


Review

Mortierella Species as the Plant Growth-Promoting Fungi Present in the Agricultural Soils

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Abstract: In the most recent scientific reports based on the DNA or RNA-analyses a widespread presence of the filamentous fungi, *Mortierella* in various environments has been shown. Some strains of this genus belong to the plant growth-promoting fungi (PGPF) and are found in the bulk soil, rhizosphere and plants tissues. These microorganisms are also often found in the extremely hostile environments, responsible for improving access to the bioavailable forms of P and Fe in the soils, the synthesis of phytohormones and 1-aminocyclopropane-1-carboxylate (ACC) deaminase, and last but not least the protection of agricultural plants from pathogens. Furthermore, earlier reports classified *Mortierella* spp. as the saprotrophic microorganisms isolated from the forest litter, and nowadays their status as a very valuable decomposers in the agricultural soils was confirmed. The key features like the ability to survive under very unfavorable environmental conditions and the utilization of carbon sources contained in polymers like cellulose, hemicellulose, chitin make these fungi efficient as the agricultural inoculants. The growing interest in the application of *Mortierella* spp. is mainly due to the potential use of this genus in the increase of the nutrient uptake efficiency, positive effect in crop protection against adverse conditions, and reduction of chemical fertilizers and pesticides applied. Moreover, activities of *Mortierella* species selected from the wild or cultivated plants influence the soil microbiota and support the performance of the beneficial microorganisms enhancing significantly crop yield.

Keywords: *Mortierella*; agricultural soils; plant growth-promoting fungi; endophytes; siderophores; phosphorus; phytohormones; phyto regulators; crop productivity



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1. Introduction

Soils are very diverse systems consisting of various types of organic and inorganic components. One of the most essential constituents of the soil are microorganisms with the ability to degrade a number of compounds and to create a very dynamic soil environment of the transformed substances acting as decomposers. Their activities result in a higher bioavailability of the key elements such as N, organic C, P, Fe, and other substances not exclusively for themselves, but also for other organisms which is crucial in agricultural soils [1,2]. The reduced application of inorganic synthetic fertilizers in favor of biofertilizers containing microorganisms has an influence in the increasing uptake and availability of mineral nutrients for plants. A specific group of these environmentally friendly microbial fertilizers can be effectively applied on the seeds, plant surfaces, or to the soil in order to promote plant growth by supplying them with the nutrients indispensable for their proper functioning [3]. The development and availability of the new methods of identification of microorganisms within the last 20 years led to the detection of plant growth-promoting *Mortierella* species in the soils all over the world. The present paper is focused on the plant

growth-promoting abilities and the other properties of *Mortierella* species which seem to be helpful in enhancing plant development in agricultural applications.

2. From the Pioneering Microorganisms to the Important Agricultural Inoculants

2.1. Isolation and Identification of *Mortierella* spp. from the Soils of the World

Over the last two decades numerous studies indicated the occurrence of *Mortierella* species in diversified environments, e.g., rocks, caves, mines, asbestos fibers, rivers, lakes, plant tissues soils, and rhizospheres (including agricultural areas) at each latitude [4–9]. Recently, researches employing molecular methods revealed that not only the *Aspergillus* and *Penicillium* genera, but also *Mortierella* strains are the most abundant filamentous fungi in the soils around the world [10–16]. Moreover, the *Mortierella* omnipresence may be confirmed by in the environment the effects of 35-year application of an organic fertilizer to the agricultural soil in China (Anhui Province) in order to promote plant growth. *Mortierella elongata* was found to be the dominant fungal species in this soil [17].

New species of *Mortierella*, being constantly discovered, are the most common soil-inhabiting fungi. Moreover, they are one of the largest genus of Mucorales within Zygomycetes. In turn, filamentous fungi with aseptate hyphae (coenocytic hyphae) belong to the Mortierellales order. *Mortierella* species form colonies often described as pale white, white or whitish (sometimes little dark whitish at the center) zonate, forming a typical rosette pattern [7,8,15,18,19]. In the course of time, the reverse side of the colonies may become yellowish. Cottony aerial hyphae of *Mortierella* species form one of the simplest sporangia (without or with rudimentary columella) which are pigmented or colorless [11]. The *Mortierella* colony growth may be accompanied by the garlic-like odor [15,20]. After incubation at 5–10 °C, these fungi are known as forming sporangia on the nutrient-poor media [21], such as water agar [11]. Contrarily to these results, *Mortierella antarctica* investigated by Ozimek et al. [8] failed sporulation on this medium (water agar) at low temperatures and the genetic analysis was required to confirm the species affiliation. However, Kuhlman [22] observed that neither the low temperature nor the different substrates affected the type of spore formation of *Mortierella* species, i.e., *M. ericetorum*, *M. parvispora*, *M. bainieri*, *M. candelabrum*, *M. elongata*, *M. minutissima*, *M. pulchella*, *M. zychae* and *M. marburgensis*. On the other hand, the studied *Mortierella* species often formed spores on the hemp seed agar or/and diluted Pablum agar. It is probable that this medium was prepared from Pablum—a product for malnutrition of infants consisting of the ground and precooked oatmeal, yellow corn meal, bone meal, dried brewer's yeast, and powdered Alfalfa (*Medicago sativa*) leaf [23]. In addition to the mineral compounds, Pablum is rich in vitamins A, B₁, B₂, D, E and reduced iron. Due to its composition, “Pablum Cereal Agar” is recommended as a medium stimulating sporulation of fungi [24,25]. Furthermore, Gao et al. [26] obtained very good sporulation of *Mortierella isabelina* on medium with xylose. The lack of morphological characteristics of *Mortierella* in the past has resulted in difficulties in identification of the species and can lead to the problems with the storage of fungal strains in the collections. Moreover, the comparison of culture-based and culture-independent methods mostly supports the higher taxonomic precision of the methods based on DNA or RNA analyses which allowed to confirm the abundance of *Mortierella* species in different environments [10].

