



Impacts of the Green Revolution on Rhizosphere Microbiology Related to Nutrient Acquisition

Mary Dixon ^(D), Carley Rohrbaugh, Antisar Afkairin and Jorge Vivanco *

Department of Horticulture and Landscape Architecture, Colorado State University, Fort Collins, CO 80525, USA * Correspondence: j.vivanco@colostate.edu

Abstract: The Green Revolution (GR) involved selective breeding of cereals and the use of high fertilizer inputs with the goal of increasing crop yields to alleviate hunger. As a result of both greater use of inorganic fertilizers and the introduction of semi-dwarf cultivars, grain yield increased globally and hunger was alleviated in certain areas of the world. However, these changes in varietal selection and fertilization regimes have impacted soil fertility and the root-associated microbiome. Higher rates of inorganic fertilizer application resulted in reduced rhizosphere microbial diversity, while semi-dwarf varieties displayed a greater abundance of rhizosphere microbes associated with nitrogen utilization. Ultimately, selection for beneficial aboveground traits during the GR led to healthier belowground traits and nutrient uptake capabilities.

Keywords: Green Revolution; rhizosphere microbiome; wheat; rice; maize; sorghum; barley

1. Introduction

In the 1960s, intensive breeding efforts and agricultural practices aiming to increase yield resulted in the Green Revolution (GR). The GR was a technological revolution that was centered on the development of high-yielding, hybrid crops in conjunction with modern fertilization regimes [1]. Before the GR, synthetic fertilizers were not commercially available, and farmers often relied on organic amendments, such as compost and animal manure, to meet crop demand. Growers produced greater yield because of GR innovations, such as year-round production, increased cropping area, greater fertilizer use, use of chemical pesticides, and introduction of high yielding varieties [1,2]. Steady gains in cereal crop yield were a result of the interplay of improved varieties and heavy fertilization [2,3].

High yielding cereal crops developed during and after the GR have also been shown to be more responsive to nitrogen (N) and phosphorus (P) application as compared to traditional cultivars [1]. GR-era rice varieties necessitated greater applications of high-N fertilizer to enhance yield [4]. Mutant alleles used during the GR, including *sd1* and *Rht*, are associated with inhibited N uptake, which may explain the different fertilizer requirements among old and new varieties [5]. The *sd1* gene is the predominant dwarfing gene in rice and has been shown to be associated with a loss-of-function of a gibberellin20-oxidase (GA200x) gene (*Os200x2*) [6]. The enzyme GA20ox catalyzes gibberellin (GA) biosynthesis and shoot elongation, so deficiencies in GA would result in dwarfism, a feature that was of interest during the GR [7,8]. Similarly, *Rht* alleles in wheat were shown to express insensitivity to GA [9]. Because GA mediates the activity of nitrate transporters and N uptake [10], cultivars expressing GA suppression would have reduced N uptake capabilities. Thus, to accumulate greater yield, GR-era cultivars would have required greater fertilizer application.

With repeated application of high rates of chemical fertilizers, modern crops have become dependent on chemical fertilizers for healthy growth [11]. Further, high N application has led to N leaching, which causes eutrophication and reduced aquatic population abundance [12]. Therefore, one of the unintended consequences of the GR was the contamination of water systems with excess synthetic chemical fertilizers [13] that created biodiversity imbalances, such as the Red Tide of microscopic algae [14].



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When excessive synthetic fertilizers are applied to soils, imbalances are also created in soil microbial communities. At high rates of synthetic fertilizer application, soil microbial functionality and symbiosis are often reduced or are non-apparent [15]. For instance, at high rates of N fertilization, N-fixing bacteria were highly diminished when compared to unfertilized soils [16]. Similarly, addition of P fertilizers has been shown to decrease the abundance of P-solubilizing bacteria, including *Pseudomonas* and *Bacillus* [17]. These effects are important because soil microbes are essential to plant nutrient acquisition, and recent rhizosphere microbiome projects have revealed a complex network of other beneficial microbes that are involved in nutrient acquisition [18–20]. For example, phosphate solubilizing bacteria, such as Pseudomonas and Bacillus, exude hydrogen (H) ions, organic acids, and chelating agents to solubilize sparingly soluble forms of soil P [18]. Other beneficial bacteria facilitate N transfer, and in legumes, symbiosis can be formed with N-fixing rhizobia that transform atmospheric N to plant available forms in return for photosynthates [21]. Further, there are many beneficial fungi that form symbiosis with plants. Mycorrhizal fungi alter soil structure by creating aggregates and increasing the root surface area. These fungi facilitate uptake of essential nutrients, primarily P [22] and potassium (K) [23].

