

Crop domestication and improvement reshape root traits and the structure and function of their associated microbiome

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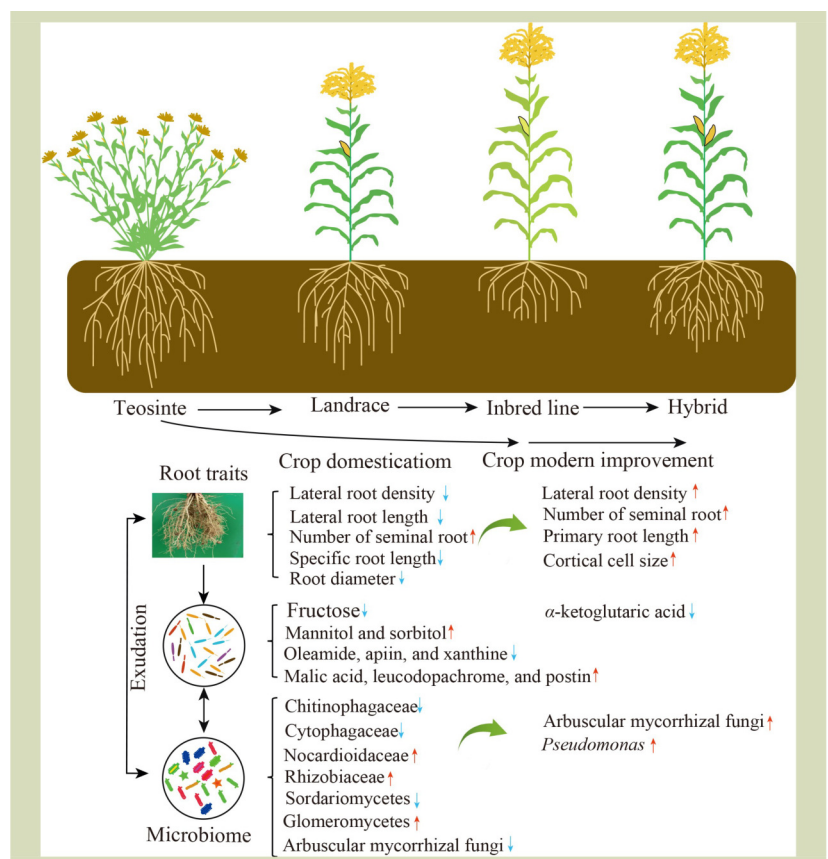
KEYWORDS

Crop domestication, heterosis, microbiome, root development, exploitation strategy

HIGHLIGHTS

- Crop domestication decreased crop genetic diversity while increasing the complexity of root traits and simplifying the structure and function of their microbiome.
- Modern crops have a great genetic potential for manipulating root traits and associated functional microbiome communities.
- Exploitation of crop domestication strengthens future crop root systems and microbiome resilience.

GRAPHICAL ABSTRACT



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ABSTRACT

Beneficial root-microbiome interactions offer enormous potential to improve crop performance and stress tolerance. Domestication and improvement reduced the genetic diversity of crops and reshaped their phenotypic traits and

their associated microbiome structure and function. However, understanding of the genetic and physiological mechanisms how domestication and improvement modulated root function, microbiome assembly and even co-selective patterns remains largely elusive. This review summarizes the current status of how crop domestication and improvement (heterosis) affected root characteristics and their associated microbiome structure and function. Also, it assesses potential mechanisms how crop domestication and improvement reshaped root-microbiome association through gene regulation, root structure and function and root exudate features. A hypothetical strategy is proposed that entangles crop genetics and abiotic interactions with beneficial microbiomes to mitigate the effects of global climate change on crop performance. A comprehensive understanding of the role of crop domestication and improvement in root-associated microbiome interaction will advance future breeding efforts and agricultural management.