The positive contribution of these fungi in the agricultural soils (Table 1) as well as in the plant tissues should lead to the discovery of the optimal culture conditions and spore-forming media enabling analysis of the complex interactions between plants and microorganisms. It is worth highlighting that the pathogenic species are very rare in this genus, that is why *Mortierella* species are very promising sources of plant growth-promoting inoculants for agriculture [27].

Table 1. The *Mortierella* species identified in the agricultural soils.

Mortierella Species	Crop/Cultivar	Country (Area)	Ref.
<i>Mortierella</i> sp. (1–5) strains; <i>M. alpina</i> ; <i>M. hyalina</i> ; <i>M. isabellina</i> ; <i>M. spinosa</i> ; <i>M. ramanniana</i> var. <i>angulispora</i> ; <i>M. ramanniana</i> var. <i>ramanniana</i>	soil samples from avocado and citrus field	Nd	[28]
<i>M. polycephala</i>	wheat rhizosphere soil (<i>Triticum aestivum</i> cv. Baldus)	Netherlands (Utrecht)	[14]
<i>Mortierella</i> sp.	soil samples from potato	Czech Republic (Lipová near Kašperské Hory)	[29]
<i>M. elongata</i> ; <i>M. gamsii</i> ; <i>M. nanna</i> ; <i>M. parvispora</i>	soil samples from maize (<i>Zea mays</i>)	India (Meghalaya)	[30]
<i>M. gamsii</i> ; <i>M. nanna</i> ; <i>M. parvispora</i>	soil samples from French bean (<i>Phaseolus vulgaris</i>)	India (Meghalaya)	[30]
<i>M. chienii</i>	soil samples from bamboo grove	Taiwan (near Tainan)	[31]
<i>M. polygoonia</i>	soil samples from <i>Solanum tuberosum</i>	Netherlands (Wegeningen)	[32]
<i>M. ambigua</i> ; <i>M. indohii</i> ; <i>M. zychae</i>	soil samples from agricultural fields	Korea	[15]
<i>M. elongata</i>	soil samples from maize	China	[17]
<i>M. alpina</i> ; <i>M. gamsii</i> ; <i>M. capitata</i> ; <i>Mortierella</i> sp.	soil samples from apple orchards (<i>Malus domestica</i>)	Mexico (Chihuahua)	[33]
<i>Mortierella</i> sp.	rhizosphere soil samples from maize and sorghum	Brazil (Minas Gerais)	[34]
<i>Mortierella</i> sp.	rhizosphere soil samples from <i>Gossypium</i> species— <i>G. hirsutum</i> cv. TM-1 <i>G. barbadense</i> cv. Hai 7124	China (Shandong)	[13]
<i>Mortierella</i> sp.	soil samples from banana (<i>Musa acuminata</i> Cavendish cv. Brazil) farms	China (Hainan)	[35]
<i>Mortierella</i> sp.	soil samples from ginseng (<i>Panax ginseng</i>) farm	China (Jilin)	[36]

nd—lack of data.

2.2. *Mortierella* Features Useful for Agricultural Inoculation

According to literature, plant growth-promoting microorganisms (PGPM) are divided into plant growth-promoting bacteria (PGPB) or rhizobacteria (PGPR) as well as plant growth-promoting fungi (PGPF) [37]. In the case of PGPM or precisely PGPF, filamentous fungi have a significant advantage over bacteria resulting from their growth. Filamentous mycelium stabilizes the soil structure, penetrates the pores of soil and the solid substrates like rocks and minerals into their cavities, slots and cracks followed by their physical changes related to the structure and size. In order to occupy large areas by hyphae, they excrete acidic compounds useful in drilling microtunnels in the solid surroundings [38,39]. The recent researches focused on the interactions between minerals (abiotic compounds) and filamentous fungi (biotic compounds) interoperable in bioweathering [39–41].

Microorganisms isolated from the extremely nutrient-poor (oligotrophic) environments, e.g., bare rocks, sandstones, newly created dunes, and areas destroyed by fires may be used as very efficient components of biopreparations used in agriculture [38,39]. Their radially-spreading mycelium, covers small fragments of the fragmented substrate. As it was discovered by scientists, the microfungal activity was observed near the weathered stalactite collected from the Penico cave located in South Portugal [42]. The identification of fungi by rRNA sequencing revealed that some spherical cells were *Mortierella* sporangiospores. The photographs taken in scanning electron microscopy demonstrated not only the presence of the subeuhedral, but also rounded shaped calcite crystals where the *Mortierella* hyphae was detected. The fungal hyphal tips and networks around crystals suggested microbial calcite dissolution [42]. These documented properties of the *Mortierella* species fungi may explain the prevalence of their occurrence in the cultivated soils.

Fungi belonging to the *Mortierella* genus are regularly recorded in Arctic, Antarctic, and Alpine soils where with the low temperatures of ground and water the activities of a number of processes in the oligotrophic conditions decreases [43–45]. Some of *Mortierella* isolates defined as psychrotrophs or psychrophiles are referred to as “snow mold” due to the ability to adapt to severe conditions (low temperatures) [46,47]. Psychrotrophs and psychrophiles grow at low temperatures, i.e., about 5 °C or below, with the optimum temperature at about 15 °C or lower for psychrophiles or above 15 °C with maximal growth at higher than 20 °C for psychrotrophs [8,48].

