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Significance of the Diversification of Wheat Species for the Assembly and Functioning of the Root-Associated Microbiome

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Wheat, one of the major crops in the world, has had a complex history that includes genomic hybridizations between *Triticum* and *Aegilops* species and several domestication events, which resulted in various wild and domesticated species (especially *Triticum aestivum* and *Triticum durum*), many of them still existing today. The large body of information available on wheat-microbe interactions, however, was mostly obtained without considering the importance of wheat evolutionary history and its consequences for wheat microbial ecology. This review addresses our current understanding of the microbiome of wheat root and rhizosphere in light of the information available on pre- and post-domestication wheat history, including differences between wild and domesticated wheats, ancient and modern types of cultivars as well as individual cultivars within a given wheat species. This analysis highlighted two major trends. First, most data deal with the taxonomic diversity rather than the microbial functioning of root-associated wheat microbiota, with so far a bias toward bacteria and mycorrhizal fungi that will progressively attenuate thanks to the inclusion of markers encompassing other micro-eukaryotes and archaea. Second, the comparison of wheat genotypes has mostly focused on the comparison of *T. aestivum* cultivars, sometimes with little consideration for their particular genetic and physiological traits. It is expected that the development of current sequencing technologies will enable to revisit the diversity of the wheat microbiome. This will provide a renewed opportunity to better understand the significance of wheat evolutionary history, and also to obtain the baseline information needed to develop microbiome-based breeding strategies for sustainable wheat farming.

Keywords: wheat, domestication, rhizosphere, root microbiome, microbial interactions, symbiosis

Abbreviations: BP, Before Present; DAPG, 2,4-Diacetylphloroglucinol; AM, Arbuscular Mycorrhizal; ISR, Induced Systemic Resistance; MIR, Mycorrhiza-Induced Resistance; SAR, Systemic Acquired Resistance; QTL, Quantitative Trait Loci; IAA, Indole-3-Acetic Acid; ACC, 1-Aminocyclopropane-1-Carboxylate; PSB, Phosphate-Solubilizing Bacteria.

INTRODUCTION

Plants interact with a myriad of microorganisms, and plant-microbe interactions are now considered a key facet of plant evolution, adaptation and ecology (Simon et al., 2019), both for wild and domesticated plants (Hassani et al., 2018). Hence, the plant needs to be seen as a holobiont (i.e., macro-organism and its associated microbiota), which requires a more integrated perspective on the significance of their microbial partners and the extended plant phenotypes they confer (Haichar et al., 2008; Vandenkoornhuyse et al., 2015).

The vast majority of plant microorganisms are in interaction with roots (Moënne-Loccoz et al., 2015). There are three distinct root-associated compartments for microorganisms, which are (i) the root endosphere (i.e., root internal tissues), (ii) the rhizoplane (i.e., the interface between the root surface and soil), and (iii) the rhizosphere (i.e., soil in the immediate vicinity of the root) (**Figure 1A**). Endophytic microorganisms inhabit the endosphere, where probably they have direct access to certain plant metabolites (Reinhold-Hurek and Hurek, 2011). They are often transmitted horizontally (Edwards et al., 2015), but some of them may be transmitted vertically (Liu et al., 2012; Hodgson et al., 2014; Truyens et al., 2015). Many of them if not most are thought to benefit their plant host (Schulz and Boyle, 2006; Reinhold-Hurek et al., 2015). In the rhizosphere, where soil is under the direct influence of the root (Hiltner, 1904), microorganisms from the surrounding soil are attracted by and benefit from rhizodeposits including root exudates (Zhalnina et al., 2018), leading to microbial proliferation and enhanced activity, i.e., the rhizosphere effect (Buée et al., 2009). Plant genotype influences the rhizosphere microbiota (Badri and Vivanco, 2009; Berg and Smalla, 2009; Micallef et al., 2009; Bouffaud et al., 2014), because different plant genotypes display different root properties and lead to different rhizosphere conditions for microbial partners. In turn, rhizosphere microorganisms can be either beneficial, pathogenic or have no effect on the plant (Vacheron et al., 2013; Nowell et al., 2016; Parnell et al., 2016). These plant-microbe interactions are essential for the ecological functioning of soil ecosystems (Lu et al., 2018).

Wheat, of the *Poaceae* family, is one of the major crops in the world with rice and maize. The crop provides 20% of calories in the human diet (Gill et al., 2004). Durum wheat is of significance as a food crop to make for example pasta, couscous, burghul, and bread wheat is used to prepare bread, pastries, etc. The Food and Agricultural Organization of the United Nations predicts a production of 776 million tons of wheat in 2022, an increase of 118 million compared to 2012. Demand for wheat is increasing with the change of diet in several large countries, such as China or India (Brisson et al., 2010). This increase in production needs to be achieved despite the growing number of challenges facing the crop, including climatic change, diminishing water resources, restrictions in the use of fertilizers and pesticides, and the risk caused by new and more aggressive pests (Tian et al., 2021). Intensive cereal systems for increasing yields are environmentally deleterious in the long-term (Lobell et al., 2009), and developing sustainable crops based on ecological intensification is essential. Exploiting the potential of wheat interactions with soil microorganisms that can enhance plant productivity, by contributing to plant nutrition and health (Bhattacharyya and Jha, 2012; Vacheron et al., 2013) is a promising strategy to reach this goal. This will require a better, more comprehensive understanding of the microbial community associated with wheat, and to identify new avenues to exploit them for sustainable wheat farming.

Recent methodology improvements, especially in sequencing technologies, have enabled to revisit our knowledge of the interactions between wheat and root-associated microbial community. For instance, the wheat microbiome has been recently described, with a focus on environmental factors driving microbiome assembly and identifying beneficial microorganisms important for sustainable wheat farming (Kavamura et al., 2021). This review aims at putting into perspective the growing knowledge on wheat-microbe interactions, by considering the evolutionary history of wheats and then its implications for the wheat microbiome. The particular patterns of microbial selection in the different root compartments (rhizosphere, rhizoplane, and endosphere) are described, ranging from bacteria and archaea to fungi and other microeukaryotes. Finally, we focus on the functional diversity of the wheat root microbiome and its implication for wheat growth and health.

WHEAT PARTICULARITIES OF RELEVANCE FOR PLANT-MICROBE INTERACTIONS

Hybridization, Polyploidy, and Domestication History

The *Triticum* and *Aegilops* ancestors of bread wheat (*Triticum aestivum*) and durum wheat (*Triticum durum*) underwent hybridization, as well as polyploidization events (Haberer et al., 2016) involving genomes A, S, B and D (**Figure 2A**). The A and S genomes arose by divergence from a common ancestor circa 7 million years Before Present (BP) (Pont et al., 2019). D genome might have originated from homoploid hybrid speciation of A and S genomes, 5–6 million years BP (Glémin et al., 2019). Two wild diploid wheats ($2n = 14$), i.e., *Triticum urartu* (AA genome) and a close descendant of *Aegilops speltoides* (BB genome) (Pont et al., 2019), hybridized about 500,000 years BP and gave a tetraploid wild wheat ($2n = 28$) termed *Triticum dicoccoides* (wild emmer wheat; AABB genome) (Pont et al., 2019). A second hybridization took place about 10,000 years BP, between domesticated emmer and a direct ascendant of the current diploid species *Aegilops tauschii* (DD genome), giving rise to a wild hexaploid wheat ($2n = 42$; AABBDD genome) at the origin of domesticated *T. aestivum*. Hexaploid wheat might have arisen from more than one crossing event (Dvorak et al., 1998). In both hybridization events, the seven chromosomes of each genome (A, B, or D) could not pair for subsequent mitosis, which resulted in chromosome doubling and thus allopolyploidy (Glover, 2016). On one hand, hybridization can lead to a loss

of genetic diversity, since only a limited number of individuals of each species is involved in the crossing. On the other hand, polyploidy may lead to particular gene expression patterns, and probably also to particular properties in terms of root exudation, root uptake, etc. (Saia et al., 2019; Iannucci et al., 2021), which can be expected to impact on microorganisms.

Wheat has undergone several domestication events. The wild einkorn *Triticum monococcum* subsp. *beoticum* (genomically close to *T. urartu*; Fricano et al., 2014) was domesticated and gave *T. monococcum* subsp. *monococcum,* a crop seldom cultivated nowadays (Salamini et al., 2002) (and therefore is not portrayed in **Figure 2A**). The wild emmer wheat *T. dicoccoides* (AABB genome) gave rise to the domesticated emmer wheat *T. dicoccon* (perhaps on several independent occasions (Özkan et al., 2011)), which later evolved into durum wheat *T. durum* (**Figure 2A**). The cross between wild emmer and the ascendant of *A. tauschii* (DD genome) either (i) resulted in an unknown hexaploid wild wheat, from which derived the domesticated wheat *T. aestivum* (Salamini et al., 2002), or (ii) was concomitant with the domestication event itself. Agronomic traits of wheat changed gradually upon domestication. As for other *Poaceae*, domesticated wheat presents bigger grains and higher seed number per spike (Salamini et al., 2002). Wheat domestication resulted also in lower root biomass (Waines and Ehdaie, 2007), with more fine roots and a shallower root system (Roucou et al., 2018), and with more seminal roots (Golan et al., 2018), but these traits display heterogeneity at inter and infra-species levels. Domestication represents a genetic bottleneck, with an estimated 50–60% reduction of wheat genetic diversity (Bonnin et al., 2014).

Wheat Geography

Nowadays, wild wheat habitats are still located in the area that was 10,000 years ago the Fertile Crescent (**Supplementary Figure 1**), and where *T. urartu*, *T. beoticum*, *T. dicoccoides*, *A. speltoides*, and *A. tauschii* can be found. Beyond the Fertile Crescent, wild wheats grow mainly in temperate climates between latitudes 30°N and 40°N, but they may occur also within the Arctic Circle and to higher elevations near the equator (Haas et al., 2019). Therefore, wild wheats grow under a wide range of pedoclimatic conditions, which means they may encounter different types of soil microbial communities.

Whereas wild wheats are mostly winter type, domesticated wheat can be either winter or spring type (i.e., does not need vernalization), which enables to find domesticated wheat in a larger range of climatic zones (and soil conditions). In comparison with spring wheat, winter wheat is sown in the autumn, which means the root system develops and interact with soil microorganisms over a much longer duration in the year. Domesticated wheats (both durum and bread wheats) are found in a broad range of areas and climates, and are present on all continents (Di Paola et al., 2018; Mideksa et al., 2018; Dong et al., 2019; Tidiane Sall et al., 2019). They are therefore likely to be included in a diversity of cropping systems and farming practices (i.e., regarding tillage, fertilizers, etc.) in contrasted conditions of soil and climate, which means exposure to very different types of soil microbial communities (Chaudhary et al., 2017; Dong et al., 2017; Gajda et al., 2017; Somenahally et al., 2018; Wang et al., 2018).

Selection and Modern Breeding

Growth of domesticated wheats in diverse environments and climatic conditions required local adaptations (Dwivedi et al., 2016). Farmers, through mass selection, led to the creation of particular, still genetically heterogeneous (Bonjean, 2001) wheat genotypes (called landraces) well-adapted to local environments (Kiszonas and Morris, 2018) and to specific stresses (Feldman and Kislev, 2007). Thus, the growth of landraces results in stands consisting of mixtures of many different closely related genotypes. Considering features important for plant-microbe interactions, this means an expected heterogeneity in terms of root system traits, plant physiology, rhizodeposition patterns and rhizosphere chemistry within a given plot.

Modern breeding aimed at higher yield. Genealogical selection (Gayon and Zallen, 1998) resulted into (i) limited plant-to-plant genetic heterogeneity within these cultivars, (ii) preferential allocation of N and C compounds to shoots rather than roots, probably leading to reduced rhizodeposition for microorganisms (Lindig-Cisneros et al., 1997), (iii) enhanced mineral uptake (Zhang et al., 2020; Cantarel et al., 2021), and (iv) particularities in root functioning and rhizosphere chemistry (George et al., 2014).