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1 Introduction

Microbes growing on plant surfaces and tissues are critical for plant growth, development, adaptation and diversification^[1–3]. As expected, the genetic background of plants modulates the composition and diversity of microbial communities^[4–7]. In turn, beneficial root-associated microbiome interactions can adjust plant performance to cope with abiotic stresses^[3,8–11]. Crop domestication and improvement led to markedly increased productivity in modern agricultural systems^[12], while at the same time the genetic diversity has been significantly reduced by direct and indirect selection during these processes compared to their wild ancestors^[13]. Consequently, crop domestication and improvement likely had an adverse impact on the composition and function of the associated microbiota^[14–18]. Thus crops will be selective for soil microbiomes present in modern agricultural systems^[19]. Recent studies have found that root exudates are pivotal for the selection of microbial communities that colonized the rhizosphere during wheat domestication^[14]. The selective pressure for favorable root metabolism and rhizosphere microbiome composition might provide opportunities to improve crop performance under abiotic stresses^[10]. Increasing evidence has revealed that microbiome heritability has the potential to understand crop eco-evolution and the associated microbiome structure and function, thus contributing to improve agricultural productivity and sustainability^[11,20,21]. For example, a recent study indicated that Oxalobacteraceae have a significantly higher heritability compared to other families in low-nitrogen soil, thus improving maize lateral root development and nutrient use

efficiency^[11]. Extensive studies have revealed that crop domestication and improvement can influence root development and the structure and function of the root-associated microbiome^[14,16–18]. However, the lack of a mechanistic understanding of microbiome heredity is the primary obstacle to apply beneficial microbiomes to crop breeding. While it is relatively straightforward to compare microbial communities associated with different crop genotypes, understanding the domestication and improvement of these communities is inherently complex. The structure and function of microbial communities are influenced by a multitude of factors, including crop genetic traits and varying environmental conditions^[3,8,11,20]. Therefore, to accurately interpret the conclusions presented in this review, it is crucial to consider the specific conditions under which these observations were made. This includes acknowledging the dynamic nature of microbial communities and how they can shift in response to genetic and environmental changes. In this review, we summarized current advances in how crop domestication and improvement alter root development and associated microbiome interactions. Moreover, we discuss how functional microbiome feedback affects root development. Finally, we propose a strategy how knowledge on crop genetics and domestication can be exploited to strengthen future crop root systems and how to transfer microbiome resilience to generate resilient crop cultivars. In addition, this review focuses primarily on the role of the bacterial and fungal components of the microbiome during crop domestication and improvement. Other microorganisms such as archaea, viruses and protists, though significant, fall outside the scope of this review.

2 Crop domestication shapes root-associated microbiome interaction

2.1 Impact of domestication on microbiome structure and function

Crop domestication reduced the genetic diversity of crop species compared to their wild ancestors^[13], altering the associated microbiome diversity and community composition (Fig. 1, Table 1)^[6,14,16–18]. For example, from wild ancestors to landraces to modern common bean cultivars, the relative abundance of Chitinophagaceae and Cytophagaceae in the rhizosphere gradually decreased, while Nocardioidaceae and Rhizobiaceae gradually increased. The alteration in microbiome composition influenced the specific root length and nodule development of the common bean cultivars^[6]. In general, modern crops tend to have less beneficial associations with the microbiome^[14,16–18]. In maize, the beta diversity of prokaryotes and fungi in rhizosphere communities gradually decreases along the maize evolutionary lineage from teosinte via

landraces to modern maize^[16]. Several studies indicated that the maize wild ancestor teosinte had the potential to recruit a significantly different functional microbiota compared to other genetic groups (landraces and modern inbred lines)^[17,34]. For example, nitrogen-acetylglucosaminidase activity of teosinte significantly differs from maize cultivars (sweet corn and popcorn) in the rhizosphere^[34]. More recently, it was demonstrated that wild wheat accessions had dominant microbial taxa related to nutrient transformation and acquisition compared to wheat cultivars^[14]. Consistently, fewer nitrogen-related bacteria under sufficient nitrogen conditions were supported in elite maize germplasm^[4]. A recent study investigating rice domestication demonstrated that modern cultivated rice displays decreased in arbuscular mycorrhizal symbiosis compared to wild rice genotypes, which influenced mycorrhizal phosphorus acquisition^[26]. Moreover, an experiment on arbuscular mycorrhizal symbiosis of 27 crop species indicated that wild progenitors were able to more beneficially interact with arbuscular mycorrhizal symbiosis compared to domesticated crops, regardless of soil phosphate availability^[28].