The studies on the molecular mechanisms underlying cold adaptation of *M. isabellina* M6-22 in the extreme environmental conditions [47] confirmed the presence of a higher content of polyunsaturated fatty acids (PUFAs), which maintained the better membrane fluidity for microbial adaptation to low temperatures. Moreover, the agricultural soils are periodically influenced by low temperatures, especially within the range of the temperate climate. Among all fungi identified in the soils of samples from the Wyoming’s Agricultural Experimental Station in the USA about 8% of isolates were ice-nucleationactive (INA) and all of them were *M. alpina* strains [49].

Among 20 genera of psychrotrophic fungi originating from Arctic soils of Franz Joseph Land and growing at 0 °C on malt extract agar (MEA), *Mortierella* isolates belonging to the following species: *M. alpina*, *M. exigua*, *M. hyalina*, *M. minutissima*, and *M. parvispora* were present [50]. A number of *Mortierella* fungi (oligotrophs) were able to grow slowly on the carbon- and/or nitrogen-free silica gel media. The growth on the carbon-deficient media suggests that the low level of available carbon in the soil should not be the limiting factor of growth of some *Mortierella* species. *Mortierella hyalina* was able to grow at 0 °C as a psychrooligotrophic fungus on a silica gel containing N-source and C-deprived source [50].

The multiple agricultural biopreparation containing potentially useful microorganisms do not improve crop yields. One of the reasons for that may be the screening of strains which covers their ability to improve bioavailable forms of P, K, Fe, and others in the soil, while the occupation of niches by inoculants depends on the availability of the C substrate [51]. Free-living saprophytic fungi perform the major role in the carbon delivery from the decomposition of plant residues where many of the nutrients contained in the soil are deposited [40]. The periodic lack of bioavailable macro- and micro-element forms, the availability of which depends practically on the intensity of microbial transformations, is noticed under adverse environmental conditions.

Saprotrophic fungi, which degrade the polymers such as cellulose, hemicellulose, chitin, render plant residues more amenable to decomposition for other microorganisms forming the organic soil which is necessary for good quality of agricultural soil [52]. Saprotrophic *Mortierella* species are often isolated among forests soils and dead wood fungal communities [53,54]. For instance, *Mortierella minutissima*, *M. alpina*, and *M. verticillata* were identified in the forest soil in Romania [6] and one of *Mortierella* sp. selected by Gawas-Sakhalkar and Singh [55] revealed a high cellulase activity. In the studies on cellulose

degradation in rye straw the ability to decompose plant remnants was also identified for *Mortierella verticillata* and *Mortierella humilis* [56].

Furthermore, Jackson [57] investigated fungi from the species of *M. spinosa*, *M. elongata*, *M. alpina*, *M. humicola*, *M. minutissima*, *M. horticola*, and *M. exigua* in the pasture soil and described a strong chitinolytic activity in the strains from root surface. Additionally, *M. alpina* was also found to decomposed hemicellulose. Again, the unargued potential of *Mortierella* was indicated in the experiments where peat substrate enriched with chitin was used in the cultivation of lettuce seedlings (*Lactuca sativa* var. *capitata* 'Alexandria') [58].

Two of the *M. alpina* rhizospheric isolates were characterized by a protease activity and both protease and urease activities were analysed for *Mortierella simplex* [55]. Additionally, there are reports of other activities of these fungi, e.g., in xylose (*M. isabellina*) [26] and starch (*Mortierella alliacea* and *M. alpina*) [59,60] degradation as well as a high amylolytic activity observed for *Mortierella* sp. and *M. minutissima*.

Access to carbon contained in different polymers like cellulose, hemicellulose, and chitin combined with staying active at lower temperatures provides fungi belonging to the *Mortierella* genus advantageous in the unfavorable soil conditions.

3. Plant Growth-Promoting Abilities of *Mortierella* Species

Mortierella species, representing plant growth-promoting abilities (Figure 1) are isolated from the agricultural soils (bulk soil, rhizosphere soil) (Table 1).

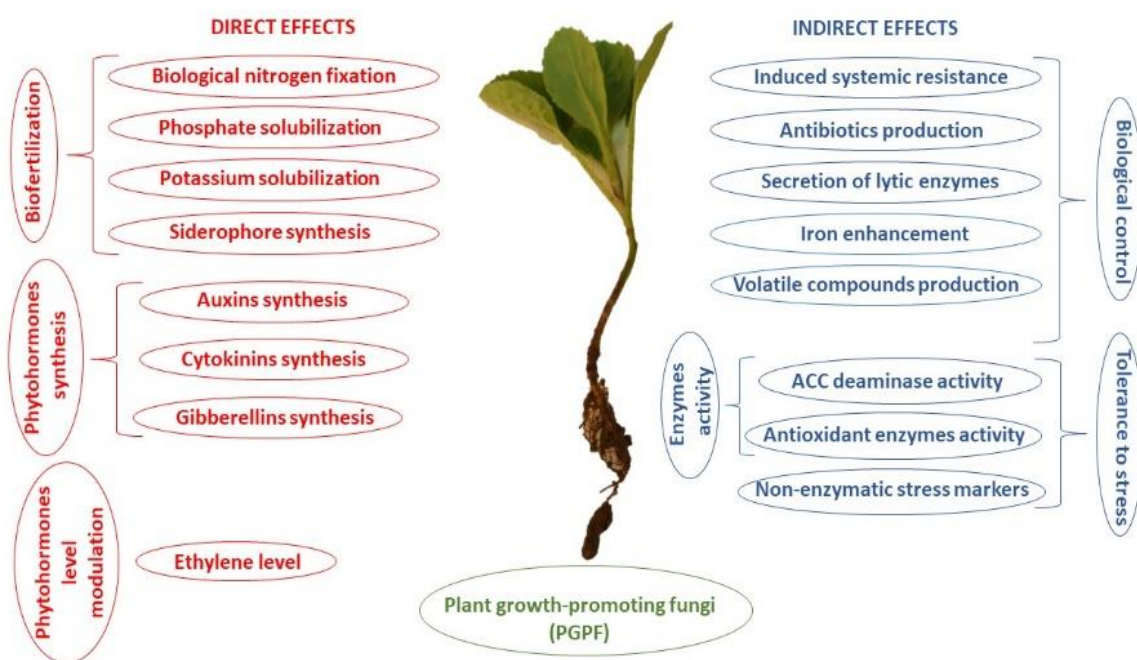


Figure 1. Direct and indirect effects of plant growth-promoting fungi [4,61–63].

