The Plant-Growth-Promoting Fungus, *Mortierella elongata*: Its Biology, Ecological Distribution, and Activities Promoting Plant Growth[1]

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This publication is intended to provide biological information of the soil fungal taxa *Mortierella elongata*. *M. elongata* is one of the most ubiquitous fungi living in the soil. The preliminary data generated from our recent studies indicated that *M. elongata* is one of the most abundant taxa (>0.5% of total soil fungi) living in the agriculture soils collected from north Florida, including pastures, cotton fields, and peanut fields. Our recent studies showed that *M. elongata* can perform plant-growth promotion across different types of crops, including bahiagrass, corn, tomato, squash, and watermelon (Zhang et al. 2020). Compared to the well-known species that have plant-growth-promotion abilities (e.g., mycorrhizal fungi, Trichoderma), growers, agents, and stakeholders are not familiar with "*Mortierella*" despite the important role these fungal taxa play in promoting the growth of their crops. Only very recently, growing studies started to focus on the function of this basal fungus. It is important to transfer the updated knowledge generated from research to Extension, given that this fungus might have potential to serve as a bioindicator of soil health or as a bio-N-fertilizer in the future. This publication provides a brief overview of *Mortierella* from biological, taxonomical, ecological, and functional perspectives to help readers learn the biology and potential modes of action of this fungus.

Summary

Mortierella is a widespread genus of fungal generalists that are detected as root endophytes and saprophytes in many natural and agricultural habitats, including forests, pastures, and croplands. *Mortierella elongata* has been observed to promote the growth of many plant species, including cottonwood, pine, oak, grass, tomato, corn, and *Arabidopsis* spp. The growth-promotion ability of *M. elongata* is plant-species independent. This evidence suggests that *M. elongata* is a potential bioindicator and biocontrol agent for crop production and soil health. The taxonomy, biology, and distribution of *M. elongata* and its potential modes of action on plant-growth promotion are discussed in this article.

Taxonomy

M. elongata is one of the most common representatives of genus *Mortierella*, a genus that contains more than 100 validated species (Ainsworth 2008). *Mortierella,* within the family Mortierellaceae of the order Mortierellales, belongs to Mucoromycota, an early-diverging phylum of fungi. Mucoromycota is comprised of Glomeromycotina (arbuscular mycorrhizal fungi), Mortierellomycotina, and Mucoromycotina (Bidartondo et al. 2011; Spatafora et al. 2016).

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Biology

Of over 100 recognized species of *Mortierella*, only *M. wolfii* is reported to be a pathogenic species as a cause of abortion in cows (Davies et al. 2010). Although the ecological functions of most *Mortierella* spp. are unknown, a recent study with a few *Mortierella* spp. suggest their promising influences on plant-growth promotion, lipid production, and chitin decomposition.

Mortierella spp., the filamentous fungi (fungi that form threadlike structures known as hyphae), are thought to include the first terrestrial fungi to evolve distinct fruiting bodies. Most *Mortierella* spp., including *M. elongata*, are culturable and can grow fast under different culture conditions. In general, the mycelia of *M. elongata* in culture are white, with a rosette-like surface appearance and no pigment (Figure 1A). The culture grows well at room temperature (between 20°C and 25°C). The zygospore, sporangiophores, sporangia, and chlamydospores may be present (Figure 2). The formation of different spore types is media dependent. For example, SAB-sucrose agar, hay extract agar, and 2% malt extract agar (MEA) are more suitable for zygospore formation of the heterothallic strains (Gams et al. 1972). The SEA medium (but not MEA) is more suitable for the sporulation of sporangia. Chlamydospores can be produced on MEA (Gams 1976).