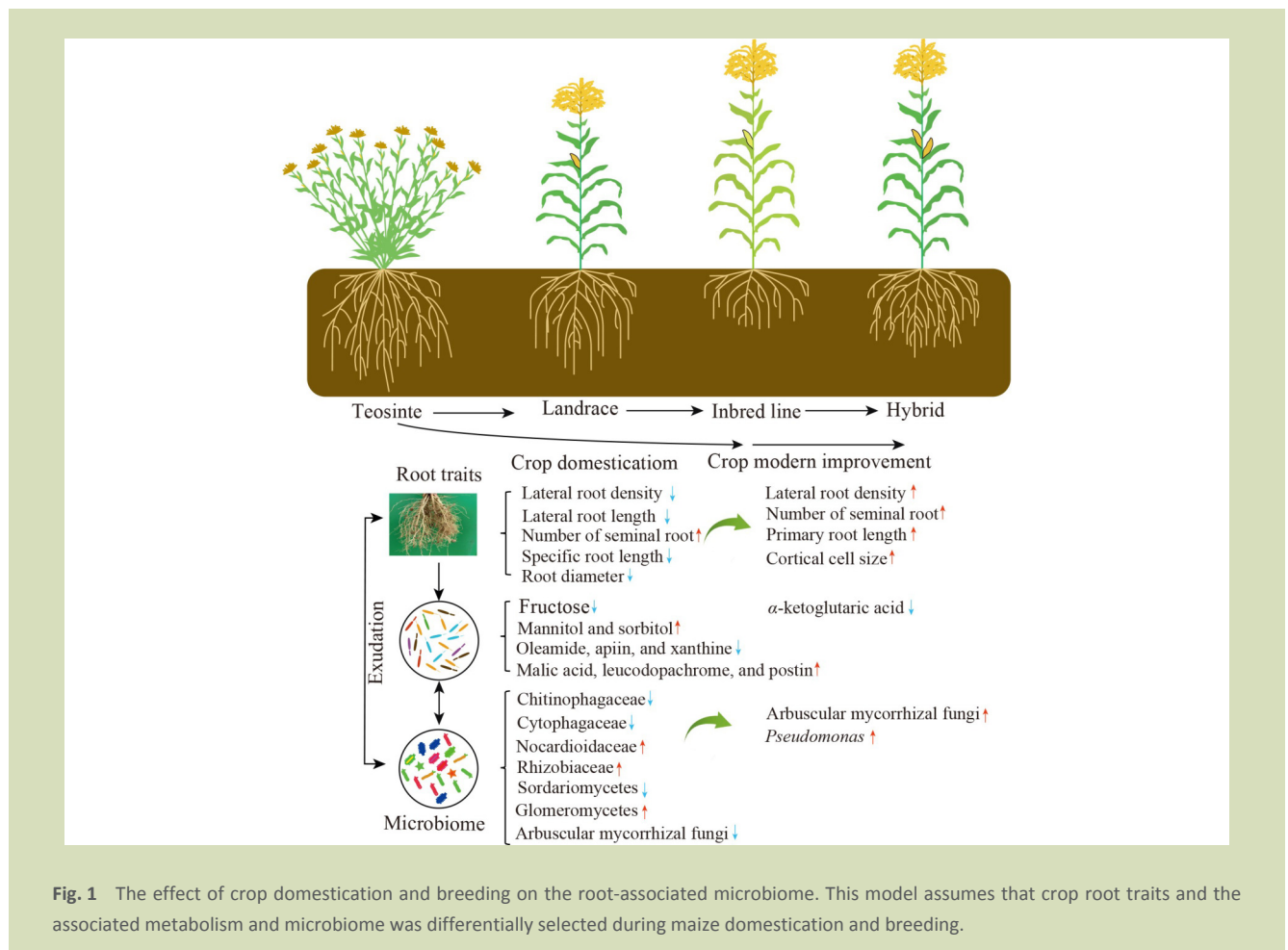


Table 1 Changes of root traits and their associated microbiome structure and function during crop domestication and breeding