Recent studies of rhizosphere soils or endophytes of various plant species proved that the presence of *Mortierella* provides a higher resistance at soil-borne pathogens or/and improve plant growth (Table 2) [9,33,64,65].

Table 2. The effect of inoculation of agricultural plants with the plant growth-promoting *Mortierella* species.

<i>Mortierella</i> sp. (Co-Inoculants)	Origin of <i>Mortierella</i> sp.	Host Crops	Effect on Plant and Soil	Ref.
<i>Mortierella</i> sp. (<i>G. aggregatum</i>)	rhizospheric soil from mature <i>L. leucocephala</i> grown in Hawaii	leucaena (<i>L. leucocephala</i>)	<ul style="list-style-type: none"> - higher: shoot DW - higher: P content (by 17% in the shoots of unfertilized plants; by 73% in the shoots of plants fertilized with PR) 	[66]
<i>Mortierella</i> sp. (<i>G. mosseae</i> and/or <i>G. aggregatum</i>)	salt-affected coastal soil in China	Virginia saltmarsh mallow (<i>Kosteletzkya virginica</i>) as a potential seed crop for saline soils	<ul style="list-style-type: none"> - higher: root and shoot DW - increased: urease, neutral phosphatase, alkaline phosphatase, activities in the bulk soil and rhizosphere - increased: catalase activity in the bulk soil - increased: Pi_{av} concentration 	[67]
<i>Mortierella</i> sp. (<i>G. mosseae</i>)	salt-affected coastal soil in China	castor bean (<i>Ricinus communis</i> cv. “Zi Bi”)	<ul style="list-style-type: none"> - higher: shoot and root DW - higher: chlorophyll and P content in the leaves - increased: urease, invertase, neutral phosphatase and alkaline phosphatase activities in rhizosphere 	[68]
<i>M. elongata</i>	soil from 35-year experiment	corn (<i>Zea mays</i>)	<ul style="list-style-type: none"> - higher: plant DW - higher: IAA and ABA concentrations in the roots - increased: N-acetyl-glucosamidase, neutral phosphatase, β-glucosidase activities in the soil - increased: Pi_{av} concentration, dissolved organic C, available N in the soil 	[17]
<i>Mortierella</i> sp. strain HI-27 (<i>Rhizoglossus</i> <i>fasciculatum</i>)	rhizospheric soil from mature <i>L. leucocephala</i> grown in Hawaii	avocado (<i>Persea americana</i> cv. ‘Hass’)	<ul style="list-style-type: none"> - higher: shoot DW and shoot height - higher: shoot P content 	[69]
<i>M. alpina</i> CS10E4	<i>C. sativus</i> grown in India	saffron crocus (<i>Crocus sativus</i>)	<ul style="list-style-type: none"> - higher: plant biomass, size of corms, number of adventitious roots, number of apical sprouting buds, crocus stigma DW - increased: chlorophyll content, production of total phenolics, flavonoids, carotenoids (apocarotenoids) and JA 	[9]
<i>M. elongata</i> PMI 77 <i>M. elongata</i> PMI 94 <i>M. elongata</i> PMI 624	<i>Populus deltoides</i> <i>P. trichocarpa</i> grown in the USA	watermelon (<i>Citrullus lanatus</i>) corn (<i>Zea mays</i>) tomato (<i>Solanum</i> <i>lycopersicum</i>) squash (<i>Cucurbita</i>) bahiagrass (<i>Paspalum notatum</i>)	<ul style="list-style-type: none"> - higher: plant height, DW and leaf area 	[70]

DW—dry weight; PR—phosphate rock; Pi_{av} —bioavailable P; IAA—indole-3-acetic acid; ABA—abscisic acid; JA—jasmonic acid.

3.1. *Mortierella* Fungi—Effective in Increasing Bioavailable Forms of P in Agricultural Soils

The fungal agricultural inoculants are free-living fungi or arbuscular mycorrhizal fungi (AMF) screened for plant growth-promoting abilities (Table 2) [68]. Innovations in the laboratory technology expanded our understanding of multiple interactions between plant and microorganisms resulting in the growth of crops. One of the most important traits of plant growth-promoting strains is enhancing the bioavailability of certain essential elements like P, K, and Fe. The sorption of bioavailable P (P_{iav}) from the soil solution on the surface of the soil minerals is one of the limiting factors of the crop productivity. *Mortierella* species are described as the phosphate solubilizing fungi (PSF) [71–74], e.g., *Mortierella* sp. isolated from Andisol of Hawaii increased the concentration of P_{iav} [75].

Another mechanism reducing the P loss from the soil and improving the P_{iav} level is desorption of P (“run off”) from the surface of the soil particles. Osorio et al. [76] investigated the effectiveness of *Mortierella* sp. to desorb Pi from the soil minerals: goethite, allophane kaolinite, and montmorillonite distributed in a number of agricultural soils [77]. Sorbed P_{iav} can be held very strongly on the surfaces of some minerals, especially the one which is bounded by iron and aluminum hydroxides [78]. *Mortierella* sp. was effective in desorbing P_{iav} from the soil minerals (except from allophane) differing in their P_{iav} sorption capacity. The highest concentration of desorbed P_{iav} was found for montmorillonite and kaolinite. The desorption also depended on the production of oxalic acid by *Mortierella* sp. [76].