During the Green Revolution (from 1950 to late 1960s), crosses with semi-dwarf varieties were implemented (Brancourt-Hulmel et al., 2003). Hybrids were produced (Šramková et al., 2009). Chromosome engineering methodologies have been employed to transfer specific disease genes from other members of the tribe Triticeae into wheat, conferring new immune system defenses against phytopathogens (Rong et al., 2000; Niu et al., 2011). More recently, molecular markers and quantitative trait loci (QTLs) (Peng et al., 2003; Pestsova et al., 2005; Peleg et al., 2011) have been used successfully to facilitate breeding, whereas CRISPR-Cas9 (Kiszonas and Morris, 2018) and genome sequencing (Trebbi et al., 2011; Jia et al., 2013; Ling et al., 2013; Maccaferri et al., 2014; Soriano et al., 2016; International Wheat Genome Sequencing Consortium [IWGSC], Appels et al., 2018) open new perspectives, with potentially an impact on wheat-microbe interactions.

TAXONOMIC DIVERSITY OF MICROORGANISMS IN THE RHIZOSPHERE AND ROOTS OF WHEAT

Importance and Analysis of Root-Associated Wheat Microbiome

Soil type (Donn et al., 2015; Simonin et al., 2020) as well as cultivation history (Hilton et al., 2018) and practices (e.g., tillage, soil amendments) are the main factors shaping wheat root microbiota (Ahlawat et al., 2018; Kavamura et al., 2018). The second most important factor is the wheat genotype, both at the species and intra-species (varieties) levels (Mahoney et al., 2017; Stromberger et al., 2017; Ellouze et al., 2018; Naz et al., 2018;

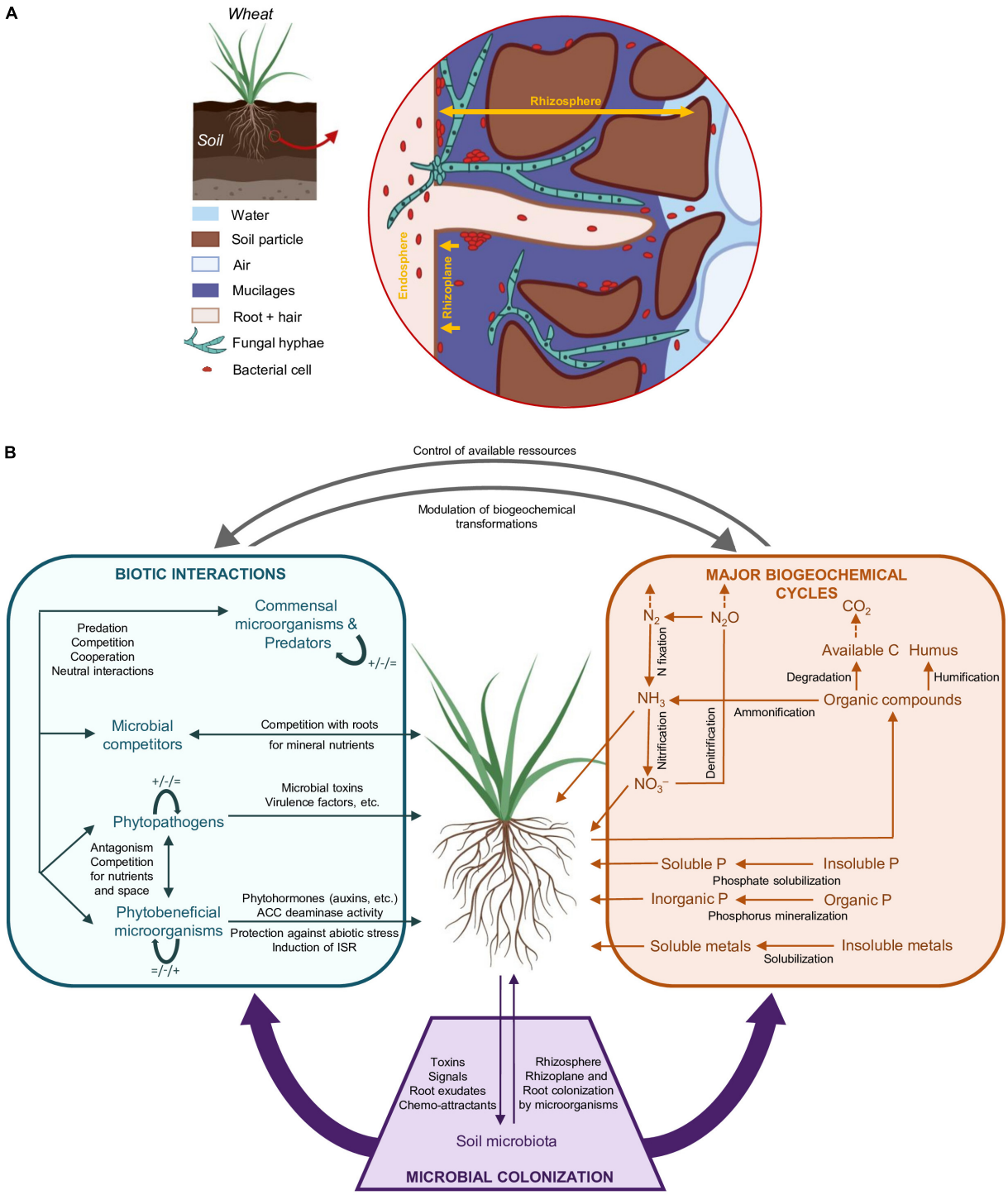

FIGURE 1 | Relationship between wheat roots and soil/microbial components. **(A)** Structure of the rhizosphere, rhizoplane, and endosphere (not to scale). The rhizosphere is the soil in the immediate vicinity of the root, where the root has a major direct impact on soil organization and microbial functioning. The rhizoplane is the interface between the root surface and the soil. The endosphere corresponds to root internal tissues. Adapted from York et al. (2016) and Ding et al. (2019). **(B)** Major root-level microbial contributions to biotic interactions and biogeochemical cycles linked to plant growth and health. Root colonization by microorganisms is mediated by plant signals and exudates, which attract or repel soil microorganisms. Biotic interactions in the rhizosphere include plant-microorganism interactions and microorganism/microorganism interactions, with beneficial (+), deleterious (-) or neutral effects (=). Major microbial transformations are indicated for C, N, and P biogeochemical cycles. Metal biotransformations are not reviewed. A particular microbial taxon may be involved in several different biotic interactions (left box) and biotransformations (right box). ISR, Induced Systemic Resistance; ACC, 1-AminoCyclopropane-1-Carboxylate. Dashed arrows are used for abiotic volatilization phenomena.

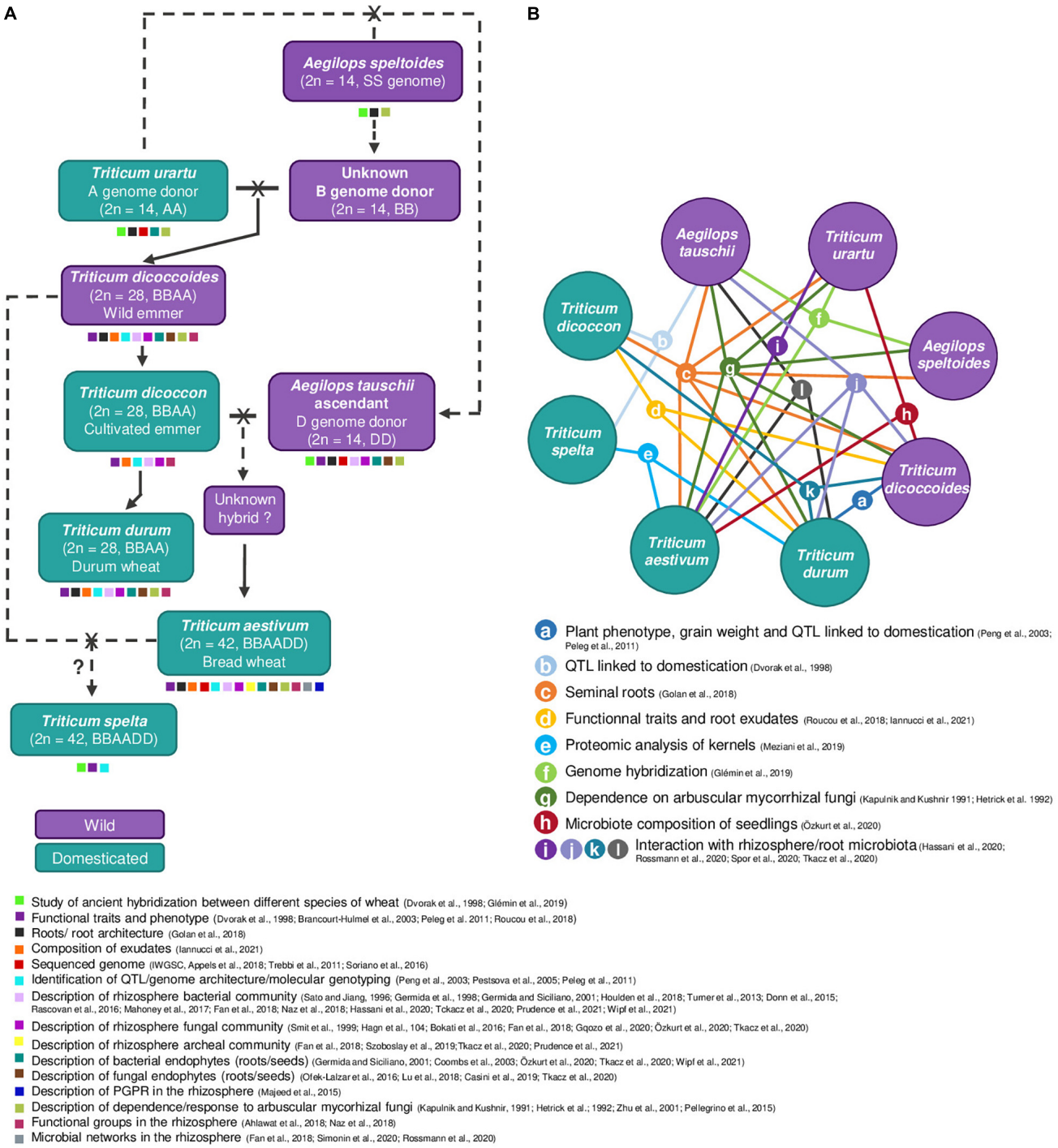

FIGURE 2 | The origin of durum and bread wheat, and literature comparisons. Wild wheats are represented in purple, while domesticated wheats are in turquoise. **(A)** Wild and domesticated species involved in wheat evolution and leading to pasta (*T. durum*) and bread (*T. aestivum*) wheats are indicated (adapted from Mujeeb-Kazi, 2006), as well as examples of key scientific issues investigated with them (shown with small squares with the color code indicated below the panel). The ancestors of pasta and bread wheats underwent hybridization and polyploidization events involving genomes A, S, B, and D. A simplified version of wheat evolutionary history is depicted. The A and S genomes arose by divergence from a common ancestor (not shown) circa 7 million years Before Present (BP) (Pont et al., 2019). The B genome probably descends from the S genome and is therefore a close relative of *Aegilops speltoides* (SS) (Fricano et al., 2014). A first hybridization event is speculated to have taken place between A (*T. urartu*) and S (*A. speltoides/A. mutica*) genomes, 5–6 million years BP (Glémin et al., 2019), leading to the D genome upon homoploid hybrid speciation. A second hybridization event took place about 500,000 years BP between this B genome donor

(Continued)

FIGURE 2 | and *T. urartu* (A genome), leading to the wild tetraploid *T. dicoccoides*, and later to the domesticated emmer *T. dicoccon*. A third hybridization event (10,000 years BP) involved *T. dicoccon* and an ascendant of current *A. tauschii* (D genome), leading to the hexaploid wheat *T. aestivum*. It is unclear whether the latter hybridization and domestication events took place at the same time or not, and the wild form of the hexaploid hybrid remains unknown. A fourth cross, between *T. aestivum* and *T. dicoccon*, is probably at the origin of the hexaploid wheat *Triticum spelta* (Fricano et al., 2014). Wheat genomes are composed of 14 (AA, BB or DD), 28 (AABB), or 42 chromosomes (AABBDD). Dashed arrows are used for uncertain events. In the history of Triticeae, other domestication events also occurred but without leading to species extensively cultivated nowadays, as for example the wild einkorn *Triticum monococcum* subsp. *beoticum* (A genome, genomically close to but not interfertile with *T. urartu*; Fricano et al., 2014) was domesticated to become *Triticum monococcum* subsp. *monococcum* (not shown). **(B)** Key literature comparisons between individual wheat species are indicated using colored lines connecting the corresponding species included; the type of comparison is shown using letters a-l, and is specified in the legend, along with the corresponding reference(s). The figure points to an unbalance in the consideration of wheat species, as previous investigation have studied *T. durum*, *T. aestivum*, and *T. dicoccoides* extensively, *T. urartu*, *T. dicoccon*, and *A. tauschii* to a lesser extent, but the other species have been seldom considered. We identified eight studies comparing wheat genomic and phenotypic properties and seven others comparing the microbiota associated to different wheat species, which shows that plant properties and microbiota properties are described to the same extent. Multiple comparisons between *T. durum*, *T. dicoccon*, and *T. dicoccoides* were made (five studies), probably because this represents a good model for domestication studies, but only one considered the microbiota (h). Only 3 of 15 studies, with a focus on seminal roots (c) or arbuscular mycorrhizal fungi (g), covered all main events of wheat history.