While disruption of plant-microbe associations is difficult to track, numerous studies highlighting changes in the abundance or function of soil bacteria across a domestication gradient have indicated that modern crops interact differently with beneficial microbes in the soil compared to wild varieties and landraces [24–27]. Because crop domestication has led to a decrease in genetic diversity of cultivated compared to wild crops, the capability of establishing symbiosis between plants and beneficial microbes may have been negatively impacted at domestication [28]. Breeding efforts after crop domestication involved increasing yield, compacting growth, and reducing shattering [8]. GR breeding efforts have similarly focused on enhancing aboveground traits [29]. However, because belowground traits were not emphasized, disruption of microbial symbiosis may have occurred as a function of domestication and was further accentuated by the GR.

In this review, we delineate how the microbiology and function of beneficial microbes in the rhizosphere of staple crops has been impacted by the breeding efforts and fertilization practices of the GR. This review outlines these effects on staple crops heavily modified by the GR: wheat, rice, maize, sorghum, and barley.

2. Microbe Facilitated Nutrient Acquisition

Soil microbes cycle nutrients required to sustain plant growth, and many beneficial microbes mobilize essential elements from sparingly soluble soil sources through processes such as decomposing organic matter and dissolving precipitates [30,31]. Some soil microbes work symbiotically with plants by utilizing their root exudates [30]. Further, exuded labile carbon enhances microbial growth which, in turn, improves N acquisition [32].

Nitrogen acquisition is further enhanced through symbiosis with beneficial soil bacteria. Common soil bacterial phyla, including *Actinobacteria*, *Acidobacteria*, and *Bacteroidetes*, contain members capable of nitrification and ammonification [33]. Nitrogen conversion pathways present within soil microorganisms support plant nutrient assimilation by converting N from sparingly available to bioavailable forms [34]. Soil microbes also exude organic anions which solubilize P through ligand exchange and precipitate dissolving reactions. These reactions are invaluable to plant nutrient acquisition because P is limited in bioavailability due to processes such as fixation, immobilization, and sorption which result in an accumulation of sparingly soluble P sources in the soil. High concentrations of soil K are similarly stored in sparingly available pools that can be exploited by soil bacteria [35]. Many soil bacteria are capable of solubilizing K, and some genera can solubilize up to 175 mg/L K [32,35]. Because of their ability to solubilize essential nutrients from sparingly soluble sources, some beneficial soil microbes reduce the need of synthetic fertilizers. However, because a marker of the GR was increased fertilizer application, those plant-microbe interactions may have been impacted in newer cultivars.

3. Influence of the Green Revolution on the Rhizosphere Microbiome of Staple Crops *3.1. Wheat*

Wheat is a longstanding component of global agriculture. Wild wheat [(*Triticum turgidum* ssp. *dicoccoides*) (Körn. ex Asch. & Graebner) Thell.] appeared in the Fertile Cresent approximately 500,000 years ago, and early forms of domesticated wheat (*T. turgidum* ssp. *dicoccum* Schrank ex Schübl) were cultivated over 10,000 years ago [36]. Traits modified by farmers during early wheat cultivation included development of a non-brittle rachis, presence of a naked grain, and increased grain size [36]. The GR later introduced new plant breeding goals for wheat varieties. The International Maize and Wheat Improvement Center (CIMMYT) was established to improve bread (*T. aestivum*) and durum (*T. durum* Desf.) wheat varieties during the GR in the mid-1900s. The germplasm developed by the CIMMYT showcased semi-dwarfism, photoperiod insensitivity, and increased grain yield [37,38].