Mortierella sp. isolate was detected in the soil dominated by montmorillonite [79]. The values of pH in the soil solution inoculated with microorganism at the end of the incubation period were significantly lower as compared to the non-inoculated samples. Osorio et al. [19] observed that *Mortierella* sp. effectively dissolved the rock phosphate by decreasing pH of the medium from 7.7 to 3.0. The low molecular weight of organic acids, like oxalic, malic, acetic, formic, gluconic, citric, lactic, 2-ketogluconic, and tartaric and citric acids secreted by filamentous fungi are considered to be one of the main mechanisms of the inorganic phosphate solubilization by *Mortierella* sp. [40,66,72]. Two *Mortierella* species cultivated on three different media synthesized various acids. In the presence of NH_4Cl in the culture, mainly acetate, succinate and formate were excreted, while *M. ramanniana* synthesized lactate, succinate, acetate, and formate [80]. Moreover, silicates and aluminosilicates levels might be dissolved by the product of microfungal activity, the organic acids, i.e., oxalic acid [40]. This acid has also the capacity to desorb P from mineral surfaces contributing to the increase of bioavailable P in the environment [75,81–83].

In the agricultural soils (Table 1), P_{iav} is supplemented with chemical fertilizers obtained from phosphate rocks, which are non-renewable resource. The problem lies in the fact that P_{iav} applied in many soils is fixed by cations resulting in low P-fertilization-use efficiency. In the acidic soils, most phosphate anions are fixed mostly by Fe and Al cations and in alkaline soils Ca cations are responsible for phosphate anions precipitation. The microbial solubilization of P-minerals naturally located in the soils or re-fixation of applied phosphates provide stable P_{iav} source which is very important for sustainable agriculture [84].

Ceci et al. [85] showed the ability of *M. globalpina* to mobilize P from insoluble forms. This strain isolated from the soil on the solid medium with 5% insoluble tricalcium phosphate (TCP) as the only P source revealed halo zone of about 11.7 mm with growth diameter of 30.0 mm after seven days of incubation. The microscopic observations of mycelia obtained on a liquid medium with TCP have shown mineral precipitates loosely attached on the surface of fungal biomass and embedded in the fungal biomass.

Zhang et al. [67] (Table 2) investigated the interactions between phosphate solubilizing *Mortierella* sp. (PSM) with *Glomus aggregatum* and *G. mossae* (arbuscular mycorrhizal fungus—AMF). The inoculation of PSM isolated from the salty coastal soil samples in China (and one of the AMF strains) caused promotion of growth of halophyte, *Kosteletzkya virginica*, at free different salinity levels. *K. virginica* is a salt-tolerant plant effective in amelioration of the very saline soil conditions and in saline agriculture [86]. After combined inoculation

of *Mortierella* and *Glomus* species, the higher concentration of Pi_{av} in all the inoculated bulk soils at different salinity levels were observed (as compared to the non-inoculated bulk soil and to the soil inoculated only with *Glomus* species). This promoting effect was very strong at the 100 mM NaCl level of salinity and about 40% higher shoot DW and above 100% higher root DW were achieved (as compared to the non-inoculated control at the same salinity conditions). These results may suggest that, there are non-stress conditions for *Mortierella* sp. at particular salt concentration in the soil [67].

Various proportions of two inoculants: *Mortierella* sp. (PSF) and *Glomus mosseae* (AMF) were prepared to study their efficiency in pot experiment [68]. Fungi were introduced to the rhizosphere soil of castor bean (*Ricinus communis*) seedlings, an important plant cultivated in China. With the increased ratio of *Mortierella* sp. to *G. mosseae*, the extension of AMF root colonization, elevation of Pi_{av} concentration in the soil solution and higher shoot and root weight were observed. This might also result in positive interactions between *Mortierella* sp. and *G. mosseae* and with the native microorganisms and beneficial changes in the activity of the soil enzymes (Table 2) [68].

The efficiency of phosphate solubilizing microorganisms as inoculants in the agricultural soils should not be studied only in vitro. The higher Pi_{av} level in the soil solution should not be the only criterium for screening PSM activity. On the other hand, the lack of the higher level of Pi_{av} in the soil after inoculation with PSM does not indicate inactivity of the inoculant. The content of Pi_{av} is changing very dynamically and the best effect of PSM efficiency can be the higher level of P in the inoculated plant and the higher yield [67]. Osorio and Habte [66] inoculated *Leucaena leucocephala* with *Mortierella* sp. isolated from the rhizosphere of mature *Leucaena leucocephala* and indicated this fungus as a very efficient phosphate rock (PR) solubilizer. In the experiment with *Mortierella* sp. (PSM) and *Glomus* sp. as coinoculant of the plant, the amount of Pi_{av} increased (over 73%) in the treatment with PR application, caused the higher content of P in the shoots and higher shoot DW of *L. leucocephala* (about 29%) (Table 2).

Two *Mortierella alpina* and one *M. simplex* strains isolated from rhizosphere revealed phosphatase activity [55]. In the preliminary screening of fifty six isolates from Arctic soils, *M. alpina* PG40 demonstrated the strongest phosphatase activity among *Mortierella* strains. *M. simplex* PG26 and *Mortierella schmuckeri* PG45 strains had low activity of this enzyme [55]. In most soils, the mineral compounds have a smaller share of the total pool of this element than the organic phosphorus compounds where the phosphate group is attached by proteins, sugars, lipids, and nucleotides. Phosphatases are enzymes synthesized by plant roots and microorganisms which are often induced by low concentration of Pi_{av} in the soil solution [24]. On the other hand, at the low level of anions bioavailable for plants ($H_2PO_4^-$ and HPO_4^{2-}), the decrease in crop productivity is proved.