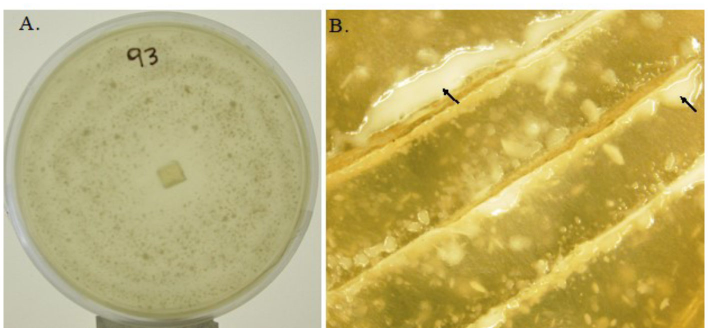

Figure 1. *M. elongata* (PMI93 isolate) growing on an MMN medium (A). Lipid release (examples shown by arrow) when the culture is injured with sharp object (B).
Credits: Liao et al. (2019)

M. elongata metabolism in culture is mostly based on utilization of simple carbon (e.g., D-glucose, D-trehalose and D-mannose) (Uehling et al. 2017). In nature, *M. elongata* can utilize N-acetyl glucosamine (chitin monomer) as carbon and nitrogen sources and serve as the most important chitin decomposers in the soil (Gray and Baxby 1968). Many *Mortierella* species have been validated to be excellent candidates for lipid production (e.g., linoleic acid, α-linolenic acid, and arachidonic acid) (Kendrick and Ratledge 1992; Meeuwse et al. 2012; Kikukawa et al. 2018; Vadivelan and Venkateswaran 2014). *M. elongata* is able to produce these lipids in culture (Figure 1B) and in the rhizosphere (Liao et al. 2019). Most of these polyunsaturated fatty acids are essential components that mediate vital biological functions of organisms. While coculturing with plants, *M. elongata* forms a biofilm on plant roots, indicating their ability to directly interact with root cells as the fungal endophyte (Figure 3).

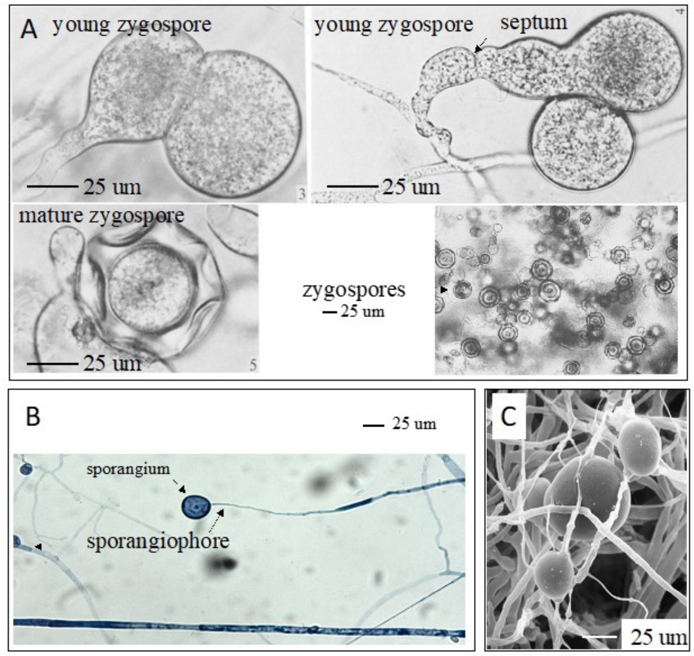

Figure 2. Morphological characterization of *M. elongata* in culture. (A) Zygospore: *M. elongata* can be heterothallic and have diploid reproductive stage in its life cycle. After the compatible hyphal tips contact each other, the progametangia grow out, fuse, and form gametangia. The swollen gametangia develop a septum at their lower part to delimit the future zygospore. The zygospores can be formed at temperatures between 20°C and 30°C. (B) In the asexual reproduction process, the special hyphae of *M. elongata* form sporangiophores (50 µm–>300µm), which bear sporangia (10–30 µm diameter). Sporangiospores are then produced in the sporangia. (C) Chlamydospores. *M. elongata* can form thick-walled spores (chlamydospores) in order to survive in harsh conditions (e.g., hot, cold, or dry seasons, or unfavorable nutritional conditions).
Credits: A: Gams et al. (1972), RightsLink License Number 4900820129589; B: Khalid Hameed; C: ZyGoLife Research Consortium

