



Review

A review on the impact of domestication of the rhizosphere of grain crops and a perspective on the potential role of the rhizosphere microbial community for sustainable rice crop production

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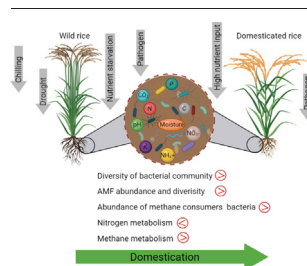
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HIGHLIGHTS

- Rhizomicrobiome studies affected by rice domestication are summarized.
- Microenvironment-host-microbe interactions drive rhizomicrobe functioning.
- Rice domestication affects AMF, nitrogen fixers, and methane consumers.
- Advantages of holobiont approach to better understanding rhizomicrobiome dynamics.
- Studies on AMF, nitrogen fixers, denitrifiers, and methane consumers are proposed.

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ABSTRACT

The rhizosphere-associated microbiome impacts plant performance and tolerance to abiotic and biotic stresses. Despite increasing recognition of the enormous functional role of the rhizomicrobiome on the survival of wild plant species growing under harsh environmental conditions, such as nutrient, water, temperature, and pathogen stresses, the utilization of the rhizosphere microbial community in domesticated rice production systems has been limited. Better insight into how this role of the rhizomicrobiome for the performance and survival of wild plants has been changed during domestication and development of present domesticated crops, may help to assess the potential of the rhizomicrobial community to improve the sustainable production of these crops. Here, we review the current knowledge of the effect of domestication on the microbial rhizosphere community of rice and other crops by comparing its diversity, structure, and function in wild versus domesticated species. We also examine the existing information on the impact of the plant on their physico-chemical environment. We propose that a holobiont approach should be explored in future studies by combining detailed analysis of the dynamics of the physicochemical microenvironment surrounding roots to systematically investigate the microenvironment–plant–rhizomicrobe interactions during rice domestication, and suggest focusing on the use of beneficial microbes (arbuscular mycorrhizal fungi and Nitrogen fixers), denitrifiers and methane consumers to improve the sustainable production of rice.

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1. Introduction

A whole new environment is created for microorganisms in the vicinity of roots as plant root systems develop and grow through the soil. This new environment, the rhizosphere, strongly differs in many ways from the soil outside the influence of the root system (Edwards et al., 2015). Numerous studies have been carried over the past hundred years to describe and understand the biological activity in the rhizosphere as this specific environment was recognized to play a key role in the health and growth of crops, as well as all plants in general. A large proportion of these studies focused on the production of root-derived compounds as nutrient substrates and as signaling molecules for bacteria and fungi in the rhizosphere, and the utilization of these root-derived products is believed to be the basis for the increase in observed biological activity (Munoz-Ucros et al., 2021). Roots produce and secrete a plethora of potential biologically-active compounds, many of which are not yet known. Utilization of the biological activity in the rhizosphere in a direct manner to support and improve plant/crop production systems has, however, rarely exploited successfully, except in cases where the relationship between microorganisms and plant roots are specific, such as in case of rhizobium and leguminous plants and to a lesser extent, arbuscular mycorrhizal fungi and their host plants.

What has often been disregarded is the fact that growing roots also change other physical-chemical aspects of the environment in the vicinity that impact the organisms, including microorganisms, that inhabit this space. Roots not only produce organic substrates, but also alter the pH, and the concentration of inorganic compounds, including nitrogen (N) and phosphorus (P) compounds, as well as the physical and moisture conditions, thereby creating new voids (or barriers) (Read et al., 2003; Yu et al., 2013; Perez-Jaramillo et al., 2017; Reid et al., 2021). Although changes induced in the soil by roots have been extensively studied by soil physicists and chemists, as well as by plant physiologists, rarely have they involved the dynamics of the community of microbes present in the rhizosphere, the rhizomicrobiome.