The positive effects of *Mortierella* sp. were observed with neutral and alkaline phosphatase activity in the soil (Table 2) [68]. Li et al. [17] also proved the increase of the soil phosphatase activity in the soil inoculated with *Mortierella elongata*, which correlated with improved maize growth.

3.2. Siderophore Producing *Mortierella* Species—Efficient in the Increase of Fe Bioavailability

Iron is an essential micronutrient required for the plant and microbial growth. When present at lower content in the agricultural soils, Fe is responsible for reduction of plant productivity. In the upper soil layers under aerobic conditions, Fe solubility is low and it is mostly found in the form of Fe^{3+} which is not available to plants [87]. One of the specific mechanisms developed by microorganism is synthesis of Fe^{3+} -complexing compounds followed by the transportation and accumulation of Fe. Siderophores are known to be synthesized and excreted by soil fungi as a response to Fe starvation in the environment and as a consequence, microbial inoculants with this ability may strongly enhance the plant growth and resistance through the sequestration of Fe from the soil [88,89].

To the best of our knowledge, only few studies have explored the capability of *Mortierella* species to Fe-complexation. In 1972, Bozarth and Goenaga extracted mycoferri-

tine, the iron-binding protein, from mycelium of *Mortierella alpina* isolated from the soil [90]. After separation from the lyophilized mycelium, this protein contained 17% of Fe. On the basis of the results obtained from HPLC-analysis, it was indicated that rhizoferrin (polycarboxylate-type siderophore) was synthesized by *Mortierella vinaceae* cultivated under Fe-limiting conditions [91].

M. alpina CS10E4 strain investigated by Wani et al. [9] also formed orange halo zone on (CAS)-blue agar. Although siderophores are mainly specific for Fe^{3+} , these chelating compounds also bind other metals, such as Cd^{2+} , Cu^{2+} , and Zn^{2+} [92–94]. The presence of optimal dose of bioavailable heavy metals in the soil might promote plant growth.

Mortierella turficola CQ1 strain isolated from the rhizosphere of *Panax ginseng* (Korean ginseng) showed positive reaction on (CAS)-blue agar. Moreover, on the liquid media amended with different concentrations of Zn^{2+} (50 to 250 $\mu\text{g/mL}$), the percentage of siderophore units in the culture of this strain was the highest at 200 $\mu\text{g Zn}^{2+}/\text{mL}$ [95].

Until now, there is limited data concerning siderophore production by *Mortierella* species, especially these isolated from the area of harsh climatic conditions. Among four tested *Mortierella* strains isolated from Spitzbergen soils only *M. verticillata* DEM32 was capable of releasing these low-molecular mass compounds with a high affinity to Fe and change the color of solid medium after incubation at three different temperatures (Figure 2) (data not published). Moreover, except for some plant growth-promoting activities detected at lower temperatures [8], this fungus also revealed the production of siderophores at conditions found in the temperate climate soils making it an attractive inoculant for the agricultural soils.



Figure 2. Production of siderophores by *Mortierella* strains on the Chrome azurol S agar medium at three temperatures of incubation, 4, 9, and 15 °C (data not published). Arrangement of the strains on the plate: clockwise from top left—*M. verticillata* DEM32 (MV32); *M. antarctica* DEM7 (MA7); bottom from left—*M. antarctica* DEM4 (MA4); *M. antarctica* DEM10 (MA10) (the psychrotrophic strains isolated from the Spitzbergen soils).

3.3. Production of Phyto regulators by PGP-Mortierella Fungi

Among phyto regulators, phytohormones are chemicals involved in a variety of physiological and biochemical processes of plants at very low concentrations. The most important and well-characterized phyto regulator is 1-aminocyclopropane-1-carboxylate (ACC) deaminase and among phytohormones of well-established importance are auxins, gibberellins, cytokinins, ethylene, abscisic acid, but also brassinosteroids, jasmonates, and salicylic acid [96–100]. It is known that environmental fungi are also able to produce some phyto regulators, e.g., phytohormones (Table 2) [4,97,101].

Among auxins, the key hormone produced by fungi is indole-3-acetic acid (IAA). IAA biosynthesis can be tryptophane (Trp)-dependent or independent. IAA was found both in the culture medium and inside the fungal mycelium [97]. The higher level of IAA can be the result of the lower sensitivity of microorganisms to IAA or the differences in

the regulation of IAA biosynthesis. In fungi, two pathways were identified, the indole-3-pyruvic acid (IPY) and the indole-3-acetamide (IAM) ones [101,102]. The knowledge of the complex cross-regulatory relations between hormone pathways which are useful in the regulation of plant development and stress responses [98,103–105] still requires deeper research and understanding. Soil microorganisms and plant endophytes producing phytohormones have a great physiological importance for microbe-plant interactions. Among other free living fungi, *Mortierella* species are known to produce a variety of phytohormones, like IAA, gibberellic acid (GA), and ACC deaminase [8,70]. Their activity in the agricultural soil may play significant role in growth improvement and stress tolerance of cultivated plants enhancement.

