



Endophytes: Improving Plant Performance

Camilla Fagorzi * and Alessio Mengoni

Department of Biology, University of Florence, Via Madonna del Piano 6, 50019 Sesto Fiorentino, Italy

* Correspondence: camilla.fagorzi@unifi.it

Endophytes represent microorganisms that reside within plant tissues, without typically causing adverse effects to the plants, for a substantial part of their life cycle, and are primarily known for their beneficial role to their host plant [1]. Specific endophytes may have evolved with their host as a holobiont, providing excellent working models for evolutionary theory or could be a source of yet unknown novel molecules, with potential pharmaceutical, agricultural or environmental significance [2–4].

The discovery of endophytes and the recognition of their relevant role dates to 1866, when De Bary detected microbial cells inside plant tissues [5]. The first microorganisms to be termed endophytes were fungi; only later were bacteria found to be massively present in plant tissues [6]. Extensive studies defined subgroups of endophytic communities, with ‘obligate’ or ‘facultative’ microorganisms, depending on the metabolites of the plant for survival in the first case, or being able to associate with the plant from the rhizosphere and atmosphere in the second one [7–9]. Estimates of microbial community density range around orders of magnitude of 10^3 – 10^4 bacterial cells per gram of tissue, but in some parts (e.g., root nodules) it can also reach an order of magnitude of 10^7 [10–12].

A bibliographic search with the keyword “Endophyte” on the PubMed database from 1946 to 2022 sorted out a total of 12,372 entries, while 9547 and 3410 entries are sorted for more specific “Fungal Endophytes” and “Bacterial Endophyte”, respectively (16 August 2022). While for “Endophytes” (mainly fungi) already in 1946 two papers are indexed, the first paper indexed with “Bacterial Endophytes” dates to 1975. Indeed, only later it was recognized that many bacterial taxa colonize the internal tissues of plants, without harming them. In the last 15 years, an increasing trend of research papers is witnessing the interest of the scientific community toward microbial endophytes (Figure 1), mainly for fungal endophytes, though interest in bacterial endophytes is increasing.

Endophytes are studied for different purposes, spanning from the search for relevant activities (e.g., biocontrol, bioremediation, metabolite production, plant growth and resistance) to ecological investigation, including adaptation to harsh conditions. For instance in medicinal plants, endophytes have been shown to participate in or modulate the biosynthesis of bioactive molecules [13,14]. In heavy-metal accumulating plants, bacterial endophytes have evolved resistance to the toxic effects of metals [15], while in plants that contain antimicrobial metabolites (e.g., many aromatic plants) the endophytic microbiome shows specific adaptation toward the essential oil of the different plant chemotypes [16].

Where do endophytes come from? Clearly, for many endophytes, the soil is their original habitat. Once the presence of the plant roots is perceived, many bacteria are attracted and proliferate around the roots, also forming biofilms over the root surface. These new habitats are called rhizosphere and rhizoplane, meaning the soil environments close to the roots and the root surface, respectively [17].

Citation: Fagorzi, C.; Mengoni, A. Endophytes: Improving Plant Performance. *Microorganisms* **2022**, *10*, 1777. <https://doi.org/10.3390/microorganisms10091777>