Belowground traits have also been indirectly impacted by domestication and the GR. Domestication and GR breeding efforts have, for instance, influenced the root exudate profile of wheat and the resultant microbial composition in the rhizosphere. Wheat root exudates have been shown to differ in composition across a domestication gradient between modern durum wheat, a primitive domestic wheat, and a wild wheat relative [39]. Similarly, rhizosphere bacterial communities from modern (semi-dwarf) cultivars have been shown to be different from traditional (tall) cultivars [26]. Tall varieties not only expressed a greater level of connectedness when compared to semi-dwarf varieties, but also tall and semi-dwarf varieties showed different relative phylum abundances. Modern, semi-dwarf varieties had a greater proportion of *Verrucomicrobia*, *Acidobacteria*, and *Planctomycetes* in the rhizosphere than traditional, tall varieties [26]. These bacterial groups are common in soil environments, and many members of *Verrucomicrobia* and *Acidobacteria* have been shown to move toward and proliferate on root-released exudates [40]. Sources of nutrients unavailable to plants, such as hydrolysable N, are transformed by these rhizosphere bacterial taxa and are then taken up by the plant root [41].

The higher proportion of beneficial microbes in the rhizosphere of modern wheat may also be a result of root architecture. Modern wheat root systems have a larger proportion of fine roots than ancestral wheat [42], and the presence and length of fine roots has been shown to influce rhizosphere bacterial community structure in plants, such as moso bamboo (*Phyllostachys edulis*) [43] and peach (*Prunus persica*) [44]. Similarly, the Rht-B1 allele present in modern wheat has been shown to be correllated to an increase in the longest root length and total root length of wheat root systems [45]. However, although the dwarfing gene has been linked to increasing root length [45], modern wheat root systems are more shallow than ancestral wheat [42,46]. Although Rht gene may partially modulate root growth, wheat roots may also be undergoing topsoil foraging in modern agroecosystems. The differing depths of root systems in modern and ancestral wheat may relate to more competitive resource acquisition efficiency of modern cultivars because the shallow soil hoizons are associated with nutrient-rich topsoil [42,47].

The competitive performance of modern wheat varieties is also a result of dramatic changes to commercial wheat production practices, including higher inorganic-N fertilizer use and monoculture cropping systems. These changes in fertilization and production may have influenced the wheat rhizobiome. Increasing inorganic N fertilization has been shown to destabilize bacterial community structure in the rhizosphere of wheat [48]. Reductions in bacterial abundance and diversity have lasting impacts on soil health. Soil microbial community diversity is a predictor of soil health because of the ability of these bacteria to both form beneficial relationships with plant systems and to serve as bioindicators for soil ecosystems [49]. Increasing levels of inorganic N fertilization led to a reduction in soil bacterial richness and diversity, including *Acidobacteria* and *Planctomycetes* members [50], which may therefore impact soil health. However, at tillering, the abundance of *Actinobacteria* and *Proteobacteria* members increased. This change in abundance can be explained by

wheat root exudation; organic acid exudation may have resulted in recruitment of microbes adapted to high N conditions [51].

3.2. Rice

Asian rice (*Oryza sativa* L.) is one of the most globally important food crops [52,53]. During domestication from two subpopulations (Or-I and Or-II) of the wild progenitor, *O. rufipogon*, two major subspecies (*O. sativa* ssp. japonica and *O. sativa* ssp. indica) developed [53]. Compared to wild rice, modern Asian cultivars have larger seeds, stronger determinate growth, stronger apical dominance, and non-shattering seeds [53]. Although rice is one of the most protected crops globally, production has dramatically increased beginning with the GR [52]. Increased rice production following the GR is attributed to GR-era farming technologies and development of elite cultivars that are semi-dwarf and early maturing [52].

The higher performing rice varieties developed during the GR were semi-dwarf and resistant to lodging, traits regulated by the *sd-1* gene [54]. The *sd-1* semi-dwarfing gene encodes the enzyme GA20ox, which catalyzes GA biosynthesis [54]. Varieties with the GA20Ox2 (*sd-1*) mutation inactivate synthesis of GA at the primary growth stage of rice, thus leading to smaller plant height [54,55]. Overexpression of GA20ox not only reduced plant height, but also increased adventitious root growth in rice [55]. Greater adventitious root growth alters soil structure and increases root exudation of phosphatases, siderophores, phytohormones, and organic acids. Exudation of these compounds because of adventitious root formation supports relationships with copiotrophic bacteria that proliferate in nutrient-rich soils [56,57]. The relative abundance of these bacteria may increase with N additions [57].