Distribution

M. elongata is one of the most prevalent species of soil fungi. It can grow saprotrophically in the soil and is also isolated as an endophyte from healthy plant roots (Liao et al. 2019; Bonito et al. 2016). *M. elongata* adapts very well to a wide range of environmental conditions. For example, *M. elongata* has been reported or isolated from fell-field soils in the Antarctic (Weinstein et al. 2000), tundra soils in Alaska (Gams et al. 1972), alpine forests in Norway (Robinson 2001), arid agricultural regions of India (Niu et al. 2018), coastal regions of Mexico, long-term corn fields in China (Li et al. 2018), and cottonwood, forage, and cotton fields in North America (Liao et al. 2019) (Figure 4). *M. elongata* grows well in a range of soil types from pH levels of 4 to 7 and prefers litter and upper organic soil horizons. The DNA sequence-based methods aid in rapid quantification and identification of soil microorganisms in situ. Using this approach, *Mortierella* spp. (including *M. elongata*) were detected in high abundance (0.3%–0.8% of total soil fungi) in the soils in forests, pastures, and agriculture fields (Figure 4).

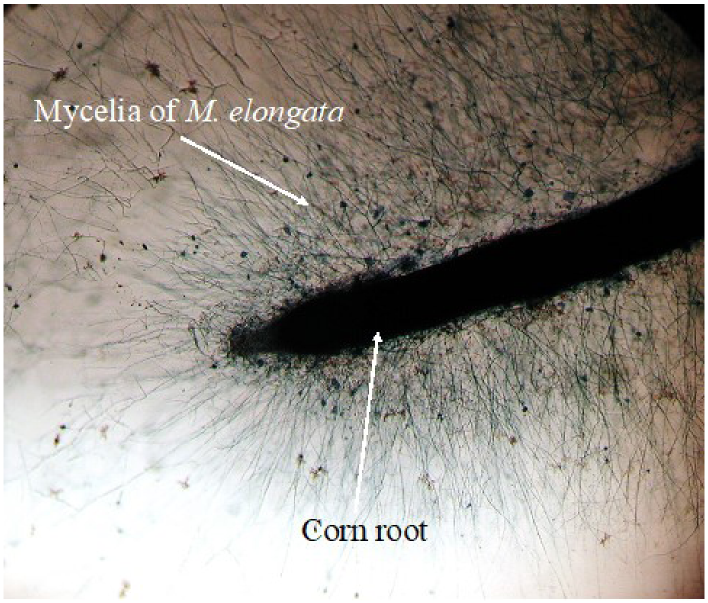

Figure 3. Image of the mycelia of *Mortierella elongata* (PMI93) forming biofilm in association with a corn root tip.
Credits: Liao et al. (2019)

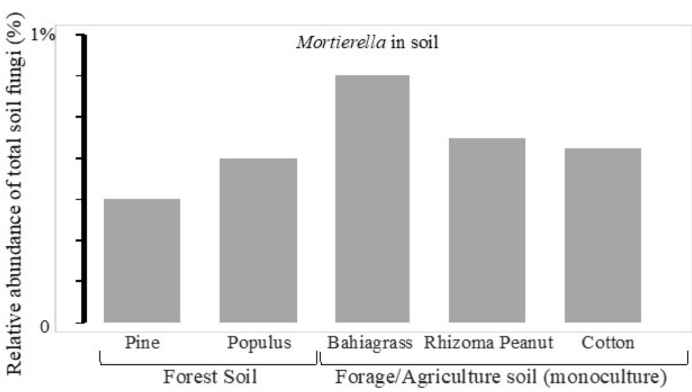

Figure 4. *M. elongata* was detected from the shallow soils (0–10 cm, in depth) of pine forests, cottonwood (*Populus*) forests, forage fields, and cotton fields. In general, around 0.3% to 0.8% of total soil fungi is *M. elongata*.
Credits: Liao, unpublished data

