing – original draft; writing – review and editing. **Jimmy Ciancas Jiménez:** Investigation. **Peggy Elizabeth Álvarez Gutiérrez:** Investigation; supervision; visualization. **Ramón Alberto Batista-García:** Conceptualization; funding acquisition; investigation; supervision; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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