M. alpina synthesized over 70 mg of IAA/L with Trp in medium [9]. In the research of efficient agricultural inoculant to the application in lower temperatures accompanying in a sprouting in temperate climate *Mortierella* spp. isolated from Spitzbergen were investigated [8]. *M. verticillata* DEM32 synthesised the highest amount of IAA at 15 °C with initial dose of Trp (about 1.5 mM). Moreover, at the same conditions the root and shoot weight of Winter wheat seedlings (*Triticum aestivum* cv. Arcadia), inoculated with this strain, was significantly higher (about 40%). At 9 °C psychrotrophic *M. antarctica* also produced IAA, however, no Trp was added in the medium confirming promoting effect on wheat seedlings. Additionally, both strains synthesized GA for growth promotion and elongation of plant cells. Among various plant growth-promoting fungal mechanisms is the synthesis of ACC deaminase. This commonly known phytohormone is produced in order to control the ethylene content. Higher ethylene level in the plant tissues is often the result of various stresses and can lead to strong growth inhibition of the crop. *M. antarctica* DEM7 demonstrated the ability to synthesize ACC deaminase (cleaving plant ethylene precursor) [106] at 9 °C, 15 °C, and 20 °C, but with the highest efficiency at the lowest temperature [8]. Genome characteristics of *M. elongata* selected from the field soil showed the presence of biosynthesis genes of ubiquitous plant hormones IAA and abscisic acid (ABA) (Table 2) [17]. ABA-mediated signalling is not only involved in the plant developmental process but its higher concentration may be increased by the plant resistance to the biotic and abiotic stresses [107]. Li et al. [17] detected 40% increase of ABA and IAA in maize roots inoculated with saprotrophic *M. elongata*. Moreover, the plant biomass, soil enzyme parameters and concentration of bioavailable nutrients also increased (Table 2).

The fungal activity causes also higher concentration of regulators in its host plant tissue or/and they may affect plants auxin-responsive genes [108]. It is also known that *Mortierella* produces and accumulates IAA in its mycelia. After inoculation, the IAA level in roots colonized by fungus was significantly higher. Furthermore, the jasmonic acid (JA) level in plants colonized by *M. hyalina* tissue was over five-times higher compared to the concentration of its phytohormone in roots inoculated with other tested fungi [107,108]. Endophytic fungi (described below) produce and accumulate phytohormones in their mycelia.

4. Endophytic *Mortierella* Strains

Endophytes are microbiota, i.e., bacteria and fungi able to colonize internal tissues of plants without symptoms [106]. They are isolated from different parts of plants, e.g., roots, stems, leaves, fruits, bulbs, and seeds [109,110]. Moreover, they can extend their niches, e.g., from roots to the aerial parts of the plant [111]. The intracellular growth of the endophytic fungi such as *Mortierella chlamydospora* and *M. indohii* results in the penetration of the cortex cells of the plant [112].

Understanding the interaction between endophytes and host-plants allows to notice the importance of composition of the plant's microbiome for its optimal development and immunity [113]. The close associations of endophytes with agricultural plants could be beneficial in crop growth promotion based on the usefulness of products resulting from the trophic interactions [106].

Investigations involving *Mortierella* revealed that *Mortierella candelabrum* was found in the seeds of *Crataegus azarolus* [109]; *M. hyalina*, *M. isabellina*, and *M. ramanniana* were

isolated from the cones of *Pinus densiflora* growing in Japan and these fungi also were found among early stage decomposers of cones on the ground [110].

These endophytes were also isolated from the roots of *Holcus lanatus*—a grass occurring in humid soils in temperate zones around the world [114,115]; *Huperzia serrate*—a very important medicinal plant native to eastern Asia used for over 1000 years in China [116] and *Pteridium aquilinum*—a species common in moorlands and pastures of Great Britain (*Mortierella* sp. 1, *M.* sp. 2 and *M. ramanniana* var. *ramanniana* L.) [117]. Root-derived isolates of the endophytic fungi commonly existing in agricultural plant tissues could be beneficial for crops biopreparates. A few *Mortierella* strains: *M. gamsii*; *M. verticillata* and *Mortierella zonata* were found in *Fragaria vesca* roots growing in Essex in United Kingdom [118]. Moreover, remarkable growth parameters of *F. vesca* (number and length of leaves and roots) were associated with the occurrence of *Mortierella* endophytes in its tissues. *M. hyalina* and *M. indohii* were the most abundant species among this genus identified in the endophytic microbiome of tomato roots [111].

The *Populus trichocarpa* endophyte *M. elongata* PMI93 can alter the genes expression of host-plant involving GA, JA and ethylene signalling which results in an improvement of plant growth and plant DW (over 30% of DW in one year) [113].

The investigation of the microbiome composition in the healthy wild plants seems to be crucial for their optimal growth and development and is a significant direction in the development of sustainable agriculture. The morphological and physiological traits of the host plant, *Crocus sativus*, an important spice and medical plant, were improved in the presence of the endophytic *M. alpina* CS19E4 strain [9]. From 14 different sites in India, the fungal endophytes of the same plant (*C. sativus*) were analyzed and the efficient endophytes were isolated [119].

These endophytic fungi are also effective in the synthesis of phytohormones, e.g., IAA was detected in the mycelia of *M. hyalina* [52]. As a result, higher auxin and jasmonate levels in its host plant (*Arabidopsis thaliana*) tissues were demonstrated and the growth of *Arabidopsis* was promoted.

5. Contribution of the *Mortierella* Species in the Healthy Condition of Plants and Soils

Among plant growth-promoting microorganisms, the potential bio-inoculants should be able to increase agricultural production and immunity of the arable crops linking different activities [120] and lead to the limitations of toxic products application [121]. The diverse activities of *Mortierella* fungi is evidenced to effectively support plant immunity. These microorganisms are present in the healthy plant population on plantations and wild gatherings.