Potential Modes of Action of *Mortierella elongata* on Plant-Growth Promotion

The beneficial associations between *Mortierella* and plants have only recently begun to be understood. *M. elongata* enhanced the biomass of roots and aboveground tissues, enhanced leaf expansion, and increased the amount of chloroplasts in cottonwood (Liao et al. 2019), pine (Figure 5), and corns (Li et al. 2018). *M. elongata* in the soil can increase the activities of soil degradation enzymes of C and P (e.g., phosphatase and beta-glucosidase) (Li et al. 2018). Some other species of *Mortierella* also have been reported to be beneficial fungi of plants. For example, *Mortierella hyalina* enhanced biomass of cress (*Arabidopsis*) (Johnson et al. 2018). *Mortierella alpina* enhanced the stress tolerance of saffron crocus (*Crocus sativus*) by promoting the production of tetraterpenoid-associated phytohormones (Wani et al. 2017). Overall, these recent findings suggest that genus *Mortierella* plays an important role in soil and plant health. The underlying mechanisms of *Mortierella* associated with plant-growth promotion are still largely unknown. The potential modes of action of *Mortierella* on plants are only starting to be uncovered, possibly including (1) enhancing plant growth-hormone production (e.g., IAA, GA, and ABA) (Liao et al. 2019; Li et al. 2018); (2) suppressing plant defense responses (Johnson et al. 2018; Liao et al. 2019); and (3) mediating plant lipid pathways (Liao et al. 2019).

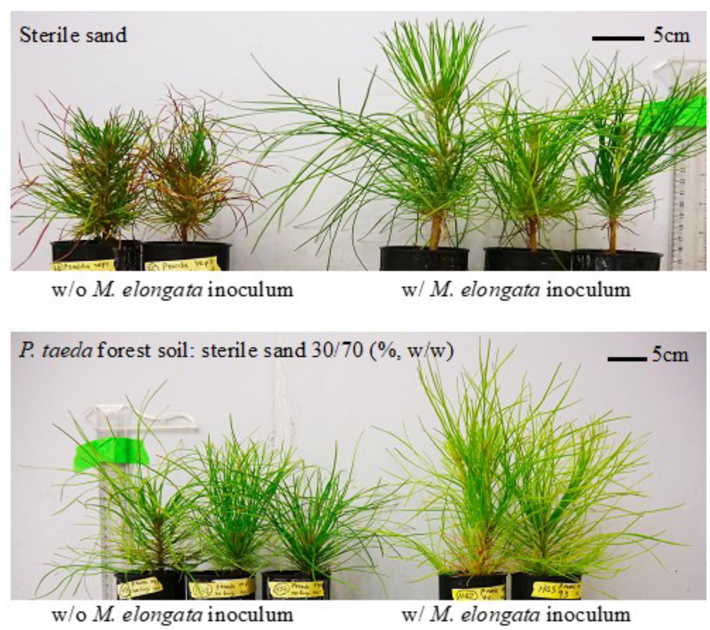

Figure 5. Growth enhancement of loblolly pine (*Pinus taeda*) in response to inoculation of *M. elongata* (Isolate PMI93). After inoculation, seedlings of *P. taeda* were grown in sterile sand or natural soil systems (30% soil collected from *P. taeda* forest, Durham, NC, mixed with 70% sterile sand [w/w]) for 10 months.
Credits: Hui-Ling Liao, UF/IFAS

Mortierella elongata–Bacteria Endophyte Interactions

M. elongata living in the soil harbor diverse bacteria taxa inside their hyphae cells (Sato et al. 2010; Uehling et al. 2017; Ohshima et al. 2016). These bacteria can alter the morphology and metabolism of their host fungi and at the same time rely on their fungal partner for the support of amino acids. It is not known if such a fungal-bacterial symbiont system might be associated with the growth-promotion activities of *M. elongata*.

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