Evolutionary transect	Crop species	Root development	Microbiome structure and function	Reference
Domestication (from wild relatives to domesticated)	Maize	Increased seminal root number		[22–24]
	Maize	Reduced lateral root density; Reduced root hair length; Reduced root diameter		[25]
	Maize	Increased specific root length; Reduced mean root diameter	Depleted arbuscular mycorrhizal fungi	[26,27]
	Bean		Enriched Nocardioideaceae and Rhizobiaceae; Depleted Chitinophagaceae and Cytophagaceae	[6]
	Wheat		Enriched Glomeromycetes; Depleted Sordariomycetes	[28]
	Rice	Reduced root volume; Reduced crown root length; Reduced lateral root length	Depleted arbuscular mycorrhizal fungi	[26]
Improvement (from inbred to hybrid)	Maize	Increased seminal root number; Increased lateral root density; Increased primary root length; Increased cortical cell size		[12,29,30]
	Wheat	Increased total root length; Increased longest root length; Increased root surface area; Increased averaged diameter; Increased root volume; Increased root tip number		[31]
	Maize	Increased seminal root number		[22]
	Maize		Enriched <i>Pseudomonas</i>	[32]
	Maize		Enriched arbuscular mycorrhizal fungi	[33]

Crop domestication does not only influence plant nutrient acquisition but also alters plant immunity. For example, domesticated wheat is able to support more Glomeromycetes (plant symbionts) rather than Sordariomycetes (fungal plant pathogens) in the rhizosphere compared to wild wheat^[35]. These results reveal that crop domestication influences functional profiles of the associated microbiome^[14,16]. Nevertheless, converse findings have been reported for other crop species^[22,36]. Elite barley cultivars have more Actinobacteria in their rhizospheres, which is adaptive for arid environments, compared to wild barley^[36]. Also, modern sunflower lines had a lower relative abundance of putative fungal pathogens than wild and native American sunflower (*Helianthus*) lines^[22]. These results indicate that several host traits may be supplemented by beneficial microbial traits and thereby improved resistance to adapt to local environments during crop domestication. However, systemic studies are required to understand whether and how divergent domestication processes result in convergent selection of microbiome features that confer beneficial functions to the host.

2.2 Impact of domestication on root development

During crop domestication, genetic diversity decreased from wild ancestors to modern cultivars^[13], which substantially influenced root system architecture (Fig. 1, Table 1). Recent investigations in maize have demonstrated that seminal root number increased during maize domestication^[23]. Similarly, fewer seminal roots were observed in teosinte compared to early landraces^[24]. Archaeological records also supported the notion that maize domestication resulted in increased seminal root formation^[37]. Subsequently, the increased seminal root number acquired during maize domestication decreased when modern maize was adapted to limited water availability^[23]. Moreover, several experiments demonstrated that wild crop ancestors had a greater number of narrower, shorter, more branched nodal roots compared to modern cultivars^[24,37]. As main root characteristics, higher lateral root density, increased root hair length and a larger root diameter were observed in wild ancestors of different crops^[25,38], resulting in a larger root system and improved abiotic stress tolerance^[27]. In a greenhouse experiment, maize landraces had an increased specific root length, while a smaller mean root diameter and reduced root colonization by arbuscular mycorrhizal fungi

were observed compared to modern temperate maize cultivars^[39]. In addition, anatomical features were affected during crop domestication^[24,37]. Compared to the wild maize ancestor teosinte, landraces had a larger mean xylem and stele area^[24]. These changes in root anatomical and architectural features during crop domestication reflect the adaptation to local environmental stress^[11,23,24]. These domesticated and adapted root functional properties might have had a selective role in the composition and colonization of beneficial microbiomes, thus representing a reciprocal interaction with the host plants. Nevertheless, future work needs to consider the potential legacy effect of root trait formation and how this affects microbiome structure and function.