Kinnunen-Grubb et al., 2020; Iannucci et al., 2021). Growth stage and plant physiology matter less (Houlden et al., 2008; Donn et al., 2015), despite significant shifts after tillering (Wang J. et al., 2016) and when heading starts (Hilton et al., 2018).

In the case of wheats (Triticeae tribe), most work on rhizosphere and root microbiomes has focused on bread wheat *T. aestivum*, whereas durum wheat *T. durum* has received little attention (**Figure 2B**). Therefore, knowledge on other *Triticum* species and *Aegilops* species is very incomplete (Özkurt et al., 2020; Tkacz et al., 2020).

Other species of the Triticeae tribe have been considered mostly for comparison with *T. aestivum* and *T. durum*, to decipher the impact of domestication and selection on the wheat microbiome (Golan et al., 2018; Roucou et al., 2018; Meziani et al., 2019) (**Figure 2B**). For instance, the interactions with *Glomeromycota* fungi have been compared between wild (*T. urartu, A. speltoides*, etc.) and domesticated wheats (*T. aestivum,* etc.) (Kapulnik and Kushnir, 1991; Hetrick et al., 1992).

Microorganisms are subjected to stronger plant selection in the root endosphere than the rhizosphere (Compant et al., 2010; Fitzpatrick et al., 2018), including in the case of wheat. This materializes by greater dominance effects in the wheat endosphere, i.e., with fewer taxa but in greater relative abundance, both for bacteria and fungi (Lu et al., 2018; Özkurt et al., 2020; Tkacz et al., 2020; Prudence et al., 2021). While the rhizosphere was extensively studied, fewer studies have focused on the root endosphere of wheats (Germida and Siciliano, 2001; Bokati et al., 2016; Özkurt et al., 2020; Tkacz et al., 2020). In addition, the bacterial community has been more investigated than the archaeal and fungal communities. Information about the archaeal community of wheat rhizosphere and root endosphere exists almost only for *T. aestivum*, and this community has been documented by culture-independent methods only (Fan et al., 2018; Szoboszlay et al., 2019; Tkacz et al., 2020; Prudence et al., 2021), archaea being difficult to isolate with methods routinely used in rhizosphere ecology. Very few studies have focused on fungi in the root endosphere, whether with culture-dependent (Bokati et al., 2016) or culture-independent methods (Bokati et al., 2016; Ofek-Lalzar et al., 2016; Özkurt et al., 2020). It must be kept in mind that the various root-associated compartments, i.e., root endosphere, rhizoplane and rhizosphere, are not always straightforward to distinguish from one another from an experimental point of view, which complicates comparisons between studies.

Rhizosphere, Rhizoplane, and Root Endosphere Microbiomes of Bread Wheat

Rhizosphere Microbiome

The rhizosphere bacterial community of *T. aestivum* is dominated at almost 40% by *Proteobacteria*, as indicated by culture-independent methods (**Table 1**). The other dominant phyla (10–15%) are *Acidobacteria*, *Actinobacteria*, and *Bacteroidetes*, whereas the remaining phyla represent <5% each (Turner et al., 2013; Donn et al., 2015; Rascovan et al., 2016; Mahoney et al., 2017; Fan et al., 2018; Tkacz et al., 2020; Prudence et al., 2021). Culture-dependent methods point to *Proteobacteria* and *Actinobacteria* (each representing about 25%) and then *Firmicutes* (10%) as main phyla in the *T. aestivum* rhizosphere (**Table 2**; Juhnke et al., 1987; Sato and Jiang, 1996a,b; Germida et al., 1998; Germida and Siciliano, 2001). Within the *Proteobacteria*, the *Gammaproteobacteria* are the most abundant, with especially the families *Pseudomonadaceae* and *Xanthomonadaceae* (Donn et al., 2015).

In the *archaea,* the *Thaumarchaeota* represent more than two thirds of the rhizosphere community of *T. aestivum*, the *Euryarchaeota* <10%, and a range of unidentified phyla a total of about 20% (**Table 1**; Fan et al., 2018; Szoboszlay et al., 2019; Tkacz et al., 2020; Prudence et al., 2021). In the studies cited in **Table 1** and **Figure 3B**, the *Crenarchaeota* were not detected in *T. aestivum* rhizosphere. One investigation also considered lower taxonomic levels, showing that the *Nitrosphaeraceae* (*Thaumarchaeota*) was the most abundant family in the rhizosphere (Prudence et al., 2021).

The rhizosphere fungal community of *T. aestivum* is dominated by *Ascomycota*, which represent 40–50% of the total community with culture-independent (**Table 1**; Fan et al., 2018; Lu et al., 2018; Gqozo et al., 2020; Tkacz et al., 2020) and culture-dependent methods (**Table 3**; Smit et al., 1999; Hagn et al., 2003). The other dominant phyla are *Basidiomycota* and *Chytridiomycota* (5–15% each; **Table 1**). At genus level, *Mortiella* (phylum *Mucoromycota*), *Verticillum* (*Ascomycota*),

TABLE 1 | Occurrence of phyla in the rhizosphere of *T. aestivum*, as documented by culture-independent methods.

Phyla	Occurrence (%)[a]			Number (and list[b]) of *T. aestivum* genotypes	Number of countries	References
	Min	Max	Mean			
Bacteria						
Proteobacteria	16.5 (Bawburgh, UK; a)	52.0 (Villa Saboya, Argentina; l)	38.6	14 (a, b, c, d, e, f, g, h, i, j, k, l, NS)	5	Turner et al., 2013; Donn et al., 2015; Rascovan et al., 2016; Mahoney et al., 2017; Fan et al., 2018; Tkacz et al., 2020; Prudence et al., 2021
Acidobacteria	0.5 (Gundibinyal, Australia; k)	23.4 (Bawburgh, UK; a)	11.5	14 (a, b, c, d, e, f, g, h, i, j, k, l, NS)	5	Turner et al., 2013; Donn et al., 2015; Rascovan et al., 2016; Mahoney et al., 2017; Fan et al., 2018; Tkacz et al., 2020; Prudence et al., 2021
Actinobacteria	1.0 (Villa Saboya, Argentina; l)	26.0 (Gundibinyal, Australia; k)	12.9	14 (a, b, c, d, e, f, g, h, i, j, k, l, NS)	5	Turner et al., 2013; Donn et al., 2015; Rascovan et al., 2016; Mahoney et al., 2017; Fan et al., 2018; Tkacz et al., 2020; Prudence et al., 2021
Bacteroidetes	0.9 (Villa Saboya, Argentina; l)	28.0 (Pullman, WA; g)	14.6	14 (a, b, c, d, e, f, g, h, i, j, k, l, NS)	5	Turner et al., 2013; Donn et al., 2015; Rascovan et al., 2016; Mahoney et al., 2017; Fan et al., 2018; Tkacz et al., 2020; Prudence et al., 2021
Chloroflexi	0.5 (Northern China; NS)	6.3 (Bawburgh, UK; a)	0.9	7 (a, k, l, NS)	4	Donn et al., 2015; Fan et al., 2018; Tkacz et al., 2020; Prudence et al., 2021
Cyanobacteria	0.5 (Norwich, UK; a)	3.0 (Bawburgh, UK; a)	0.2	1 (a)	2	Turner et al., 2013; Tkacz et al., 2020
Firmicutes	9.6 (Norwich, UK; a)	20.9 (Bawburgh, UK; a)	2.9	2 (a, NS)	3	Turner et al., 2013; Rascovan et al., 2016; Prudence et al., 2021
Armatimonadetes	1.0 (Pullman, WA; d)	4.6 (Pullman, WA; e)	1.2	9 (b, c, d, e, f, g, h, i, j)	1	Mahoney et al., 2017
Planctomycetes	0.2 (Northern China; NS)	8.9 (Villa Saboya, Argentina; l)	1.0	4 (a, h, l, NS)	3	Turner et al., 2013; Rascovan et al., 2016; Mahoney et al., 2017; Fan et al., 2018
Saccharibacteria	2.0 (Pullman, WA; i)	4.0 (Pullman, WA; b)	2.0	9 (b, c, d, e, f, g, h, i, j)	1	Mahoney et al., 2017
Gemmatimonadetes	0.5 (Northern China; NS)	7.0 (Pullman, WA; b)	2.3	10 (b, c, d, e, f, g, h, i, j, NS)	2	Fan et al., 2018; Naz et al., 2018
Verrucomicrobia	0.7 (Northern China; NS)	10.2 (Villa Saboya, Argentina; l)	2.7	12 (a, b, c, d, e, f, g, h, i, j, l, NS)	4	Turner et al., 2013; Rascovan et al., 2016; Mahoney et al., 2017; Tkacz et al., 2020; Prudence et al., 2021
Other taxa	2.0 (Villa Saboya, Argentina; l)	23.5 (Bawburgh, UK; a)	2.2	2 (a, l)	3	Turner et al., 2013; Rascovan et al., 2016; Prudence et al., 2021
Unidentified taxa	1.0 (Pullman, WA; e)	71.6 (Northern China; NS)	7.12	11 (b, c, d, e, f, g, h, i, j, k)	2	Donn et al., 2015; Mahoney et al., 2017
Archaea						
Euryarchaeota	24.5 (Bawburgh, UK; a)	24.5 (Bawburgh, UK; a)	6.1	1 (a)	1	Prudence et al., 2021
Thaumarchaeota	22.2 (Northern China; NS)	100.0 (Bawburgh, UK; a)	74.3	3 (a, NS)	3	Fan et al., 2018; Szoboszlay et al., 2019; Tkacz et al., 2020; Prudence et al., 2021
Other taxa	0.2 (Bawburgh, UK; a)	0.2 (Bawburgh, UK; a)	0.05	1 (a)	1	Prudence et al., 2021
Unidentified taxa	0.4 (Bawburgh, UK; a)	77.8 (Northern China; NS)	19.6	2 (a, NS)	2	Fan et al., 2018; Prudence et al., 2021
Fungi						
Zygomycota	16.0 (Bawburgh, UK; a)	16.0 (Bawburgh, UK; a)	2.7	1 (a)	1	Tkacz et al., 2020
Glomeromycota	0.5 (Bethlehem, South Africa; o)	1.5 (Bawburgh, UK; a)	0.8	4 (a, m, n, o)	2	Gqozo et al., 2020; Tkacz et al., 2020
Chytridiomycota	0.9 (Bawburgh, UK; a)	22.3 (Pretoria, South Africa; n)	5.4	4 (m, n, o, p)	2	Gqozo et al., 2020; Tkacz et al., 2020
Basidiomycota	0.5 (Hangzhou, China; NS)	24.3 (Bethlehem, South Africa; o)	12.6	5 (a, m, n, o, NS)	3	Smit et al., 1999; Lu et al., 2018; Tkacz et al., 2020
Ascomycota	28.3 (Bawburgh, UK; a)	60.6 (Napier, South Africa; m)	45.4	6 (a, m, n, o, NS)	3	Fan et al., 2018; Lu et al., 2018; Gqozo et al., 2020; Tkacz et al., 2020
Other taxa	12.6 (Bethlehem, South Africa; o)	39.5 (Bawburgh, UK; a)	14.2	4 (a, m, n, NS)	2	Gqozo et al., 2020; Tkacz et al., 2020
Unidentified taxa	51.0 (Northern China; NS)	63.5 (Hangzhou, China; NS)	19.1	2 (NS)	1	Lu et al., 2018

Min and Max correspond to minimum and maximum occurrences observed for each phylum in the specified references, after combining data from all replicate plants of one genotype (indicated between parentheses), at one growth stage, for one treatment in one soil of one geographic location (indicated between parentheses). For each phylum, the mean is calculated from all the values obtained from the different geographic locations and T. aestivum genotypes.