Combining the information on the biology, chemistry, and physics of the rhizosphere in a holobiont approach may significantly improve our knowledge of rhizosphere ecosystem, and enable the direct manipulation of the rhizosphere in sustainable crop production systems. An important line of study in this respect, has been the analysis of the changes in the rhizomicrobiome of a crop that have occurred during the process of domestication of their wild relatives and further breeding processes. Wild plants have properties that enable them to survive and withstand significant biotic and abiotic stress conditions, such as drought, pathogens, and lack of nutrients, to which domesticated crops are not or much less exposed to in modern agricultural practices. As a result, domesticated crops may have lost these traits during the domestication process and breeding for yield and quality. Therefore, understanding how the rhizomicrobiome functions in wild relatives growing under stress conditions, relative to the rhizomicrobiome of domesticated crops, can provide the information needed to design beneficial rhizosphere communities that support the growth of crops in a sustainable manner with less dependence on chemical inputs and irrigation.

One of the biggest accomplishments in human history has been the domestication of rice, which has provided a continuous food supply for a significant proportion of the global population (Wang et al., 2018). The major existing domesticated rice species, *Oryza sativa japonica*, *Oryza sativa Indica*, and *Oryza glaberrima*, were domesticated from the wild rice species, *Oryza rufipogon*, *Oryza nivara*, and *Oryza barthii*, respectively (Huang et al., 2012; Wang et al., 2014). A reduction in prime areas suitable for rice cultivation, combined with the growth of the human population, has driven the development of rice varieties with high yields to enhance rice productivity (Chang et al., 2021a). The growth of these varieties, however, requires significant inputs of nutrients, water, and pesticides. Wild plant species growth and survive without these massive inputs of chemicals and water. It is known that the rhizomicrobiome of wild species does play an important role in the growth of plants under these circumstances. Thus, the effective use of the benefits provided by the rhizomicrobiome present in wild rice species may help to address the need to develop more sustainable rice production systems.

In this review, we first provide information on the impact of domestication on the structure and diversity of the rhizomicrobial community of plants in general, and more specifically in rice. In this context we review the most recent information on the effect of rice domestication on crucial processes in the rhizosphere, especially methane metabolism. We then review studies on the interplay between microbial activity and root-derived organic substrates, rhizospheric pH, and the concentration of inorganic compounds, to provide insight into the impact of physico-chemical soil parameters on the rhizomicrobiome. The presented information will serve as a basis for the discussion of a holobiont approach that should be used in future rhizomicrobiome-related research directed at the practical use of beneficial rhizomicrobes as a major step in developing more sustainable rice production systems.

2. Rhizomicrobial signature of domestication

Microbial community structure and composition in the rice rhizosphere is cultivar dependent (Hardoim et al., 2011). Thus, it is not surprising that crop domestication, and the subsequent development of different cultivars, has resulted in profound changes in the composition of the microbial communities inhabiting the rhizosphere and roots (Leff et al., 2016). In fact, comparisons of the microbial communities in the rhizosphere of wild and domesticated plant species have revealed significant differences in the structure of the rhizomicrobiome of wild and domesticated species of grain crops such as barley (Bulgarelli et al., 2015), wheat (Spor et al., 2020), corn (Brisson et al., 2019), and rice (Tian et al., 2017; Alonso et al., 2020).

Intuitively, one would expect that the rhizomicrobiome of wild plant species would be more diverse than domesticated species due to rhizosphere communities of domesticated plants being exposed to uniform agricultural practices. It has been suggested that the biodiversity of the microbial community in wild plant species may be a key factor enabling indigenous plants to tolerate the large variety of stress factors to which they are exposed, including limited nutrients and water, exposure to soilborne

and foliar pathogens (Stringlis et al., 2018; Perez-Jaramillo et al., 2019), and drastic changes in temperature and salinity (Breitkreuz et al., 2021; de Souza et al., 2021; Santos et al., 2021). Szoboszlay et al. (2015) reported that teosinte (*Zea mays* ssp. *parviglumis*), the ancestor of modern maize, has significantly higher rhizobacterial abundance and diversity than modern *Zea mays* varieties. The wild ancestor of beet, *Beta vulgaris* ssp. *Maritima*, was also reported to exhibit higher rhizobacterial diversity and greater abiotic stress tolerance than domesticated sugar beet (Zachow et al., 2014). Notably, Xu et al. (2019) demonstrated that the biodiversity of the rhizobacterial community was higher in natural ecosystems than that in cultivated fields.