Received: 25 August 2022

Accepted: 1 September 2022

Published: 3 September 2022

Publisher’s Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

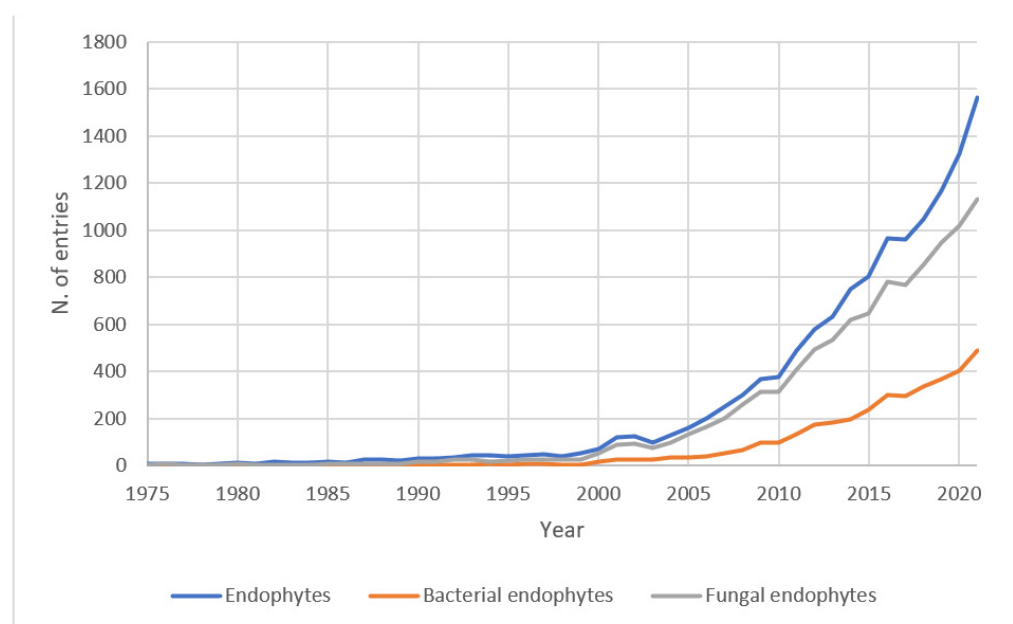


Figure 1. Number of entries by year (starting from 1975) present in PubMed database. Searches with keyword “Endophytes”, “Fungal Endophytes” and “Bacterial Endophytes” are shown.

From there, they may eventually penetrate the root tissue in presence of cracking of the root epidermis [18], but some of them have developed specific signaling to enter the plant and become symbionts (e.g., rhizobia). However, microbes are present in the dust particles also and can be brought by animals (e.g., pollinating insects). Consequently, endophytes may originate from the phyllospheric microbiome (the leaf’s surface microbiome) [19] or from the floral microbiome [20]. Endophytes originating from the floral microbiome are particularly intriguing since they can in theory propagate via seeds, then showing vertical transmission with their host plant. Indeed, seed endophytes are gaining the attention of several investigators since they could be nice examples of coevolution between host and microbe, but also a powerful way to produce seeds of crops that may harbor plant-growth-promoting microbes [21]. Such applications need detailed knowledge of the peculiarities of a microbial endophyte. In fact, not all rhizosphere or phyllosphere microbes can be endophytes. Adaptation to plant tissues seems to require a specific genetic repertoire, including metabolic and signaling functions [22,23]. However, a large part of the interest toward endophytes is focused on the ability of many of them to alleviate plant abiotic stress [24], promote plant growth and antagonize pathogens (biocontrol) [1]. The isolation and characterization of large culture collections of endophytes is constituting an important resource for sustainable food production and low-input agriculture, facing the need of exploiting marginal lands and increasing the yield of crops in a neutral climate change way [25]. However, a lot of work has still to be done, since the number of questions requires proper answers prior to a rational application of microbial endophytes in improving plant performances [26–28]. Among the outstanding questions to be answered, priorities can be given to the identification of a common set of microbial endophytes to be used as bioinoculants, to the development of setups and methods to translate knowledge from model to nonmodel plants (hence from lab-to-the-field) and to the elucidation of possible “rules of engagement” (genetic and physiological) of being an endophyte. With this Special Issue, we aim to stimulate research, opinions and reviews which, by addressing microbial endophytes, can promote the translation from laboratory discovery to field applications.

Author Contributions: Conceptualization, C.F. and A.M.; resources, C.F. and A.M.; writing—original draft preparation, C.F. and A.M.; writing—review and editing, C.F. and A.M.; funding acquisition, A.M. All authors have read and agreed to the published version of the manuscript.

Funding: This work was partially supported by the grant MICRO4Legumes, D.M.n.89267 (Italian Ministry of Agriculture) to A.M. C.F. is supported by a post-doctoral fellowship from LEGUMED project (PRIMA Foundation).