[a] *Abbrevations are used to designate United Kingdom (UK) and Washington State (WA).*

[b] *Genotypes were cultivars Paragon (a), Madsen (b), PI561725 (c), Eltan (d), Finch (e), Hill81 (f), Lewjain (g), PI561722 (h), PI561726 (i), PI561725 (j), Janz (k), Cadenza (l), SST88 (m), Kariega (n), Eland (o) or were not specified (NS).*

TABLE 2 | Occurrence of phyla in the rhizosphere of *T. aestivum*, as documented by culture-dependent methods.

Phyla	Occurrence (%)			Number (and list[a]) of *T. aestivum* genotypes	Number of countries	References
	Min	Max	Mean			
Bacteria						
Proteobacteria	9.4 (Watrous, Canada; NS)	77.0 (Kawatabi, Japan; d)	23.7	6 (a, b, c, d, f, NS)	3	Sato and Jiang, 1996b; Germida et al., 1998; Germida and Siciliano, 2001; Rascovan et al., 2016
Actinobacteria	5.0 (Watrous, Canada; NS)	88.9 (Kawatabi, Japan; d)	24.0	6 (a, b, c, d, f, NS)	3	Juhnke et al., 1987; Sato and Jiang, 1996a; Germida et al., 1998; Germida and Siciliano, 2001
Bacteroidetes	1.9 (Watrous, Canada; NS)	23.0 (Kawatabi, Japan; d)	5.9	5 (a, b, c, d, NS)	2	Sato and Jiang, 1996b; Germida et al., 1998; Germida and Siciliano, 2001
Firmicutes	3.4 (Saskatoon, Canada; b)	28.3 (Watrous, Canada; NS)	10.0	5 (a, b, c, d, NS)	2	Sato and Jiang, 1996a,b; Germida et al., 1998; Germida and Siciliano, 2001
Other taxa	55.4 (Watrous, Canada; NS)	55.4 (Watrous, Canada; NS)	7.9	1 (NS)	1	Germida et al., 1998
Unidentified taxa	60.6 (Saskatoon, Canada; a)	70.0 (Saskatoon, Canada; c)	28.5	3 (a, b, c)	1	Germida and Siciliano, 2001
Fungi						
Zygomycota	5.9 (Utrecht, The Netherlands; NS)	5.9 (Utrecht, The Netherlands; NS)	5.9	1 (NS)	1	Smit et al., 1999
Chytridiomycota	3.7 (Utrecht, The Netherlands; NS)	6.7 (Utrecht, The Netherlands; NS)	3.7	1 (NS)	1	Smit et al., 1999
Basidiomycota	32.8 (Utrecht, The Netherlands; NS)	32.8 (Utrecht, The Netherlands; NS)	32.8	1 (NS)	1	Smit et al., 1999
Ascomycota	54.6 (Utrecht, The Netherlands; NS)	54.6 (Utrecht, The Netherlands; NS)	54.6	1 (NS)	1	Smit et al., 1999
Other taxa	3.7 (Utrecht, The Netherlands; NS)	6.7 (Utrecht, The Netherlands; NS)	3.7	1 (NS)	1	Smit et al., 1999

Min and Max correspond to minimum and maximum occurrences observed for each phylum in the specified references, after combining data from all replicate plants of one genotype (indicated between parentheses), at one growth stage, for one treatment in one soil of one geographic location (indicated between parentheses). For each phylum, the mean is calculated from all the values obtained from the different geographic locations and T. aestivum genotypes.
[a]*Genotypes were cultivars PI167549 (a), Red Fife (b), CDC Teal (c), Aoba (d), GSTR 11562 (e), Pondera (f), or not specified (NS).*

and *Cryptococcus* (*Basidiomycota*) are enriched in the rhizosphere (Tkacz et al., 2020).

Rhizoplane Microbiome

The rhizoplane is very poorly documented with sequencing methods, which is surprising considering the importance of bread wheat as a crop. This situation probably results from sampling limitations for the root-sol interface and an increased focus on the root endosphere in recent years. In comparison with the rhizosphere, the rhizoplane displays a bacterial community that changes with wheat growth to a larger extent, with a decrease in *Proteobacteria* and an increase in *Actinobacteria* between the vegetative and ripening stages, as well as a decrease in *Bacteroidetes* associated with senescing roots compared to ripening stage (Donn et al., 2015). A lower abundance of *Acidobacteria* is observed at the rhizoplane in comparison with the rhizosphere (Donn et al., 2015).

Root Endosphere Microbiome

The bacterial community of the root endosphere of *T. aestivum,* in contrast with that of the rhizosphere, is dominated by *Actinobacteria* (Tkacz et al., 2020; Prudence et al., 2021). They represent about 40% of the total community based on culture-independent methods (**Table 3**), but <10% with culture-dependent methods (Germida and Siciliano, 2001; Bokati et al., 2016). They are followed by *Proteobacteria* (about 30%), and then *Bacteroidetes, Acidobacteria* and *Verrucomicrobia* (each at 5–10%). At family level, the *Streptomycetaceae* (*Actinobacteria*) dominates the endophytic community, followed by *Chitinophagaceae* (*Bacteroidetes*) and *Polyangiaceae* (*Proteobacteria*) (Prudence et al., 2021), whereas at genus level *Streptomyces, Microbispora*, *Micromonospora*, and *Nocardioides* (all in the *Actinobacteria* phylum) are prevalent (Coombs and Franco, 2003).

Root archaeal endophytes consist mainly of *Thaumarchaeota* (about 60% of the community) and *Euryarchaeota* (about 30%) (**Table 3**; Tkacz et al., 2020). It is a situation reminiscent of the one in the rhizosphere, but the abundance of *Thaumarchaeota* is lower in the root endosphere compared with the rhizosphere (Tkacz et al., 2020). The family *Nitrosphaeraceae* (*Thaumarchaeota*) also dominates in the root endosphere (about 75% of the community; Prudence et al., 2021). *Methanobacteriaceae* and *Methanocellaceae* are also present (about 10% of the community; Prudence et al., 2021).

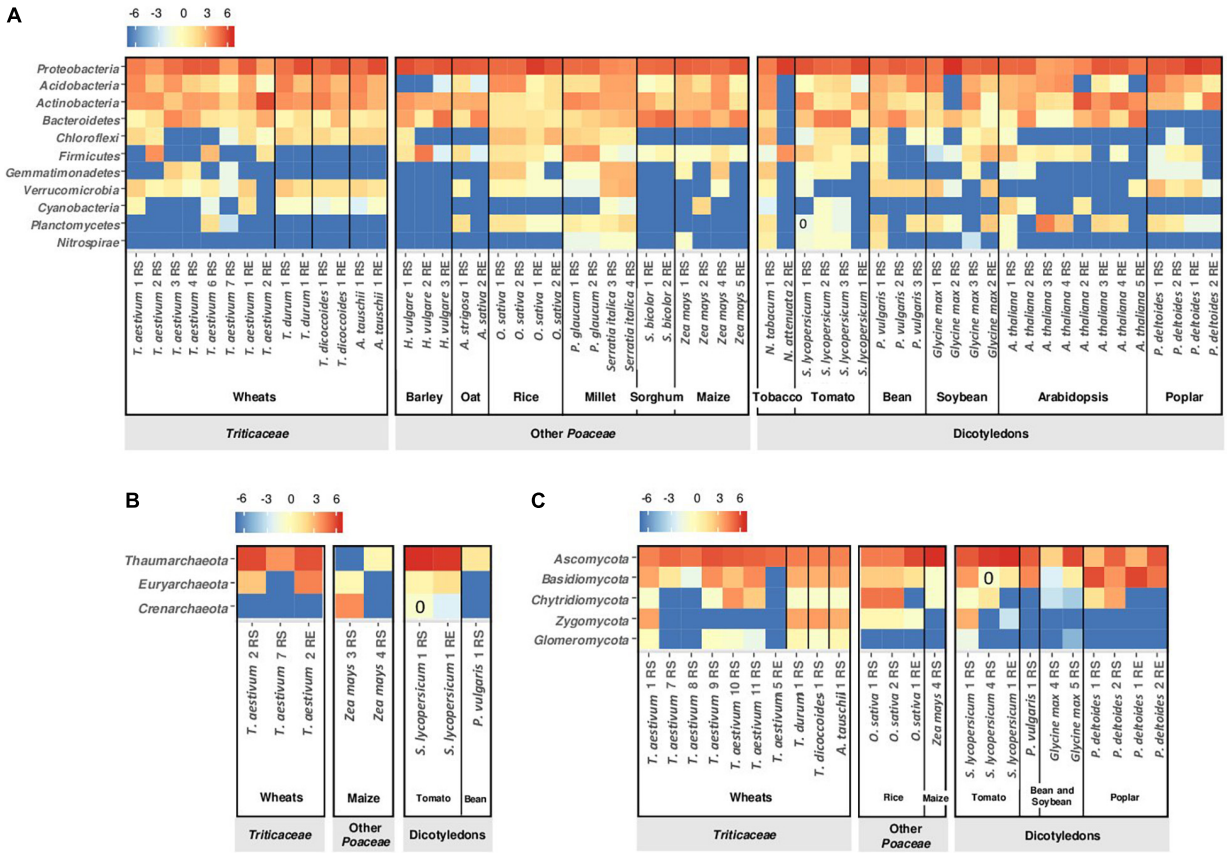

FIGURE 3 | Heatmap of major phyla affiliated with **(A)** bacteria, **(B)** archaea, and **(C)** fungi in rhizosphere soil (RS) and root/endosphere (RE) of wheats and non-wheat plants based on results from selected studies. Only phyla with relative abundance >0.5% in at least one study are shown. The color intensity in each cell denotes the transformed relative abundance [$\log_2((100x)+0.02)$] of a phylum in each study for each plant type. For details on individual conditions, see **Supplementary Table 1**.

For fungi, the predominance of *Ascomycota* in *T. aestivum* root endosphere (about 80%; **Table 3**) is documented with culture-independent and culture-dependent methods (Bokati et al., 2016; Özkurt et al., 2020). Basidiomycota represent <1% (Özkurt et al., 2020).