Interestingly, the structure of fungal rhizosphere communities appears to be more strongly influenced by crop domestication than bacterial communities, as shown for sunflower (Leff et al., 2016) and rice (Shi et al., 2019). This has been attributed to the indirect effect of domestication on soil characteristics that are modulated by differences in root traits (Pérez-Jaramillo et al., 2016), a topic that will be discussed later in this review. Notably, the role of fungi in the rhizosphere, including the utilization of root-derived products, is much greater than historically thought (Akinola and Babalola, 2021). Additionally, a study on the effect of the inoculation of the fungal pathogen, *Magnaporthe oryzae*, on wild and domesticated rice indicated that the relative abundance of the fungal pathogen was significantly lower in wild rice than in domesticated rice, suggesting that the microbial community in the rhizosphere of the wild species had some negative effect on the pathogen (Shi et al., 2018).

Arbuscular mycorrhizal fungi (AMF) are one of the most abundant inhabitants of the rhizosphere ecosystem, supplying inorganic nutrients and enhancing stress tolerance to their host plants (Munkvold et al., 2004; Jia et al., 2019; Gao et al., 2020). AMF enhanced host secondary metabolism and integrated the transcriptional response to chilling stress when plant roots were exposed to low temperatures in cucumber (Chen et al., 2013), potato (Caradonia et al., 2019), maize (Chen et al., 2014) and barley (Hajiboland et al., 2019). Liu et al. (2013) and Liu et al. (2015) extended these results and revealed that the response of rice (*Oryza sativa*)-associated mycorrhizal fungi to low temperatures was associated with increased phosphorus uptake, and nitric oxide and adenosine triphosphate production in rice. AMF also increased carbon and nitrogen metabolism in rice, a response potentially involving jasmonic acid production and the increased activity of enzymes involved in carbon and nitrogen metabolisms (Liu et al., 2013). AMF can also improve the uptake of water and mineral nutrients by host plants, the accumulation of osmolytes associated with salt stress response, as well as increase photosynthesis (Seleiman et al., 2022).

In particular, increasing evidence has been provided suggesting that the domestication of legume crops has affected their compatibility with rhizobial strains and AMF due to the reduced genetic diversity of host plants, resulting in a reduction of AMF diversity and colonization of legume roots (Liu et al., 2020). Analysis of AMF responsiveness in 27 crop species indicated stronger AMF colonization in wild progenitor crops, while domesticated crops only benefited from AMF under low phosphorus availability conditions (Parvin et al., 2021). Recent studies have also suggested that changes in the plant-AMF relationship have occurred in response to the domestication of rice. Xu et al. (2017) found that a greater number of AMF genera were detected in wild rice growing in natural wetlands than in Asian domesticated rice growing in cultivated paddy fields. A co-occurrence network analysis conducted by Chang et al. (2021b) revealed a greater number of positive correlations of AMF with more fungi in rhizosphere of wild rice than in the rhizosphere of domesticated rice. An interesting finding is that the colonization of AMFs in wild rice roots upregulates shikimic acid metabolism, resulting in an increase in phenylpropanoid synthesis which enlarges the production of lignin which, infused into the cell wall of root cells, may increase the resistance to *Magnaporthe oryzae* (Shi et al., 2018).