The positive impact of *Mortierella* sp. and *M. elongata* on the growth and development of the cultivated plants was demonstrated along with the presence of these microorganisms in the fungal community of the healthy *Pisum sativum* rhizosphere and bulk soil [121]. *M. elongata* strains were rarely detected in the samples from the infected plants. Over four hundred *Mortierella* isolates were indicated in the acidic soils of apple orchards collected in Chihuahua in Mexico, e.g., *M. capitata*, *M.* sp., *M. gamsii aurium*, *M. alpina*, but none of them were pathogenic to the apple rootstocks [33].

The presence of some microorganisms can enhance plant growth and additionally protects plants from disease and abiotic stresses through various mechanisms. A good example of this activity is the synthesis of iron-chelating compounds that are secreted by microorganisms providing them one of the most abundant elements in the soil. On the other hand, limitations in the biologically available forms of Fe (Fe^{2+}) in the soil for pathogens could contribute in the reduction of their number present in the soil [88].

Similarly, *Mortierella* species possess ability to secrete the lytic enzymes which provide compounds like cellulose, hemicellulose, pectin or chitin available as nutrients. Simultaneously, these compounds are the main structural polysaccharide components of the plant and fungal cell wall and the ability to decompose them gives the possibility to eliminate pathogenic organisms from the soil and even to dominate the environment [122].

Mortierella elongata, the endophyte of *Populus trichocarpa*, may regulate the genes associated with hypersensitive response and cell wall degradation which are responsible for the plant immunity [113].

M. hyaliana promoting aerial growth of *Arabidopsis thaliana* simultaneously showed over 30% growth inhibition of *Alternaria brassicae* on the agar plate [52]. The free of pathogenic *Fusarium oxysporum* f. sp. *cubense* (caused *Fusarium* wilt of banana) soil was dominated by *Mortierella* species constituting over 36% of the total soil abundance [35]. Very similar results were indicated by Xiong et al. [123] while investigating vanilla soil—suppressive against *Fusarium* wilt disease. About 37% of the total fungal sequences belonged to the *Mortierella* genus showing the great potential of these fungi to promote agricultural plants.

Studies indicated that more vulnerable to soil-borne pathogens were the rhizosphere soils poor in *Mortierella* species [124]. To understand the multidirectional impact of inoculant on the soil microbial populations, the genetic analyses on the reshaping microbiomes are carried out. Li et al. [125] demonstrated that the introduction of *M. capitata* to maize rhizosphere promoted its growth “by altering the root gene expression levels”, which was also the result of change in the quality and quantity of the rhizosphere bacteria.

It is worth noting that some of these filamentous fungi might produce and accumulate PUFAs like arachidonic, γ -linolenic and eicosapentaenoic acids in their mycelium [126,127]. The synthesis of the fat compounds is one of the microbial cold adaptive mechanisms [128]. For that reason, in the 1990s, mostly psychrotrophic species of *Mortierella* were isolated from Arctic, Antarctic or alpine soils [50,129]. Polyunsaturated fatty acids which are essential for the human health are also very important nutrients and are widely used in medicine, pharmaceuticals and cosmetics [127,130]. Some of PUFAs, e.g., arachidonic acid, are incorporated into the plant oxylipin pathway regulating defense processes in plants and as a result inducing plant resistance [120,131].

The effect of mixture containing lipids from *Mortierella hygrophila* on plant resistance was observed in the field experiments. The preparation composed of 30% of arachidonic acid stimulated the resistance of potato and sugar beet against *Phytophthora infestans* and *Rhizoctonia solani* and increased the yield from 11 to 14%. The mixture also limited the development of powdery mildew of grapes in about 40% [120]. Similarly, among eleven endophytes of *Crocus sativus*, *M. alpina* CS10E4 extract demonstrated antimicrobial activity and inhibited more than three pathogens (at least of about 50%) [119]. Moreover, the mechanism of enhancing the plants immunity may be based on the better control of different soil-borne pathogens by synthesis of antibiotics. In the genome of *M. elongata* also streptomycin, butirosin, and neomycin biosynthesis genes were described [17]. The strong influence of *Mortierella* on the growth of pathogenic species described Tagawa et al. [132]. *M. chlamydospora* was proposed as the one of potential agents in controlling of the potato scab pathogens, i.e., *Streptomyces*. This fungal strain isolated from the potato soil, was found to have a high antagonistic activity against *Streptomyces turgidiscabiei*. All these examples are pointing to the usefulness of some *Mortierella* spp. not only as the inoculants in order to improve crop nutrient acquisition, but also to inhibit plant pathogens.

6. Conclusions

In the face of the rapid climate change and the decrease of natural resources necessary to maintain the crop productivity at the current level, there is a clear need for new efficient solutions preserving and enhancing agricultural ecosystems. *Mortierella* species are common soil and endophytic fungi with various characteristics promoting plant growth and supporting the defense mechanisms in plants. The results achieved among a number of studies highlight positive influence of the applied *Mortierella* strains on soils activities and plants growth parameters (including crop species).

Recent studies focusing on the impact of the introduced inoculant to the soil microbiome have also proved that the activity of *Mortierella* fungi may have a beneficial effect on modifying soil microbiological composition and gene activity of some microorganisms.

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Abbreviations

ABA	abscisic acid
ACC	1-aminocyclopropane-1-carboxylate
AMF	arbuscular mycorrhizal fungi
CAS	chrome azurol S
DW	dry weight
GA	gibberellic acid
IAA	indole-3-acetic acid
JA	jasmonate acid
PGP	plant growth-promoting
PGPB	plant growth-promoting bacteria
PGPR	plant growth-promoting rhizobacteria
PGPF	plant growth-promoting fungi
PGPM	plant growth-promoting microorganisms
PSF	phosphate solubilizing fungi
PSM	phosphate solubilizing microorganisms
PUFAs	polyunsaturated fatty acids
TCP	tricalcium phosphate
Trp	L-tryptophane

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