Evolutionary History of Wheats and Microbiome Effects

Hybridization and Domestication

Inter-generic hybridizations and domestication events led to a range of wheat species with phenotypic differences between one another and with their wild progenitors (see above section). Wheat polyploidy is a trait thought to lead to slightly different bacterial community diversity in root and rhizosphere. Wipf and Coleman-Derr (2021) documented a higher abundance of *Actinobacteria* in roots of tetraploid and hexaploid species and a higher α-diversity in the rhizosphere, in comparison with diploids. Several studies investigated the impact of domestication on the microbial community of rhizosphere and root endosphere of wheat (**Figure 2B**; Kapulnik and Kushnir, 1991; Hetrick et al., 1992; Hassani et al., 2018; Özkurt et al., 2020; Tkacz et al., 2020; Wipf and Coleman-Derr, 2021). Comparison of *T. durum* and *T. aestivum* with *T. dicoccoides* and *A. tauschii* (Tkacz et al., 2020) evidenced the same bacterial phyla but not in the same proportions, depending on the wheat species and root compartment. In the rhizosphere, the abundance of *Verrucomicrobia* is lower and the abundance of *Actinobacteria* is higher for *T. dicoccoides* than the other wheats (**Figure 3A**; Tkacz et al., 2020). Wild varieties displayed higher bacterial α-diversity than domesticated ones when comparing diploid wheats (Wipf and Coleman-Derr, 2021). In the root endosphere, a higher proportion at the heading/flowering stage is found for *Bacteroidetes* in *T. dicoccoides*, *Chloroflexi* in *A. tauschii* and *Cyanobacteria* in *T. aestivum* compared with the other wheat species (**Figure 3A**; Tkacz et al., 2020). The root endosphere of seedlings displays a higher abundance of *Proteobacteria* and a lower abundance of *Firmicutes* for *T. dicoccoides* than for *T. aestivum* (Özkurt et al., 2020). Results with root samples pointed to higher α-diversity for wild polyploid wheats than domesticated polyploids, but shifts were of small magnitude (Wipf and Coleman-Derr, 2021). Higher stochasticity (e.g., priority effects) was found in *T. aestivum* than the wild species *T. dicoccoides* (Tkacz et al., 2020).

TABLE 3 | Occurrence of phyla in the root endosphere of *T. aestivum*, as documented by culture-independent and culture-dependent methods.

Phyla	Occurrence (%)[a]			Number (and list[b]) of *T. aestivum* genotypes	Number of countries	References
	Min	Max	Mean			
Culture-independent methods						
Bacteria						
Proteobacteria	16.1 (Bawburgh, UK; a)	51.1 (Bawburgh, UK; a)	33.6	1 (a)	1	Tkacz et al., 2020; Prudence et al., 2021
Acidobacteria	1.2 (Bawburgh, UK; a)	12.4 (Bawburgh, UK; a)	6.8	1 (a)	1	Tkacz et al., 2020; Prudence et al., 2021
Actinobacteria	14.9 (Bawburgh, UK; a)	60.1 (Bawburgh, UK; a)	37.5	1 (a)	1	Tkacz et al., 2020; Prudence et al., 2021
Bacteroidetes	5.1 (Bawburgh, UK; a)	11.1 (Bawburgh, UK; a)	8.1	1 (a)	1	Tkacz et al., 2020; Prudence et al., 2021
Chloroflexi	1.0 (Bawburgh, UK; a)	5.2 (Bawburgh, UK; a)	3.1	1 (a)	1	Tkacz et al., 2020; Prudence et al., 2021
Cyanobacteria	4.3 (Bawburgh, UK; a)	4.3 (Bawburgh, UK; a)	2.2	1 (a)	1	Tkacz et al., 2020
Firmicutes	3.5 (Bawburgh, UK; a)	3.5 (Bawburgh, UK; a)	1.6	1 (a)	1	Prudence et al., 2021
Verrucomicrobia	7.17 (Bawburgh, UK; a)	7.17 (Bawburgh, UK; a)	3.6	1 (a)	1	Tkacz et al., 2020
Other taxa	7.0 (Bawburgh, UK; a)	7.0 (Bawburgh, UK; a)	3.5	1 (a)	1	Prudence et al., 2021
Archaea						
Euryarchaeota	28.0 (Bawburgh, UK; a)	28.0 (Bawburgh, UK; a)	28.0	1 (a)	1	Prudence et al., 2021
Thaumarchaeota	62.0 (Bawburgh, UK; a)	62.0 (Bawburgh, UK; a)	62.0	1 (a)	1	Prudence et al., 2021
Other taxa	7.9 (Bawburgh, UK; a)	7.9 (Bawburgh, UK; a)	7.9	1 (a)	1	Prudence et al., 2021
Unidentified taxa	2.1 (Bawburgh, UK; a)	2.1 (Bawburgh, UK; a)	2.1	1 (a)	1	Prudence et al., 2021
Fungi						
Ascomycota	66.0 (Kirksville, MO; b)	99.3 (Northern Germany; NS)	82.7	1 (b, NS)	1	Bokati et al., 2016
Basidiomycota	0.7 (Northern Germany; NS)	0.7 (Northern Germany; NS)	0.7	1 (NS)	1	Özkurt et al., 2020
Other taxa	34.0 (Kirksville, MO; b)	34.0 (Kirksville, MO; b)	17.0	1 (b)	1	Bokati et al., 2016
Culture-dependent methods						
Bacteria						
Proteobacteria	17.8 (Saskatoon, Canada; c)	24.3 (Saskatoon, Canada; e)	21.0	3 (c, d, e)	1	Germida and Siciliano, 2001
Actinobacteria	4.7 (Saskatoon, Canada; c)	11.8 (Saskatoon, Canada; e)	8.0	3 (c, d, e)	1	Germida and Siciliano, 2001
Bacteroidetes	1.0 (Saskatoon, Canada; d)	4.1 (Saskatoon, Canada; c)	2.5	3 (c, d, e)	1	Germida and Siciliano, 2001
Firmicutes	0.8 (Saskatoon, Canada; e)	1.6 (Saskatoon, Canada; c)	1.1	3 (c, d, e)	1	Germida and Siciliano, 2001
Unidentified taxa	59.0 (Saskatoon, Canada; e)	73.6 (Saskatoon, Canada; c)	67.3	3 (c, d, e)	1	Germida and Siciliano, 2001
Fungi						
Ascomycota	75.0 (Kirksville, MO; b)	75.0 (Kirksville, MO; b)	75.0	1 (b)	1	Bokati et al., 2016
Unidentified taxa	15.0 (Kirksville, MO; b)	15.0 (Kirsville, MO; b)	15.0	1 (b)	1	Bokati et al., 2016

Min and Max correspond to minimum and maximum occurrences observed for each phylum in the specified references, after combining data from all replicate plants of one genotype (indicated between parentheses), at one growth stage, for one treatment in one soil of one geographic location (indicated between parentheses). For each phylum, the mean is calculated from all the values obtained from the different geographic locations and T. aestivum genotypes.

[a] *Abbrevations are used to designate Missouri (MO) and United Kingdom (UK).*

[b] *Genotypes were cultivars Paragon (a), GSTR 11562 (b), PI167549 (c), Red Fife (d), CDC Teal (e) or not specified (NS).*

Archaea were studied (Tkacz et al., 2020), but sequencing targeted bacteria and archaea together, yielding limited numbers of sequences for archaea (<5%). This approach gave similar levels of *Thaumarcheota*, in the rhizosphere and the root endosphere, for *A. tauschii, T. dicoccoides, T. durum*, and *T. aestivum*.

For fungi, *A. tauschii* presented fewer *Zygomycota* in its rhizosphere than the other wheats did (**Figure 3C**; Tkacz et al., 2020). At genus level, fewer *Mortierella* (*Mucoromycota*) were found in *A. tauschii* and more *Verticillum* (*Ascomycota*) in *A. tauschii* and *T. dicoccoides* in comparison with *T. aestivum* (Tkacz et al., 2020). The less abundant fungal phylum in *T. aestivum* rhizosphere corresponded to the *Glomeromycota* (about 1%, **Table 1**), which were more abundant in the rhizosphere of *A. tauschii* (Tkacz et al., 2020). The selection of *Glomeromycota* and the plant response to these fungi are controlled by the D genome of *A. tauschii*, in comparison

TABLE 4 | Literature comparisons of root-associated microbial functional groups considering (i) wheat of different species, wild or domesticated, (ii) landraces, ancient, or modern varieties within wheat species, and (iii) different modern cultivars within wheat species.

Microbial function	Analysis of individual microorganisms				Analysis of functional groups			
	Microorganism studied	**(i) Wheat evolution/ domestication**	**(ii) Genotype categories within wheat species**	**(iii) Wheat cultivars**	**Methodology used**	**(i) Wheat evolution/ domestication**	**(ii) Genotype categories within wheat species**	**(iii) Wheat cultivars**
Biotic interactions								
DAPG synthesis	*Pseudomonas brassicacearum* Q8r1-96			Okubara and Bonsall, 2008; Yang et al., 2018				
	Pseudomonas fluorescens Q2-87							
	Pseudomonas ogarae F113		Valente et al., 2020	Valente et al., 2020				
					PCR-RFLP and sequence analysis of *Pseudomonas* isolates			Mazzola et al., 2004
Phenazine synthesis	*Pseudomonas chlororaphis*			Mahmoudi et al., 2019				
Synthesis of antimicrobial compound(s)					*in silico* prediction from *rrs* metabarcodes			Mahoney et al., 2017
Fungal inhibition					PCR-RFLP of *Pseudomonas* isolates			Gu and Mazzola, 2003
Rhizoctonia inhibition					Agar plate assays of *Pseudomonas* isolates			Mazzola and Gu, 2002
Induction of root defense	*Pseudomonas brassicacearum* Q8r1-96			Maketon et al., 2012				
	Pseudomonas putida			Pérez-de-Luque et al., 2017				
	Rhizophagus irregularis							
	Pseudomonas brassicacearum Q8r1-96			Okubara et al., 2010				
IAA synthesis	*Azotobacter chroococcum*			Narula et al., 2000				
					Salkowski method and sequence analysis			Venieraki et al., 2011
ACC deaminase activity					Absorbance quantification of α-ketobutyrate product			Stromberger et al., 2017
Yield promotion	*Azospirillum brasilense* Cd	Pagnani et al., 2020						
	Gluconacetobacter diazotrophicus Pal5							
	Herbaspirillum seropedicae Z67							

(Continued)

TABLE 4 | (Continued)

Microbial function	Analysis of individual microorganisms				Analysis of functional groups			
	Microorganism studied	**(i) Wheat evolution/ domestication**	**(ii) Genotype categories within wheat species**	**(iii) Wheat cultivars**	**Methodology used**	**(i) Wheat evolution/ domestication**	**(ii) Genotype categories within wheat species**	**(iii) Wheat cultivars**
Biogeochemical cycles								
Malate production					*in silico* prediction from *rrs* metabarcodes			Mahoney et al., 2017
Degradation of organic compound					Biolog^{TM} plate assays		Siciliano et al., 1998	
Cellulose decomposition					Counts on cellulose Congo Red medium			Zuo et al., 2014
Urease, catalase, sucrose, and dehydrogenase synthesis					Colorimetric assays of potential enzymatic activities			Zuo et al., 2014
Nitrogen metabolism					Metabarcoding (*rrs*) predicted gene functioning			Mahoney et al., 2017
N_2 fixation					Counts on N-free Ashby's medium	Zuo et al., 2014		
					Acetylene reduction assays and *nifH* sequence analysis			Venieraki et al., 2011
					qPCR (*nifH*)	Spor et al., 2020		Rilling et al., 2018
Nitrification					Counts on improved Stephenson's medium			Zuo et al., 2014
					qPCR (*amoA*)	Spor et al., 2020		
Denitrification					Measurement of nitrate reductase potential activity			Gill et al., 2006
					qPCR (*nirK/nirS, nosZI/nosZII*)	Spor et al., 2020		
Sulfur metabolism					*in silico* prediction from *rrs* metabarcodes			Mahoney et al., 2017
Phosphorus metabolism					*in silico* prediction from *rrs* metabarcodes			Mahoney et al., 2017
Phosphate solubilization	*Azotobacter chroococcum*			Narula et al., 2000				

These comparisons were carried out at the level of individual microorganisms (whereby one or several microorganisms was/were inoculated on wheat) or entire functional groups (i.e., taking into account most or all microorganisms potentially contributing to a given microbial function). RFLP, Restriction Fragment Length Polymorphism. List of references is available in ***Supplementary Material 1****.*

with genomes A (*T. urartu*) and B (*A. speltoides*) (Kapulnik and Kushnir, 1991; Hetrick et al., 1992; Zhu et al., 2001). The analysis of 32 *T. durum* genotypes indicated that *Glomeromycota* composition depended on plant genotype, and that certain *T. durum* genotypes associated strongly with *Paraglomus* and *Dominikia*, which were undetected in other genotypes (Ellouze et al., 2018). In the root endosphere, differences between *T. aestivum* and *T. dicoccoides* seedlings were evidenced, with a

higher abundance (73 vs. 47%) of *Pleosporales* (*Ascomycota*) in *T. aestivum* than *T. dicoccoides* roots (Özkurt et al., 2020).