Adequate N fertilization rates increase the density, quality, and number of roots. With moderate increases in N fertilization, root senescence is delayed and total root absorption area increases [58]. Thicker roots have been associated with a greater abundance of Bacteroidetes in other crops [59]. Increased N fertilization has also been associated with increased exudation of compounds including sugars and phenolics in other cereal crops [51,60] (Figure 1). Exudates present in the rice rhizosphere are utilized by soil microbes. Because exudation patterns vary with genotype, the composition of the rhizosphere microbiome may also vary with genotype. For example, Nitrosomonas spp. have been detected in greater abundance in the rhizosphere of modern rice when compared to traditional rice landraces [61] (Figure 1). *Nitrosomonas* spp. are nitrifiers and facilitate N cycling. Modern rice also showed a greater concentration of oxygen on the root surface, which may in part explain the greater abundance of *Nitrosomonas* spp. [61]. In the rhizosphere of rice, there is often an abundance of Proteobacteria and Acidobacteria. However, the diversity of bacteria in the rhizosphere of wild, traditional, and modern cultivars of rice vary. Alpha diversity was found to be lowest in the rhizosphere of wild rice, moderate in the rhizosphere of traditional rice, and highest in the rhizosphere of modern rice [62]. In landraces developed prior to the GR, there was greater relative abundance of methanotrophs in the rhizosphere [62]. However, pre-GR varieties have higher methane (CH₄) fluxes and emissions when compared to post-GR cultivars [63]. This genotypic variation in CH_4 cycling may help explain the differing abundances of rhizosphere methanotrophs between traditional and modern rice.

3.3. Maize

The domestication of maize (*Zea mays* L.) from wild teosinte (*Z. mays* subsp. parviglumis) occurred 9000 years ago in Mexico [64]. There are many morphological differences in modern maize compared to teosinte. The principal distinctions between modern and wild maize are that modern maize has paired spikelets, is polystichous, has a non-disarticulating rachis, has soft glumes, and has reduced axillary branching [65]. Mutations in single genes can result in major morphological changes, and the teosinte glume architecture (tga1) gene in maize exemplifies a gene that can account for differences present in modern compared

to wild maize [66]. The tga1 gene regulates whether maize kernels are hardened or naked and may also be involved in glume lignification [66]. The phenotypic changes brought about by this gene and other genes allowed for the commercial production of maize on a global scale. Since adoption of hybrid maize varieties in the 1930s, yields have dramatically increased [67]. Initially, there was low adoption of high-performing varieties of hybrid maize by small farmers, but high yielding varieties were ultimately developed and disseminated [67,68]. The efforts by this foundation to establish high-yielding germplasm coincided with the onset of the GR [68]. In the latter half of the 20th century, maize production doubled in Asia because of adoption of both improved varieties and greater fertilizer inputs [69].



Figure 1. Differences in rice before and after the Green Revolution (GR). The left image represents rice developed before the GR and the right image rice developed after the GR. GR-era breeding and agricultural practices resulted in semi-dwarf cultivars (**A**), geater adventitious root growth (**B**), and greater root density (**C**). Introgression of the semi-dwarfing gene in GR era rice resulted in higher sugar exudation (**D**) and greater bacterial diversity (**E**) in the rhizosphere.

During the post-GR period, overarching maize breeding goals included reducing the vegetation period and increasing grain yield [70]. However, because of selection for varieties with high quality aboveground traits, belowground traits have also been influenced. Cytokinin dehydrogenase (CKX) exemplifies this change. The ZmCKX5 gene, a member of the cytokinin gene family, was found to be expressed greater in inbred lines when compared to teosintes and landraces [71,72]. This gene is positively associated with root length and total root area [72], which impacts the soil microbiome (Figure 2). Root architectural changes impact root exudates and cause formation of microhabitats in the rhizosphere [56]. These microhabitats establish different ecological niches that allow diverse microbial species to grow in the rhizosphere [56]. Thus, the rhizosphere microbiome of maize has changed over time [25]. A principal coordinate analysis (PCoA) showed microbiome composition of older maize varieties to be more tightly clustered together than modern varieties, indicating that the microbiome of older varieties have a greater degree of relatedness than modern varieties [25].