2.3 Potential mechanisms how domestication impacts microbiome structure and function

Natural and artificial selection controlling metabolic, morphological and agronomic traits are conservative, leading to the recruitment of specific functional microbiomes to adapt to distinct environmental conditions. For example, the maize domestication gene *teosinte branched1* increased crown root numbers and lateral root density, while it reduced the average lateral root length compared to wild type plants^[38]. Root development affected by crop domestication is associated with microbiome structure and function. For example, root length was positively correlated with the fungal genera *Holtermanniella* in domesticated wheat and *Microdochium* in wild wheat^[14]. Those changes of root traits are thus functionally linked with root metabolism and microbiome assembly (Fig. 1, Table 1)^[14,34,40]. In addition to root traits, root exudates are would also be expected to be selected during domestication^[14,41], thus altering the diversity and composition of the root-associated microbiome^[14]. For example, it has been demonstrated that alkaloids, terpenoids and lipids are major differential metabolites in the exudates of teosinte and tropical maize^[41]. A study in wheat primary (from wild emmer to domesticated primitive emmer) and secondary (from domesticated primitive emmer to durum landraces or modern cultivars) domestication indicated that plant defense metabolites, antioxidants, plant hormones and proteinogenic amino acids significantly increased in kernels from wild lines to modern cultivars^[42]. Similar observations of different patterns of metabolites (i.e., fructose, mannitol and sorbitol) in the rhizosphere in response to different soil types were reported during wheat domestication from wild emmer to emmer to durum wheat^[29]. Changes of root exudate during domestication have great potential to influence the root-associated microbiome in the rhizosphere and endosphere (Fig. 1, Table 1)^[14,40]. Functional diversity of crop root traits

regulated by domestication genes influence the composition of root exudates, thus contributing to beneficial root-associated microbiome interactions adaptive for abiotic stress.

3 Modern crop improvement (heterosis) shapes root-associated microbiome interactions

3.1 Impact of heterosis on microbiome structure and function

Heterosis refers to the phenomenon that hybrids perform better than the average of their inbred parents^[12,43–45] and is likely the collective effect of plant genetics and root-associated microbiomes (Fig. 1, Table 1)^[21,30,32,33,46–50]. Recent literature has shown that heterosis is reflected in crop performance but also in microbiome assembly^[21,47–50]. Recent work has revealed significant differences in microbiome compositions in maize leaves and rhizosphere between hybrids and their parents under field conditions^[21]. Another field study indicated that the maize hybrid L3 × L22 had a higher alpha diversity of bacteria in roots and fungi in the rhizosphere compared to its parental inbred lines^[50]. A pot soil experiment in rice found that rice F₁-offspring had a larger number of endophytic fungi in roots after crossbreeding^[49]. Also, soil microbial communities strongly influenced heterosis of root biomass and other plant traits in maize^[21]. Recent work with rice demonstrated that the rice hybrid LYP9 had improved tolerance to *Fusarium oxysporum* compared to the parental lines mediated by root-associated bacterial communities which affect reactive oxygen species metabolism and cell wall biogenesis^[47]. Another study provided physiological evidence that maize hybrids had increased *Pseudomonas* colonization in their roots through auxin enrichment in the rhizosphere^[30]. Those results indicate that modern hybrid breeding can directly influence root-associated microbiome structure and function and show a trend for crop hybrids to favor plant growth-promoting microbiomes, which can improve crop health and growth (Fig. 1, Table 1).

3.2 Impact of heterosis on root development

Comparisons of hybrids and their parental inbred lines revealed differences in gene expression, root development and nutrient absorption^[12]. These architectural and functional differences have the potential to shape the microbiome composition in the rhizosphere (Fig. 1, Table 1). Root phenotypic changes are the result of direct and indirect

selection during hybrid breeding as observed in maize^[31,43], wheat^[51,52] and rice^[53]. In maize, hybrids have more seminal roots, increased lateral root density, longer primary roots and larger cortical cell size compared to their parental inbred lines^[12], thus providing great potential to influence root metabolism and the associated microbial colonization and function. Seedlings of modern maize hybrids display a high degree of heterosis^[54]. Of the root traits, lateral root density displayed the highest midparent heterosis^[54], indicating that lateral roots might be the strongest driver of root-associated microbiome interactions during maize heterosis. These results indicate that heterosis-dependent root traits have the potential to enhance the association with the rhizosphere microbiome and consequently improve abiotic stress tolerance.