Post-domestication Selection

The analysis of bacterial rhizosphere isolates showed a higher diversity with a landrace compared with two cultivars of *T. aestivum*, with the genera *Aureobacter* and *Salmonella* found only in the landrace (Germida and Siciliano, 2001). With culture-independent methods, landraces presented in the rhizosphere a higher abundance of *Bacteroidetes* and a lower abundance of *Actinobacteria* in comparison with modern *T. aestivum* cultivars (Rossmann et al., 2020). Landraces also displayed a core microbiome with more bacterial genera that were specific, i.e., found only with landraces. In the rhizosphere, the fungal genus *Dominikia* (*Glomeromycota*) was detected with 80% of *T. durum* landraces but only 60% of modern genotypes (Ellouze et al., 2018). The endophytic fungal community of *T. durum* landrace Perciasacchi (winter type) is dominated by *Ascomycota* (with *Alternaria* and *Gibberella*) and that of *T. durum* landrace Tumminia (spring type) by *Basidiomycota* (and particularly *Sporobolomyces* and *Puccinia*) (Casini et al., 2019), but these landraces were not compared with durum wheat cultivars. When comparing root and rhizosphere microorganisms associated with landraces and modern cultivars of *T. aestivum*, old accessions were enriched in *Acidobacteria* and *Actinobacteria*, and modern cultivars in *Verrumicrobia* and *Firmicutes* (Kinnunen-Grubb et al., 2020). Landraces are genetically more heterogeneous than cultivars, including for traits that influence root-microorganism interactions, e.g., root system size and root exudation (Waines and Ehdaie, 2007; Haichar et al., 2008; Matthews et al., 2019; Iannucci et al., 2021), and thus at the scale of a field they are likely to select a wider range of soil microorganisms overall. At the scale of individual plants, however, the microbiota of both old and ancient bread wheats followed a neutral assembly model, and the root microbiome displayed higher stochasticity (i.e., less deterministic selection) with modern *T. aestivum* cultivars than with landraces (Kinnunen-Grubb et al., 2020).

The Green Revolution resulted in the selection of semi-dwarf cultivars. In comparison with older, tall cultivars, the rhizosphere bacterial community of semi-dwarf bread wheat cultivars displays lower levels of *Actinobacteria* (1.4 vs. 13%), *Bacteroidetes* (5.0 vs. 16%) and *Proteobacteria* (8.6 vs. 29%) and higher levels of *Verrucomicrobia* (7.9 vs. 2.9%), *Planctomycetes* (2.1 vs. 0.7%) and *Acidobacteria* (2.9 vs. 1.4%) (Kavamura et al., 2020). The latter phyla are typically well present in bulk soil, which suggests a lower selection intensity by semi-dwarf than tall cultivars (Kavamura et al., 2020). When considering rhizosphere selection of individual strains, the comparison of 192 *T. aestivum* varieties evidenced that old varieties had a higher ability than modern cultivars to recruit the bacterium *Pseudomonas ogarae* (ex-*fluorescens* ex-*kilonensis*) F113 (Valente et al., 2020). Root systems of mid and later-generation semi-dwarf wheats are smaller than those of early Green-Revolution wheats (Waines and Ehdaie, 2007), whereas the amount of simple sugars released by roots of modern wheats is higher (Shaposhnikov et al., 2016), probably due to less stringent control of sugar exudation (Pérez-Jaramillo et al., 2018). Much remains to be done to understand differences in microbial community between old and modern cultivars, notably for archaea and fungi (not considered so far).

Among modern bread wheat cultivars, differences in bacterial selection can be significant, for certain phyla (**Figure 3A**; Mahoney et al., 2017). The abundance of *Actinobacteria, Firmicutes* and *Cyanobacteria* in the rhizosphere of cultivar Madsen is lower than for cultivar Paragon (8 vs. 19%, 0.2 vs. 20%, and 0.5 vs. 2.8%, respectively; **Figure 3A**). Such differences can also be evidenced at lower taxonomic levels, and root colonization levels by *P. ogarae* F113 varied between modern *T. aestivum* cultivars (Valente et al., 2020). Different *T. aestivum* cultivars can present dissimilar abundance levels of *Thaumarchaeota* and *Euryarchaeota* (**Figure 3B**), but data scarcity does not enable to conclude on archaeal ecology (Fan et al., 2018; Tkacz et al., 2020; Prudence et al., 2021). With fungi, higher rhizosphere levels were found for *Basidiomycota* (>15% vs. <10%) in cultivars Paragon, SST88 and Eland (Gqozo et al., 2020; Tkacz et al., 2020) and for *Chytridiomycota* (about 20% vs. <10%) in cultivar Kariega (Gqozo et al., 2020; **Figure 3C**). Among 94 *T. aestivum* genotypes, variations in mycorrhizal colonization were observed following inoculation with *Rhizophagus* and *Claroideoglomus* species, which could vary depending on old vs. recent cultivars (Lehnert et al., 2017). The abundance of *Paraglomus* (*Glomeromycota*) depends on the modern *T. durum* cultivar in the rhizosphere but not in the root endosphere (Ellouze et al., 2018).

Microbiome of Wheats vs. Other *Poaceae* and Non-*Poaceae*

Wheats vs. Other *Poaceae*

Compared with other *Poaceae*, Triticea members show some specificity in the level of certain phyla in the rhizosphere or root endosphere. Using selected publications (**Supplementary Table 1**), we found trends for (i) a higher abundance of *Cyanobacteria* and *Glomeromycota* and a lower abundance of *Firmicutes* in the rhizosphere, and (ii) a higher abundance of *Chloroflexi* in the root endosphere (**Figures 3A,C**). Differences between rhizobacterial communities increase with the phylogenetic distance between *Poaceae* (Bouffaud et al., 2016), but this is not apparent when considering phyla abundance. For example, *Verrucomicrobia* are found at the same level of magnitude in the rhizospheres of millet, rice and wheat (**Figure 3A**; Shi et al., 2019), even though the former two are distant from the Triticeae tribe. Moreover, rice (the closest to wheats in **Figure 3C**) displays a higher abundance of *Chytridiomycota* in the rhizosphere than Triticeae, whereas maize (although more distant) exhibits rhizosphere levels of *Chytridiomycota* closer to those of the Triticeae. This is also the case for the root endosphere, as the abundance of *Acidobacteria* in Triticeae is higher than in barley and oat but similar to levels in rice, sorghum and maize, which are comparatively more distant from wheats (**Figure 3A**). Nevertheless, such a variability between wheats and *Poaceae* needs to be considered in light of the high variability that exists between the different Triticeae species, and even between different *T. aestivum* cultivars.

Wheats vs. Non-*Poaceae*

Differences in bacterial community composition at phylum level can be found between Triticeae and non-*Poaceae*. This includes a lower abundance in rhizosphere and root endosphere of *Bacteroidetes* (for poplar) and *Chloroflexi* (for poplar and arabidopsis) compared with the Triticeae. A higher abundance of *Thaumarchaeota* (in rhizosphere and root endosphere) and *Nitrospirae* (in rhizosphere) is observed for tomato compared with *T. aestivum* (**Figure 3B**). In the rhizosphere, *Glomeromycota* are more abundant with Triticeae members than with tomato, bean, soybean and poplar (**Figure 3C**). However, significant microbiota similarities may also be observed when considering Triticeae and *non-Poaceae* plants mentioned in **Figure 3**. For instance, *Proteobacteria* and *Ascomycota* dominate the rhizobacterial community of both wheats and dicotyledons except for two varieties of *Arabidopsis thaliana* (Bulgarelli et al., 2012).

The comparison between Triticeae and non-*Poaceae* also reveals unexpected features, as certain differences do not coincide with the divide between these two groups. Barley (the closest to wheat in **Figure 3A**), displays surprisingly a low abundance of *Acidobacteria* in comparison with the Triticeae, the other *Poaceae* and also the non-*Poaceae*. The *Thaumarchaeota* dominate the rhizospheres of wheat and tomato, but not maize (**Figure 3B**). The rhizosphere and root endosphere of dicotyledons and certain *T. aestivum* are poorly colonized by *Zygomycota*, unlike for rice, other *Triticum* species and *A. tauschii*. In fact, extensive variability exists within the Triticeae, including between *T. aestivum* cultivars, and it is not necessarily lower than the variability between Triticeae and *non-Poaceae* observed in **Figure 3**.

FUNCTIONAL DIVERSITY OF THE WHEAT MICROBIOME

Functional Network of the Wheat Root Microbiome

Microorganisms play key roles in the biogeochemical cycles of carbon, nitrogen, sulfur, etc. (Philippot et al., 2013; Louca et al., 2016; **Figure 1B**). In root environments, the plant is the major provider of organic C and stimulate microorganisms, leading to the synthesis of various microbial metabolites, many of them with feed-back effects on the plant (Raaijmakers et al., 2009; Compant et al., 2010; Vacheron et al., 2013). The range of possible interactions between microorganisms and plant host is very broad (**Figure 1B**), from parasitism and competition to commensalism and mutualism (Lambers et al., 2009; Newton et al., 2010). Root-associated microorganisms also interact with one another, which modulates their own interactions with the plant (Raaijmakers et al., 2009; Huang et al., 2012). Due to the importance of root metabolism and rhizodeposition, it can be expected that exudate differences between wheat genotypes have the potential to materialize in significant differences in the implementation of biogeochemical cycles and biotic interactions in the root zone, but this possibility remains poorly documented.

Microbial functioning involves a complex network of elementary transformations (e.g., the conversion of N_2 into NH_3) or interactions (e.g., the inhibition mediated by a given antibiotic), each corresponding to a particular function. Each individual microorganism is endowed with many of these functions, and typically each function is common to different strains and species, leading to functional redundancy in the microbial community (Louca et al., 2016). All microorganisms participating to the same function form a functional group, and therefore each organism is likely to belong to several functional groups (Louca et al., 2016). For root-associated microorganisms, the context of the holobiont adds a supplementary dimension when considering microbial functioning (Vandenkoornhuyse et al., 2015; Lemanceau et al., 2017; Hassani et al., 2020). Whereas taxonomic variation within individual functional groups does not seem to fluctuate extensively with soil and other environmental conditions, the functional potential of the microbiota is thought to be strongly linked to environmental conditions (soil physico-chemistry, plant genotype, and growth stage) (Louca et al., 2016; Lemanceau et al., 2017; Guo et al., 2018). Accordingly, similar environments should promote similar microbial functional communities, while allowing for taxonomic variation inside an individual functional group.

Global Functioning of the Wheat Microbiota

The emergence of metagenomics has made it possible to glimpse the global functional and metabolic capacities of a microbiota. The assessment of the rhizosphere metagenome of *T. durum* showed an overrepresentation of two categories of microbial functions (Ofek-Lalzar et al., 2016; Ofaim et al., 2017). A first category corresponded to basic metabolism, important for root colonization (Santi et al., 2013; Vacheron et al., 2013), such as chemotaxis, lipopolysaccharide metabolism, nitrogen metabolism, pentose and glucoronate interconversions, starch, and sucrose metabolism. The second category was related to secondary metabolism, e.g., anthocyanin production or xenobiotic metabolism (Ofaim et al., 2017; Lu et al., 2018). Whether metagenome differences occur between wheat species or lines of individual wheat species remains to be determined. Despite methodological limitations, functional metagenome predictions from metabarcoding-based OTU datasets did suggest microbial differences between wheat lines (Mahoney et al., 2017). These predictions differed also according to *T. aestivum* growth stage (Kavamura et al., 2018). Energy metabolism dominates in the rhizosphere microbiota during early wheat development, vs. degradation of complex organic compounds with older, photosynthetically active plants. A similar rhizosphere acclimatization was found with oat (Nuccio et al., 2020). Metatranscriptomic analysis of the rhizosphere of one *T. aestivum* genotype revealed metabolic capabilities for rhizosphere colonization, including cellulose degradation and methylotrophy (Turner et al., 2013).