Conflicts of Interest: The authors declare no conflict of interest.

References

- Compant, S.; Cambon, M.C.; Vacher, C.; Mitter, B.; Samad, A.; Sessitsch, A. The plant endosphere world-bacterial life within plants. *Environ. Microbiol.* **2021**, *23*, 1812–1829. <https://doi.org/10.1111/1462-2920.15240>.
- Vandana, U.K.; Rajkumari, J.; Singha, L.P.; Satish, L.; Alavilli, H.; Sudheer, P.D.V.N.; Chauhan, S.; Ratnala, R.; Satturu, V.; Mazumder, P.B.; et al. The Endophytic Microbiome as a Hotspot of Synergistic Interactions, with Prospects of Plant Growth Promotion. *Biology* **2021**, *10*, 101.
- Guo, B.; Wang, Y.; Sun, X.; Tang, K. Bioactive natural products from endophytes: A review. *Appl. Biochem. Microbiol.* **2008**, *44*, 136–142.
- Gouda, S.; Das, G.; Sen, S.K.; Shin, H.-S.; Patra, J.K. Endophytes: A treasure house of bioactive compounds of medicinal importance. *Front. Microbiol.* **2016**, *7*, 1538.
- de Bary, A. *Morphologie und Physiologie der Pilze, Flechten und Myxomyceten*; Engelmann: Lemgo, Germany, 1866.
- Freeman, E.M. I—The seed-fungus of *Lolium temulentum*, L., the darnel. *Philos. Trans. R. Soc. Lond.* **1904**, *196*, 1–27.
- Rosenblueth, M.; Martínez-romero, E. Bacterial Endophytes and Their Interactions with Hosts. *Society* **2006**, *19*, 827–837.
- Abreu-Tarazi, M.F.; Navarrete, A.A.; Andreote, F.D.; Almeida, C.V.; Tsai, S.M.; Almeida, M. Endophytic bacteria in long-term in vitro cultivated “axenic” pineapple microplants revealed by PCR–DGGE. *World J. Microbiol. Biotechnol.* **2010**, *26*, 555–560.
- Oldroyd, G.E.D.; Murray, J.D.; Poole, P.S.; Downie, J.A. The Rules of Engagement in the Legume-Rhizobial Symbiosis. *Annu. Rev. Genet.* **2011**, *45*, 119–144. <https://doi.org/10.1146/annurev-genet-110410-132549>.
- Porter, S.S.; Simms, E.L. Selection for cheating across disparate environments in the legume-rhizobium mutualism. *Ecol. Lett.* **2014**, *17*, 1121–1129. <https://doi.org/10.1111/ele.12318>.
- Orole, O.O.; Adejumo, T.O. Bacterial and fungal endophytes associated with grains and roots of maize. *J. Ecol. Nat. Env.* **2011**, *3*, 298–303.
- Hallmann, J.; Berg, G. Spectrum and population dynamics of bacterial root endophytes. In *Microbial Root Endophytes*; Springer: Berlin/Heidelberg, Germany, 2006; pp. 15–31.
- Maggini, V.; De Leo, M.; Granchi, C.; Tuccinardi, T.; Mengoni, A.; Gallo, E.R.; Biffi, S.; Fani, R.; Pistelli, L.; Firenzuoli, F.; et al. The influence of *Echinacea purpurea* leaf microbiota on chicoric acid level. *Sci. Rep.* **2019**, *9*, 1–11. <https://doi.org/10.1038/s41598-019-47329-8>.
- Maggini, V.; Mengoni, A.; Bogani, P.; Firenzuoli, F.; Fani, R. Trends in Plant Science Forum Promoting Model Systems of Microbiota—Medicinal Plant Interactions Trends in Plant Science. *Trends Plant Sci.* **2019**, *25*, 223–225. <https://doi.org/10.1016/j.tplants.2019.12.013>.
- Mengoni, A.; Schat, H.; Vangronsveld, J. Plants as extreme environments? Ni-resistant bacteria and Ni-hyperaccumulators of serpentine flora. *Plant Soil* **2010**, *331*, 5–16.
- Checucci, A.; Maida, I.; Bacci, G.; Ninno, C.; Bilia, A.R.; Biffi, S.; Firenzuoli, F.; Flamini, G.; Fani, R.; Mengoni, A. Is the plant-associated microbiota of *Thymus* spp. adapted to plant essential oil? *Res. Microbiol.* **2017**, *168*, 276–282. <https://doi.org/10.1016/j.resmic.2016.11.004>.
- Bowen, G.D.; Rovira, A.D. The rhizosphere and its management to improve plant growth. *Adv. Agron.* **1999**, *66*, 1–102.
- Reinhold-Hurek, B.; Hurek, T. Living inside plants: Bacterial endophytes. *Curr. Opin. Plant Biol.* **2011**, *14*, 435–443.
- Vorholt, J.A. Microbial life in the phyllosphere. *Nat. Rev. Microbiol.* **2012**, *10*, 828.
- Massoni, J.; Bortfeld-Miller, M.; Widmer, A.; Vorholt, J.A. Capacity of soil bacteria to reach the phyllosphere and convergence of floral communities despite soil microbiota variation. *Proc. Natl. Acad. Sci. USA* **2021**, *118*, e2100150118. <https://doi.org/10.1073/pnas.2100150118>.
- Abdelfattah, A.; Tack, A.J.M.; Wasserman, B.; Liu, J.; Berg, G.; Norelli, J.; Droby, S.; Wisniewski, M. Evidence for host-microbiome co-evolution in apple. *New Phytol.* **2021**, *234*, 2088–2100. <https://doi.org/10.1111/nph.17820>.
- Levy, A.; Gonzalez, I.S.; Mittelviefhaus, M.; Clingenpeel, S.; Paredes, S.H.; Miao, J.; Wang, K.; Devescovi, G.; Stillman, K.; Monteiro, F.; et al. Genomic features of bacterial adaptation to plants. *Nat. Genet.* **2018**, *50*, 138–150. <https://doi.org/10.1038/s41588-017-0012-9>.
- Levy, A.; Conway, J.M.; Dangel, J.L.; Woyke, T. Elucidating Bacterial Gene Functions in the Plant Microbiome. *Cell Host Microbe* **2018**, *24*, 475–485.
- Rolli, E.; Vergani, L.; Ghitti, E.; Patania, G.; Mapelli, F.; Borin, S. ‘Cry-for-help’ in contaminated soil: A dialogue among plants and soil microbiome to survive in hostile conditions. *Environ. Microbiol.* **2021**, *23*, 5690–5703. <https://doi.org/10.1111/1462-2920.15647>.