3.3 Potential mechanisms by which heterosis impacts microbiome structure and function

Through heterosis, maize hybrids express more genes than their parents during primary root development^[12,43,45], indicating that more dominant genes are related to root traits and root exudates in hybrids compared to their parents. For example, it was reported that α -ketoglutaric acid occurred in the rhizosphere of the inbred lines (Lo1016 and Lo964) but not in their hybrid, indicating that heterosis drives differential metabolic compositions^[55] and has the potential to influence microbiome structure and function in the rhizosphere (Fig. 1, Table 1). Several possible explanations for heterosis have been reported in distinct crop species^[30,32,46,47]. Maize hybrids tend to have more beneficial microbiomes (*Pseudomonas* and arbuscular mycorrhizal fungi) in their rhizosphere than their parental inbred lines^[32,33], which is posited to improve root development and nutrient utilization. Recent research in rice has revealed that *Pseudomonas* is significantly enriched in hybrid rice seeds compared to their parents and was associated with improved seed germination and root development^[46]. Another study in rice demonstrated that rice hybrids have enriched beneficial root microbiomes that protect against fungal pathogens (e.g., *Fusarium oxysporum*)^[47]. These observations indicate that crop hybrids can have a favorable balance between plant growth and fitness that contributes to heterosis. However, to date, no potential unifying molecular and physiological mechanism has been revealed to explain the role of the microbiome in heterosis.

4 Exploitation of beneficial microbiome communities in crop breeding

Modern crop breeding and agronomy have altered the

interactions between roots and their associated microbiome^[4]. For example, high nutrient input for crop production purposes has decreased the functional selection for soil microbiomes related to nutrient acquisition during crop breeding^[4]. Numerous lines of evidence have demonstrated that wild crop ancestors are genetically more diverse with functional genes, exudates and microbiomes controlling favorable dominant phenotypical traits (Fig. 2)^[14,16–18]. Additionally, traditional crop landraces selected from diverse ecological systems resulted in heritable variations to adapt to local growth environments^[56]. This provides the potential to recruit functional microbiomes to cope with abiotic stresses^[11,57]. For example, a maize landrace grown in a low-nitrogen soil in Mexico had a complex nitrogen-fixing microbiome associated with secretions of carbohydrate-enriched mucilage from aerial roots with this hologenotype well adapted to its nitrogen-depleted environment^[57]. However, it remains difficult to restore favorable traits lost during crop domestication, such as genes or root phenotypic and metabolic characteristics, but microbial traits of progenitors and older cultivars could be helpful for the development of new, stress-resilient cultivars to cope with global climate change. Relevant to this, it has been reported that the maize domestication gene *Teosinte branched 1* can regulate lateral root development^[38], which illustrates the potential of plant genetics to influence microbiome structure and function in the root and rhizosphere. Reintroduction of alleles coding for beneficial functional genes into elite crop lines might boost favorable interactions between root development and its associated microbiome (Fig. 2)^[58,59]. One such gene could be *Colorless2-Inhibitor diffuse* that encodes a chalcone synthase influencing the release of flavones to the rhizosphere in low-nitrogen soil, which can modulate bacterial community composition in the rhizosphere^[2]. Recently, it was shown that a functional gene (*Zm00001d048945*), which controls lateral root development in association with *Massilia*, contributes to adaptation to nitrogen deprivation^[11]. It has been demonstrated that *Phosphate Transporter 1* genes are positively associated with arbuscular mycorrhiza in a range of cereal crop species^[60]. These examples highlight the need to exploit wild relatives and landraces of crop plants and their associated microbiomes to search for beneficial microbiome-related genes to improve crop productivity for greater agricultural sustainability^[11]. Taking advantage of root-microbiome interactions as a selection target for optimizing root system architecture in breeding will result in resilient crops adapted to global climate change.