Metagenomic or metatranscriptomic studies have been useful to describe global metabolic activity in root environments, but they have not been implemented yet to compare different wheat

species or lines. Therefore, it remains difficult to assess the impact of intra-species variation, domestication and hybridization of wheats on global microbial functioning in the root zone, and this is a topic in strong need of research attention.

Microbial Interactions in the Wheat Root and Rhizosphere

Rhizosphere microorganisms develop deleterious, beneficial or neutral interactions with one another (**Figure 1B**). The extent of these interactions, and the density and complexity of the resulting interaction network depend on taxa richness, microbial abundance and activity levels (Finlay et al., 1997; Torsvik and Øvreås, 2002; Fuhrman, 2009). Wheat root system architecture and rhizodeposition traits determine the root surface that can be colonized and the amount of root exudates. Since these characteristics were affected by domestication and subsequent crop selection (Waines and Ehdaie, 2007; Shaposhnikov et al., 2016; Iannucci et al., 2021), wild wheats, landraces and modern cultivars probably display different patterns of microbial colonization and of microbial interactions in their roots and rhizosphere. Microbial interactions and competition can also be modulated by predators (nematodes and protozoa), which thrive to different extents in the rhizospheres of oat, pea and wheat (Turner et al., 2013), and perhaps also in the rhizosphere of different wheat genotypes. Microbiota network analysis of *T. aestivum* rhizosphere revealed the co-occurrences of cercozoa (protozoa), bacterial and fungal taxa, reminiscent of a predator-prey system (Rossmann et al., 2020). Co-occurrence levels were higher and trophic networks more entangled with landraces than modern cultivars, which suggests a higher level of microbial interactions in the rhizosphere of landraces.

Pathogens infecting wheat roots cause significant damage, including the take-all fungus *Gaeumannomyces graminis* var. *tritici* (Wilkinson et al., 1985), *Rhizoctonia* spp. causing root rot or damping-off (Ingram and Cook, 1990), and *Pythium* species leading to root rot (Wiese, 1987; Ingram and Cook, 1990). Differences in sensitivity to root pathogens exist according to wheat genotype. *A. speltoides* and *T. durum* are more sensitive than *T. monococcum* to *G. graminis* var. *tritici* (McMillan et al., 2014), whereas inter-cultivar variability of resistance to this pathogen is high within *T. aestivum* (Golizadeh et al., 2017). Susceptibility to *Rhizoctonia* was similar for *T. monococcum* and *T. durum*, as well as certain *T. aestivum* cultivars, whereas other cultivars of *T. aestivum* were more sensitive (Oros et al., 2013). Differences in tolerance to *G. graminis* (Golizadeh et al., 2017), root-infecting *Fusarium graminearum* (Wang et al., 2018), foot, crown and root rot-causing *Fusarium culmorum* (Erginbaş Orakcı et al., 2018) and *Pythium* (Higginbotham et al., 2004) occurred among *T. aestivum* cultivars. Wheat is also affected by parasitic nematodes, with cultivar-level differences in susceptibility of *T. aestivum* to cereal cyst nematodes *Heterodera* spp. (Cui et al., 2016) and root-lesion nematode *Pratylenchus curvicauda* (Begum et al., 2020). Apart from differences in disease sensitivity, modern *T. aestivum* cultivars tend to be more colonized by *Fusarium*, *Neoascochyta* and *Microdochium* root pathogens compared with landraces (Kinnunen-Grubb et al., 2020).

Wheat cultivars might rely on specific microbial populations for phytoprotection, which may entail pathogen inhibition (*via* competition or antagonism) or systemic induction of plant defense pathways. Fluorescent *Pseudomonas* inhibit *Pythium, Rhizoctonia* and *G. graminis* (Weller and Cook, 1986; Mavrodi et al., 2013), using 2,4-diacetylphloroglucinol (DAPG), hydrogen cyanide (HCN), or phenazines (Keel et al., 1992; Kwak and Weller, 2013; Mavrodi et al., 2013; Imperiali et al., 2017). The diversity of bacterial populations producing these compounds and rhizosphere expression of the corresponding genes depend on plant host genotype (Latz et al., 2015). DAPG and HCN-producing microorganisms can be studied *via* the marker genes *phlD a*nd *hcnABC*, respectively (**Supplementary Table 2**), and DAPG-producing microorganisms associated with different wheat genotypes have been well-studied in comparison with the case of other antagonistic compounds (**Table 4**). Modern cultivars of *T. aestivum* differentially select for and benefit from DAPG-producing *Pseudomonas* species in resident soil populations (Berg et al., 2002; Mazzola et al., 2004; Meyer et al., 2010). Cultivar differences were evidenced in the interaction with DAPG-producing *P. brassicacearum* in soil suppressive to take-all (Yang et al., 2018). Suppression of *Rhizoctonia* root rot and take-all is cultivar-dependent, through enhanced recruitment of specific *Pseudomonas* populations by cultivars less affected by disease (Mazzola et al., 2004; Yang et al., 2018). Phytopathogens may also be inhibited by other saprophytic microorganisms, including bacteria and fungi (Barnett et al., 2017), and for the latter the ability to colonize wheat roots can depend on the cultivar (Osborne et al., 2018). In addition, Arbuscular Mycorrhizal (AM) fungi (division *Glomeromycota*) also inhibit wheat pathogens *via* competition (Ganugi et al., 2019) or production of cellulases and chitinases, which may affect pathogen cell wall and provide wheat protection (Pérez-de-Luque et al., 2017), but the significance of wheat genotypes is not documented. Induced resistance is poorly documented in monocots, including wheat (Balmer et al., 2013). Induced Systemic Resistance (ISR), which involves jasmonate and ethylene signaling, is triggered in wheat by certain *Pseudomonas* strains (Balmer et al., 2013). Similarly, saprophytic fungi from *Aspergillus*, *Penicillium* and *Trichoderma* genera and protecting against Rhizoctonia wilt trigger ISR in wheat (El-Maraghy et al., 2020). Mycorrhizae also induce systemic plant resistance, termed Mycorrhiza-Induced Resistance (MIR) (Mustafa et al., 2016), which is reminiscent of ISR (Balmer et al., 2013) but displays also features of Systemic Acquired Resistance (SAR), especially the priming of salicylic acid-dependent genes (Pérez-de-Luque et al., 2017). Thus, MIR by the AM fungus *Funneliformis mosseae* upregulated several defense genes in wheat, and protected wheat from the powdery mildew pathogen *Blumeria graminis* f. sp. *tritici* (Mustafa et al., 2016). In addition, *Bacillus velezensis* CC09 stimulated SAR pathways, inducing *PR1* genes and enhancing lignin accumulation, and protected wheat from take-all (Kang et al., 2018). Little has been done to compare induced resistance in different wheat genotypes (**Table 4**). The two cultivars studied in Pérez-de-Luque et al. (2017) displayed different levels of systemic priming for chitosan-induced callose after co-inoculation with *Pseudomonas putida* and *Rhizophagus irregularis*. One of the two cultivars showed higher level of callose deposition after

co-inoculation than inoculation of *P. putida* or *R. irregularis* alone, suggesting additive or synergistic effects in some but not all genotypes, probably linked to cultivar differences in the signaling pathway leading to systemic immune priming (Haichar et al., 2016). Root expression of defense gene homologs induced by *P. brassicacearum* Q8r1-96 differed between the three wheat cultivars analyzed (Okubara et al., 2010). Since wheat species and varieties differ in their abilities to recruit microbial taxa containing strains with induced resistance potential, especially AM fungi (**Figure 2A**), it raises the possibility that some varieties are more prone to be protected by ISR. If so, this might explain some of the differences in sensitivity to diseases observed among cultivars.

Apart from plant protection, several microbial functional groups present in the rhizosphere are beneficial, by ensuring better plant growth (Vacheron et al., 2013; Lemanceau et al., 2017). However, information about their abundance and activity according to wheat genotype is scarce, even for the best described functional groups. Mineral nutrition of wheat can be promoted by different functional groups directly affecting nutrient bioavailability or stimulating plant development through microbial modulation of its hormonal balance (Finkel et al., 2017). Wheat growth can be promoted by microorganisms that produce phytohormones, such as Indole-3-Acetic Acid (IAA) (Spaepen et al., 2007), cytokinins and gibberellin, or secondary metabolites interfering with auxin, such as DAPG (Landa et al., 2003) and nitric oxide (NO) (Molina-Favero et al., 2008). Inoculation with different P-solubilizing, IAA-producing strains of *Azotobacter chroococcum* carried out on three cultivars of *T. aestivum* showing contrasted P responses resulted in enhanced N, P, K uptakes, probably as a consequence of phytohormone effects, but without difference between wheat genotypes (Narula et al., 2000). In contrast, cultivar differences were found following *Azospirillum* inoculation, when considering phenotypic traits such as root system architecture or plant height, especially during early growth phases, but without an effect on grain yield (Kazi et al., 2016). Using the Opata × synthetic mapping population, one QTL region on chromosome 1A was identified for *Azospirillum* adhesion to wheat roots (Díaz De León et al., 2015). DAPG, at low concentration, induces the plant's auxinic pathways, which stimulates root exudation and branching (Brazelton et al., 2008; Combes-Meynet et al., 2010). Application of wheat root exudates to a soil modified the composition of the DAPG-producing community in a cultivar-specific manner (Gu and Mazzola, 2003). The activity of DAPG-producing *Pseudomonas* in the rhizosphere and DAPG accumulation on the rhizoplane of *T. aestivum* is influenced by specific cultivar-bacterial strain associations (Bergsma-Vlami et al., 2005; Okubara et al., 2010). Variability is also observed between old and modern cultivars, as colonization by *P. ogarae* F113 and expression of *phl* genes (coding for DAPG production) are higher for ancient genotypes of *T. aestivum* (Valente et al., 2020). Not much data is available on the effect of wheat genotype on the abundance or activity of other phytohormone-producing microorganisms (**Table 4**). 1-aminocyclopropane-1-carboxylate (ACC) is the precursor of ethylene in plants and more ACC is produced in case of stress, which may have deleterious effects on plant growth (Glick, 2014). ACC deaminase activity, which catalyzes the cleavage of ACC into ammonium and alpha-ketobutyrate (Glick, 2005, 2014), is found in many microorganisms living in the rhizosphere (Bouffaud et al., 2018). This activity can improve the growth and yield of *T. aestivum* under salt stress and drought conditions, acting as an ACC sink that lowers ethylene level without stopping stress-induced reactions (Zahir et al., 2009; Shakir et al., 2012; Hassan et al., 2014). The abundance of microorganisms with ACC deaminase activity in the rhizosphere varies with plant genotype (Bouffaud et al., 2018), and the abundance, composition and activity of the corresponding functional group depends also on *T. aestivum* cultivar (Stromberger et al., 2017). Under drought or well-watered conditions, the response of *T. aestivum* to inoculation with ACC deaminase-producing bacteria is genotype dependent, as some cultivars showed higher root length while others had increased above-ground biomass (Salem et al., 2018). The ability of these bacteria to promote drought resistance may depend on wheat genotype (Stromberger et al., 2017). The significance of ACC deaminase activity has not been studied for wheat species other than *T. aestivum* (**Figure 2A**). *Pseudomonas* producing phenazine (usually studied for its antimicrobial properties) are thought to be involved in drought resistance as well. Indeed, when inoculated, their presence on roots (at population levels that are wheat cultivar dependent; Mahmoudi et al., 2019) leads to added protection of seedlings against drought in cultivars that are genetically drought resistant (Mahmoudi et al., 2019). Moreover, *Pseudomonas* producing phenazine were shown to be abundant in non-irrigated soil (Mavrodi et al., 2012, 2013). Furthermore, resistance to drought (along with other abiotic stress like salinity or metals; Seguel et al., 2016; Aguilera et al., 2018; Ganugi et al., 2019) may be conferred by AM fungi following the induction of particular metabolomic responses in wheat roots (Bernardo et al., 2019). This protection varies with *T. aestivum* cultivars and QTLs have been identified, especially on chromosomes 3D and 7D (Lehnert et al., 2017). More generally, genome-wide association studies for the establishment of AM symbiosis have highlighted QTL regions on chromosomes 3A, 4A, and 7A in *T. aestivum* inoculated with *Rhizophagus intraradices*, *Claroideoglomus claroideum* and *Claroideoglomus etunicatum* (Lehnert et al., 2017) and on chromosomes 1A, 2B, 5A, 6A, 7A, and 7B for *T. durum* when inoculated individually with *Funneliformis mosseae* or *Rhizoglomus irregulare* (De Vita et al., 2018). Depending on the species (*T. aestivum* or *T. durum*), changes in rhizosphere microbiota traits due to drought will differ, suggesting that different wheat genotypes recruit their own specific microbiota to help alleviate abiotic stresses (Azarbad et al., 2018, 2020).