3. Functional changes in the rhizomicrobiome during domestication

Several studies have provided evidence that the recruitment of microbial communities in the rhizosphere of plants is largely driven by the functional,

rather than the structural, properties of the rhizosphere community (Mendes et al., 2014; Yan et al., 2017). Mendes et al. (2014) demonstrated that the functional properties of the rhizomicrobiome were strongly linked to factors influencing the growth of plants. Recent studies on the metagenomics of crops versus their wild relatives have provided a wealth of information on changes that have occurred in the rhizomicrobial functionality of barley (Bulgarelli et al., 2015), and maize (Schmidt et al., 2020) during domestication. Tian et al. (2018), in a comparison of the rhizomicrobiome and root transcriptome of wild and domesticated rice varieties, found that root genes involved in ‘Glutathione metabolism’ were positively associated with the relative abundance of bacterial and fungal taxa in the rhizosphere of wild rice, while root genes involved in ‘Caffeine metabolism’ were significantly and positively correlated with the enriched bacterial and fungal taxa in the rhizosphere of domesticated rice. The products of glutathione metabolism are involved in the storage and distribution of reduced sulfur within the plant regulating sulfur nutrition, but also represent essential components of plant response to environmental stresses (Shan and Yang, 2017). Additionally, the results of sequencing of the shotgun metagenomes indicated that specific genes, such as those involved in carbon and amino acid metabolisms, were primarily enriched in the rhizosphere of wild rice, while others, such as those involved in nitrogen and lipid metabolisms, were enriched in the rhizosphere of domesticated rice (Tian et al., 2022).

Chemotaxis, the ability of motile bacteria to change their direction of movement in response to stimuli, has been shown to provide motile bacteria with a competitive advantage in reaching the rhizosphere (Scharf et al., 2016). In this regard, Sun et al. (2021) observed that the abundance of bacterial chemotaxis genes in the rhizospheres of wild rice was greater than that in the rhizosphere of domesticated rice. The enrichment of chemotaxis genes in the rhizosphere of wild rice accessions may reflect their role in the assembly of the rhizosphere microbiome in wild rice rhizosphere, with the resulting assembly being a factor contributing to enhanced stress tolerance.

One of the most notable changes in the functionality of the rhizomicrobiome in response to rice domestication is related to methane metabolism (Tian et al., 2022). Key enzymes involved in both methane production and utilization are overrepresented in rhizomicrobiome samples obtained from wild rice accessions, relative to domesticated accessions. Also, taxa of methanotrophic *Anaerolineae* and *Methylocystaceae* (methane consumers) were found to be overrepresented in the microbial rhizosphere community of wild rice species relative to domesticated rice cultivars, suggesting that methane emissions from paddy soil are lower where wild rice is growing, compared to paddy soils where domesticated rice is growing (Shenton et al., 2016; Tian et al., 2022). These results suggest that the rhizomicrobiome of wild rice maintains a different balance in methane production and utilization relative to related domesticated rice accessions, which may result in a lower production of methane from the soil. This finding is highly relevant to improving the sustainability of the rice production since rice paddies have been reported to represent a major source of anthropogenic methane emission (Cui et al., 2015; Chen et al., 2019). Methane released during rice growth accounts for approximately 20 % of global methane emission (Ke et al., 2014; Edwards et al., 2015). These findings were confirmed by Conrad et al. (2009), who reported that methane emission from soils planted with wild rice was lower than it was in soils planted with domesticated rice during the 35-day period following tillering.

4. Root and (abiotic) soil properties affect the rhizomicrobiome

A number of studies have demonstrated that soil is a key factor determining the composition and structure of the rhizomicrobiome (Schlemper et al., 2018). In this regard, pH (Zhang et al., 2018), nutrients, moisture, and organic matter (Santoyo et al., 2017; Munoz-Ucros et al., 2021) have been reported to be the most important factors among soil-related factors. This seems logical as the microbial community comprising the rhizosphere is primarily recruited from the surrounding soil microbiome, which is both directly and indirectly affected by these same soil-related factors.