5 Conclusions

Crop domestication and breeding from ancient progenitors to modern cultivars driven by the interplay of environment and

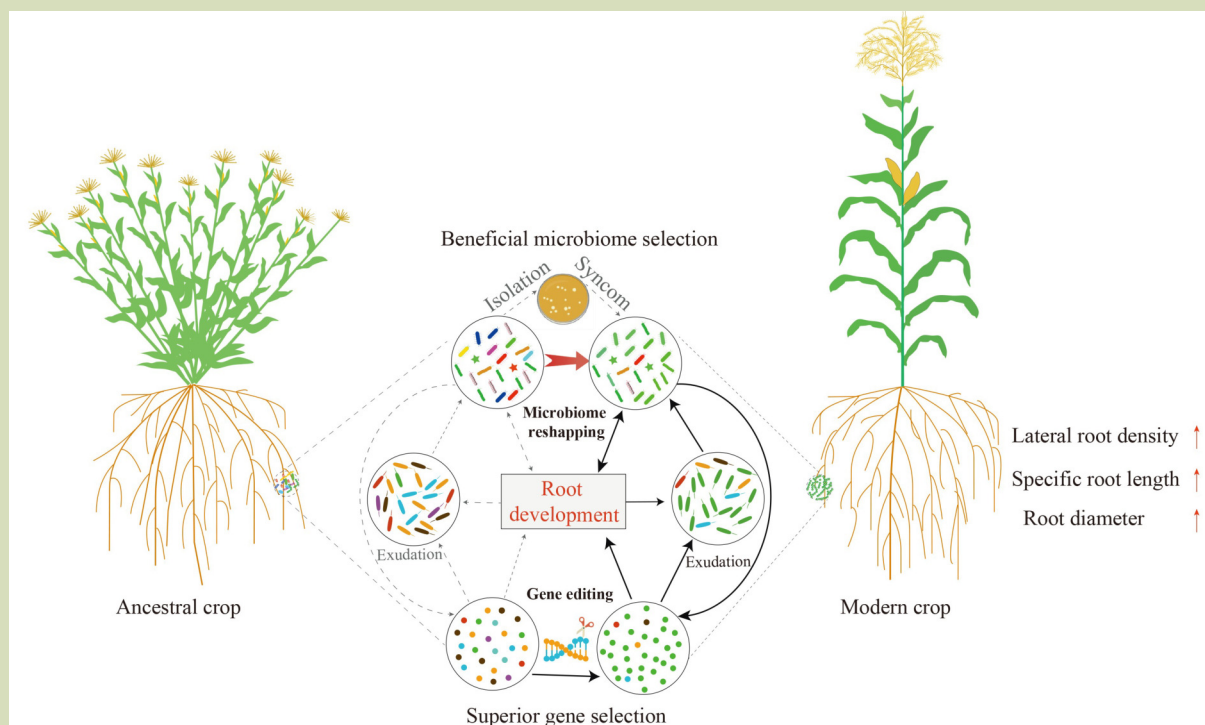


Fig. 2 Schematic illustration of the exploitation of beneficial microbiomes from ancestral crops to improve crop breeding. Targeted modification of the superior genes and beneficial microbiome to improve beneficial interactions among root development, root exudates and the rhizosphere microbiome.

human interventions has resulted in alterations on many levels from gene function and metabolism to root architecture and its associated microbiome. During this process, the structure and function of the microbiome tended to lose its ability to establish beneficial heritable and environment-adaptable interactions with the root system. Mechanistic studies focusing

on how crop domestication and breeding influence the adaptation and diversification of the root-associated microbiomes could contribute to the generation of environment-adapted cultivars. Further experiments are required to be able to exploit heritable beneficial microbiomes to adapt to abiotic stresses.

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Compliance with ethics guidelines

Xiaoming He, Frank Hochholdinger, Xinping Chen, and Peng Yu declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

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