25. Riva, V.; Mapelli, F.; Bagnasco, A.; Mengoni, A.; Borin, S. A Meta-Analysis Approach to Defining the Culturable Core of Plant Endophytic Bacterial Communities. *Appl. Environmental Microbiol.* **2022**, *88*, e02537-21.
26. Busby, P.E.; Soman, C.; Wagner, M.R.; Friesen, M.L.; Kremer, J.; Bennett, A.; Morsy, M.; Eisen, J.A.; Leach, J.E.; Dangl, J.L. Research priorities for harnessing plant microbiomes in sustainable agriculture. *PLoS Biol.* **2017**, *15*, e2001793.
27. Dundore-Arias, J.P.; Elie-Fadrosch, E.A.; Schriml, L.M.; Beattie, G.A.; Brennan, F.P.; Busby, P.E.; Calderon, R.B.; Castle, S.C.; Emerson, J.B.; Everhart, S.E.; et al. Community-Driven Metadata Standards for Agricultural Microbiome Research. *Phytobiomes J.* **2020**, *4*, 115–121. <https://doi.org/10.1094/PBIOMES-09-19-0051-P>.
28. Vaccaro, F.; Cangioli, L.; Mengoni, A.; Fagorzi, C. Synthetic plant microbiota challenges in nonmodel species. *Trends Microbiol.* **2022**. <https://doi.org/10.1016/j.tim.2022.06.006>.