Most studies, however, provide a static picture of the rhizomicrobiome. They provide a characterization of the microbial community as it is assembled during the growth of the roots through the soil at a single or a few fixed points and as it is influenced by the abiotic parameters present in the bulk soil at the same time points. What is needed for a proper understanding of the dynamics of the rhizosphere community and the interaction between plants and microbes in this micro-environment, is a detailed knowledge of the dynamics of the plant-microbe interactions during the growth of roots in the immediate vicinity of the growing root and the abiotic conditions present in these immediate surroundings; thus, taking into account that the abiotic conditions in this micro-environment may be very different from those in the surrounding bulk soil. Hinsinger et al. (2003), in their review, provided a good overview of the differences in the abiotic parameters of pH, nutrient concentration, and CO₂ that occur in the first few millimeters extending out from the root surface. Notably, the cation-anion balance in the root tissue, as affected by the availability of either NH₄-N or NO₃-N, is a key factor among the abiotic parameters determining the conditions in the rhizosphere.

These abiotic conditions not only directly impact the structure of the rhizomicrobiome but also have an indirect effect, by determining the quality and quantity of root exudates and other root-derived products. Vives-Peris et al. (2020) indicated that abiotic stress conditions, such as drought, nutrient starvation, and high salinity, have a significant impact on the quantity and type of products exuded by plant roots. For example, phosphorus deficiency induces increased secretion of some organic acids, such as citramalic and salicylic acids, which contribute to the solubilization of soil phosphorus by decreasing soil pH, and greater amounts of proline are exuded into the soil when plants are subjected to salinity and osmotic stress. Both of these changes in exudate secretion will have a specific effect on the rhizomicrobiome.

Up to date, we could not find any data in the literature on how crop domestication has impacted the abiotic conditions present in the rhizosphere environment, although some authors have implied that the abiotic conditions in the rhizosphere may differ in wild vs. domesticated crops, for instance by the deeper rooting of wild species the moisture conditions in soil may be affected (Perez-Jaramillo et al., 2017). In this regard, an analysis of the impact of domestication on root architecture may provide an indication on how domestication can affect the abiotic parameters in the immediate vicinity of roots, and how this may affect the plant-rhizomicrobiome interaction Kavamura et al. (2020) reported that tall cultivars of wheat, which have a higher mean specific root length and longer, thinner roots than semi-dwarf cultivars, assemble a different rhizosphere microbial community. Perez-Jaramillo et al. (2017) identified a significant correlation between the composition of the rhizosphere microbiome and specific root length in domesticated and wild, common-bean accessions. Szoboszlai et al. (2015) also observed a greater number of thick roots in the wild ancestor of maize, relative to domestic cultivars, which resulted in a substantial change in the structure of the bacterial and fungal rhizocommunity and a higher bacterial abundance in the wild ancestor, compared to the domesticated maize cultivars. Whether the same principle applies to rice domestication is still unknown. Yet, for rice, Fernández-Baca et al. (2021) found that the abundances of microbes correlated well with increases in both rice root and shoot biomass, including species involved in nitrogen cycling (*Anaeromyxobacter* spp.) and methane production (*Methanocella avoryzae*). With regard to the formerly mentioned *Anaeromyxobacter* spp., the newly discovered nitrogen fixers predominant in rice rhizosphere (Masuda et al., 2020), these organisms are also iron-reducing bacteria and upon addition of ferrihydrite or Fe₂O₃ to the soil, the nitrogen fixing activity significantly increased (Masuda et al., 2021) as well as the abundance of the gene transcripts of *nifD* from *Anaeromyxobacter*.

5. Future directions and perspectives in rice rhizomicrobiome research

Significant efforts have been invested in the domestication of rice through breeding programs to introduce high levels of rice productivity and resilience to climate change. However, to date, fewer studies have focused on the rhizomicrobiome and its potential utilization to improve the