Biogeochemical Cycles in the Wheat Root and Rhizosphere

The rhizosphere is characterized by the release of organic exudates and other rhizodeposits, and the uptake of mineral nutrients by roots (**Figure 1B**). The biogeochemical cycles of carbon, nitrogen and phosphorus are well-understood, and several primers are available to target microbial markers

associated with these cycles (**Supplementary Table 2**). However, microbial activities involved in other important cycles such as those of potassium, sulfur or iron are less described in the wheat root and rhizosphere (Narula et al., 2000; Sheng and He, 2011; Jacoby et al., 2017; Kumar et al., 2018).

Carbon

Carbon efflux from the root is important (Kuzyakov and Cheng, 2001) and wheat root-derived CO_2 represents between 25 and 50% of the total CO_2 efflux from soil (Kuzyakov and Cheng, 2001). Most microbial functions related to carbon in the rhizosphere are linked to degradation of organic exudates (Derrien et al., 2004; Haichar et al., 2016). The rhizosphere priming effect (i.e., the increase of microbial activity following exudation) intensifies decomposition and mineralization (Cheng et al., 2003), and is an important cause of carbon loss from the rhizosphere.

Bacteria and fungi are primary decomposers, releasing extracellular hydrolytic enzymes to catalyze decomposition of organic matter (Berg and McClaugherty, 2008). Actinobacteria, found in the rhizosphere of *T. aestivum* (**Table 1**) include different species involved in decomposition and humus formation (Wang C. et al., 2016; Bao et al., 2021). In the rhizosphere, the potential activity of microbial enzymes (mostly cellulases) associated with carbohydrate degradation differed according to *T. aestivum* cultivar (**Table 4**; Zuo et al., 2014). Moreover, endophytic microorganisms isolated from roots of ancient *T. durum* cultivars differed in their ability to degrade organic compounds compared with those from more recent cultivars (Siciliano et al., 1998). Indeed, microorganisms isolated from recent cultivar CDC Teal degraded carboxylic acids at a higher rate, whereas polymers and amino acids were degraded at a higher rate by microorganisms isolated from ancient cultivars Red Fife and PI 167549.

Nitrogen

Diazotrophs are well-represented in the plant rhizosphere, where they find sufficient energy resources for the costly functioning of the dinitrogenase that fixes N_2 into assimilable NH_3 (Herridge et al., 2008). N_2 fixation is the best studied activity when comparing different wheat genotypes (**Table 4**). The ability of N_2-fixing *Azospirillum* to colonize roots depends on *T. aestivum* cultivar, as the bacteria were detected either in the root tissues and intercellular spaces or only at the root surface (Schloter and Hartmann, 1998). *Cyanobacteria* of the genera *Nostoc* (Gantar et al., 1993) and *Azospirillum brasilense* FP2 fix N_2 when colonizing *T. aestivum* roots (Van Dommelen et al., 2009; Camilios-Neto et al., 2014). Free-living nitrogen-fixing prokaryotes contribute to nitrogen requirement of wheat (Dellagi et al., 2020), up to 76 and 32% for shoots and roots, respectively (Majeed et al., 2015). In addition, higher yields were observed for *T. aestivum* inoculated with engineered strains able to fix nitrogen constitutively (Fox et al., 2016). The diazotroph community varies in size and activity with plant species (Perin et al., 2006; Mao et al., 2013; Bouffaud et al., 2016) and cultivars of *T. aestivum*, with a higher number of rhizosphere diazotrophs for Xiaoyan than for other *T. aestivum* cultivars (Mahoney et al., 2017).

Even though N is often limiting for plant growth, wheat roots may release nitrogen in the form of NH_3/NH_4^+ in the rhizosphere (26 mg for the entire growing season, 18% of the total N yield of the plant; Janzen, 1990). Within the wheat rhizosphere, NH_3 is oxidized into NO_2^- and NO_3^- by aerobic nitrifiers. Ammonium oxidizers include ammonium-oxidizing bacteria (AOB) and ammonium-oxidizing archaea (AOA; Chen et al., 2011). Wheat domestication and selection had an effect on the interaction with nitrifiers, as they are less abundant in the rhizosphere of modern *T. durum* cultivars compared with *T. dicoccoides* and *T. dicoccon* (Spor et al., 2020). Differences in abundance of nitrifying bacteria also exist between *T. aestivum* cultivars, with higher rhizosphere numbers for cultivar Xiaoyan than the others (Mahoney et al., 2017). In addition, some *T. aestivum* landraces can inhibit nitrification in their rhizosphere (O'Sullivan et al., 2016).

Denitrifying bacteria harboring NO_2^- reductase genes *nirK*/*nirS* (Chen et al., 2011) reduce NO_2^- into NO. In the *T. aestivum* rhizosphere, denitrification is stimulated by root exudates (as denitrifiers are heterotrophs) (Wollersheim et al., 1987) and soil waterlogging (as it results in anoxia) (Hamonts et al., 2013). Thus, *T. aestivum* modulates denitrification activity and influences the composition of the denitrifying community (Achouak et al., 2019). Among modern *T. aestivum* cultivars, differences in rhizosphere denitrification activity and N_2O emissions are significant (Hayashi et al., 2015), including for cultivars that can even inhibit nitrate reductase activity (Gill et al., 2006).

Phosphorus

Phosphorus is mostly present as insoluble phosphate or organic forms in the soils. Microorganisms can degrade P-containing organic matter *via* phosphatases, thereby mineralizing phosphorus and making it potentially available for plants. Some bacteria also act as Phosphate-Solubilizing Bacteria (PSB), thanks to the production of organic acids, protons, IAA (Gyaneshwar et al., 2002). PSB have been isolated from the rhizosphere of *T. aestivum*, e.g., *Streptomyces* spp. (Jog et al., 2014), *Pseudomonas* sp. BR2 (Babana et al., 2013) and *Bacillus* sp. (Majeed et al., 2015), and the rhizosphere of *T. durum* (Cherchali et al., 2019; Di Benedetto et al., 2019). The number of culturable PSB varies with plant species (Kundu et al., 2009). Since PSB are heterotrophic, their abundance in the rhizosphere of *T. aestivum* is influenced by organic matter content (Abderrazak et al., 2017), and differences between wheat cultivars might be expected since each may exude differently (Waines and Ehdaie, 2007; Iannucci et al., 2021). Wheat cultivars differed in the abundance of microbiota sequences linked to phosphate metabolism (Mahoney et al., 2017). Inoculation with a PSB from *Azotobacter chroococcum* in the rhizosphere of three cultivars of *T. aestivum* increased the number of grains per spike, straw yield, and root biomass, but without significant difference between cultivars (Narula et al., 2000). This is the only study dealing with P solubilization activity in different wheat cultivars (**Table 4**).

In addition to bacteria, AM fungi associated to wheat can mineralize organic phosphorus. The symbiotic network formed by mycorrhizal fungi with plant roots increases the volume of soil exploited for nutrients, providing the plant with P sources

while the fungus acquires organic carbon from the plant (Hamel et al., 2004; Li et al., 2006; Pellegrino et al., 2015). The importance of AM fungi in wheat phosphorus feeding depends on the combination of plant and fungal genotypes (Hamel et al., 2004; Pérez-de-Luque et al., 2017). Indeed, the abundance of AM fungi differs between *T. durum* varieties, with a higher abundance associated with landraces than with modern cultivars (Ellouze et al., 2018). Similarly, wild wheats of genome A (*T. urartu*) and B (*A. speltoides*) showed more mycorrhizal dependence (i.e., the degree of plant growth and nutrition obtained with the help of AM fungi) than wild wheat of the D genome (*A. tauschii*) (Hetrick et al., 1992). Thus, the response to AM fungi in hexaploid wheat is probably controlled by the D genome (Kapulnik and Kushnir, 1991; Hetrick et al., 1992). Mycorrhizal dependence was lower in modern cultivars in comparison to old cultivars of *T. aestivum* (Zhu et al., 2001). Modern wheat crops seem to select their partner less (Hetrick et al., 1992; Zhu et al., 2001) and mycorrhizal dependence has been reported to decrease with wheat domestication (domesticated *T. durum* vs. wild *T. dicoccoides*; Martín-Robles et al., 2018). Indeed, in agroecosystems where different fertilization regimes are applied, modern cultivars probably rely less on microorganisms for their nutrition since they are well-provided with fertilizers (Duhamel and Vandenkoornhuyse, 2013).

CONCLUSION

Wheat, one of the three most important crops in the world, has undergone a particularly complex evolutionary history involving several inter-genus crosses, genomic hybridizations and domestication events, which resulted in the formation of several wheat species able to grow in contrasted climates and cultivated (mostly *T. aestivum* and *T. durum*) for various feed and food purposes. The implications of this very particular evolutionary history on the recruitment and functioning of root and rhizosphere microbiomes are poorly understood.

Most studies have focused on the taxonomic features of these microbiomes, describing the abundance and diversity of microorganisms associated with wheat species. The most dominant bacterial phylum corresponds to *Proteobacteria* in the rhizosphere (as for other plant taxa) and *Actinobacteria* in the root endosphere (but *Proteobacteria* for other *Poaceae* and for non-*Poaceae* taxa). In both compartments, the archaeal and fungal communities are dominated by, respectively, *Thaumarchaeota* (as for other plant taxa) and *Ascomycota* (as for the other plant taxa investigated except poplar, where *Basidiomycota* dominate).

Domestication, selection and modern breeding created wheats selecting different root and rhizosphere communities in comparison with those of their wild or ancient relatives. Evidence for the importance of genomic hybridizations relates especially to the case of *Glomeromycota*, whose mycorrhizal association is controlled by D genome factors. Otherwise, the main differences in root and rhizosphere microorganisms seem to stem from post-domestication selection, based on the information available so far. Indeed, landraces are associated with a larger microbial diversity, which probably results from their higher plant-to-plant genetic heterogeneity, and their core microbiome presents certain bacterial families not found in modern cultivars. However, at the level of individual plants, strong microbial selection takes place in the rhizosphere of landraces, with higher taxa co-occurrence levels. This is attributed to a stronger selective pressure in the rhizosphere of pre-Green Revolution wheat compared to semi-dwarf varieties and modern cultivars of *T. aestivum*. Overall, the vast majority of analyses considering wheat genetic diversity have been restricted to the comparison of different cultivars of *T. aestivum*, showing microbial variability between them, to an extent not necessarily lower than that found between Triticeae and other *Poaceae* or *non-Poaceae*.

At the functional level, much less is documented on root-associated microorganisms in comparison with taxonomic data. Information is scarce on their functional traits, both for metagenomic and metatranscriptomic investigations targeting the entire microbial community and studies dealing with particular microbial functional groups. Differences in recruitment of disease-suppressive microorganisms are seen between cultivars of *T. aestivum*, contributing to differences in wheat health. The best-documented impact of domestication and post-domestication selection concerns the ability to interact and benefit from AM fungi, which decreases along the domestication/selection gradient.

Overall, it appears that wheat evolution has resulted into crop varieties with particular microbiome profiles, which probably rely less on their underground microbial partners for provision of growth resources and protection against diseases, and thus they are more dependent on human management. The development of omics tools targeting microbial functions in the rhizosphere is expected to provide new insights into the significance of wheat domestication and diversification for wheat-microorganisms interactions. It should also facilitate the design of novel breeding strategies integrating the contribution of root symbiotic partners for sustainable wheat farming.

AUTHOR CONTRIBUTIONS

All authors contributed to the writing of this review article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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