sustainability of rice production. When studies have considered the impact and manipulation of the rhizomicrobiome to increase crop production or improve sustainability, nearly all have focused on the application and use of single microbial strains or a combination of few specific strains capable of improving plant growth, identified as plant growth-promoting microbes (PGPM) or plant growth-promoting rhizobacteria (PGPR) (Ruíz-Sánchez et al., 2011; Andreo-Jimenez et al., 2019; Labanca et al., 2020). These plant growth-promoting microorganisms, however, have not provided consistent results under field conditions due to the resilience of soil microbiome (Çakmakçi et al., 2006). This reinforces the premise that plant development, growth, health, and productivity are, in addition to their genetic composition, influenced by the entire complex of microbial communities that they host (Li et al., 2019) dynamically through time (Leite et al., 2021), as suggested by the holobiont concept (Sanchez-Canizares et al., 2017). Therefore, we suggest that when developing novel systems designed to utilize the rhizomicrobiome to improve sustainable rice production, a holobiont approach combined with a detailed analysis of the dynamics of the chemical and physical micro-environment surrounding and along the root can be used to systematically investigate the impact of plant-microbe interactions. The importance of the rhizomicrobiome in combination with the root environment and genotype was clearly shown by Oyserman et al. (2021), who found that all interacting variables explained 22 % of root dry mass variance, 8 % of shoot dry mass variance, and 26 % of root length total variance. Information gained from studying and comparing the rhizomicrobiome and physico-chemical soil properties in wild species and domestic cultivars of rice can be used to develop a strong basis for the manipulation and utilization of the rhizomicrobiome to improve sustainable production systems for rice.

We hypothesize that the rhizomicrobiome in wild rice species plays an essential role in carbon (C), nitrogen (N), and phosphorus (P) cycling. The availability of N and P to plants in wild rice species is strongly affected by the host-associated microbiome, primarily free-living nitrogen fixers and AMF, which can solubilize and deliver nutrients to their plant hosts. The productivity in present agricultural soils with high nutrient content input, especially N and P, as well as the breeding of modern cultivars, has resulted in domesticated rice losing its need and ability to form associations with beneficial microbes that significantly impact C, N and P cycles. The need for inputs of high-loads of nutrients, the associated loss of these nutrients through leaching and soil erosion, and the emission of methane (CH₄) and nitrous oxide (N₂O) are significant environmental problems that need to be addressed to improve the sustainable production of rice. Therefore, we suggest focusing primarily on increasing knowledge and use of rhizosphere microbial communities that are directly involved the C, N and P cycles in soil. This mainly comprises AMF, free living N fixers, nitrifiers, denitrifiers, as well as methane producers and consumers. The topics we suggest for further studies are those that are directed at understanding the mechanisms underlying microbiome assembly in wild rice vs. domesticated rice related to:

1. The assemblage of high diversity AMF community in wild rice in contrast to the AMF community in domesticated rice. Topics to be considered when comparing the AMF-plant relationships in wild vs. domesticated rice include: differences in the production of metabolites, including hormones such as strigolactones, what function is signaling molecules to recruit different AMF species; differences in AMF colonization niches on different root-types and in different stages of plant development; and, the interaction between AMF species and the impact of soil nutrients on those interactions.
2. Understanding the factors that drive the positive interactions of different species of AMF with their hosts and with other fungal members of the rhizomicrobiome that are enriched in wild rice relative to domesticated rice. This would provide information on the benefits of AMF to wild plant species, in regards to plant health and abiotic stress tolerance, including drought and salinity.
3. Understanding how wild rice establishes a better balance between methane producers and consumers relative to domesticated rice. Issues that

need to be addressed include: the role of the natural, native environment of wild rice, i.e., the prevailing abiotic factors of soil pH, oxygen, water, organic matter, and nutrient availability, in shaping and structuring specific methane-producing and methane-consuming communities. The role of plant physiology, more specifically, root production of specific exudates that affect methane metabolism, in wild and domesticated rice also needs to be investigated.

Knowledge developed in the suggested topics may indicate and lead to management practices and strategies for rice production that consider the factors that enable the assembly of beneficial rhizomicrobiomes in wild rice species and apply them to domesticated rice cultivars.

Legal requirements

Submissions have not been published in, or accepted for publication by, any other journal.

Data availability

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

CRedit authorship contribution statement

JC, JAV, CT and EEK wrote the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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