Figure 2. Maize root architectural changes because of the Green Revolution (GR). The left panel represents maize roots before the GR and the right panel represents maize roots after the GR. Because of higher nitrogen fertilization rates during the GR, symbiosis with diazotrophs (represented by orange triangles) was less in modern when compared to traditional cultivars (**A**). Maize cultivars developed after the GR maize showcased a lower degree of relatedness (same-colored circles represent related bacterial communities) in rhizosphere bacterial communities (**B**) likely because of more microhabitats being formed from the greater root length of modern varieties (**C**).

In addition to maize breeding goals since the GR, N fertilization rates have also changed. Inorganic N fertilizer rates have increased steadily since the early 1940s [73], a pattern that may have impacted soil health. Excess agrochemicals have been shown to deteriorate soil physical, chemical, and biological properties [74]. Beneficial members of *Pseudomonas* and *Bacillus*, for example, were shown to stimulate plant growth and promote nutrient uptake of maize in nutrient deficient soils [75]. Further, under conditions of high and continuous N fertilization, the mutualism with N-fixing diazotrophs became less efficient [25] (Figure 2). These diazotrophs express the nitrogenase nifH gene which catalyzes N fixation, and the abundance of this gene in the maize rhizosphere microbiome has decreased with time from 1949–1985 [25]. Thus, reliance on inorganic N fertilization may have weakened the ability of maize to recruit beneficial N-fixing diazotrophs.

3.4. Sorghum

After being initially domesticated in Africa, sorghum [*Sorghum bicolor* (L.) Moench] underwent major improvements for traits such as reduced shattering and increased grain width [76]. Further improvements were made during the GR. Similar to other cereal crops, semi-dwarfism was a significant breeding goal for sorghum during the GR [77], and development of semi-dwarf cultivars resulted in increased yield [78,79]. Since the 1950s, introgression of genes and development of methods to control plant height have been used in sorghum production [80]. The *dwf-1* dwarfing gene in sorghum has been mapped to a frameshift in GA200x and reduction of GA [81,82]. Suppression of GA200x reduced shoot growth, but because of the lower expression of GA receptors in roots, it had less impact on root growth [83] (Figure 3). This differing impact on root growth led to an increase in



root-to-shoot ratio, a trait that has been shown to be beneficial to growth in conditions with drought or nutrient deficiency [83,84].

Figure 3. Effect of Green Revolution (GR) genes, *dwf-1* and *sdw-1* on gibberellin (GA) biosynthesis. The *dwf-1* gene that was bred into modern sorghum suppresses GA20ox, an enzyme that is responsible for GA biosynthesis. Thus, modern sorghum varieties showcase reduced shoot growth and increased root-to-shoot ratios. Similarly, the *sdw-1* gene that was bred into modern barley results in a loss-of-function of GA20ox. The resultant deficiency of GA in sorghum and barley results in the develop of semi-dwarf cultivars [55,81,85–89].

Although the development and release of N-efficient, high-yielding sorghum was widely adopted in sorghum-growing regions, the practice of applying high rates of inorganic fertilizer was not [90]. Sorghum fertilizer application has been below recommended rates both before and after the GR, but during the 1990s, micro-dose fertilization was developed. This fertilization practice allowed for growers to apply small amounts of N fertilizer at little cost and highly promoted sorghum production [91]. High rates of chemical fertilization have been shown to decrease the diversity of soil bacteria and fungi [92], and because micro-dosing fertilization avoids high rates of chemical fertilizer than other GR-impacted cereal crops. However, because these effects on the soil microbiome and plant yield are a result of micro-dosing fertilization practices, they cannot be linked to the GR.

While soil microbial impacts cannot be directly linked to the GR, there have been experimental studies conducted on the differential effects of N fertilization on N-fixing bacterial assembly in the sorghum rhizosphere. The rate of N fertilization has been shown to be a predictor of the structure of N-fixing communities [93]. At higher rates of N fertilization, microbial expression of nifH was found to reduce in the rhizosphere when compared to low rates of fertilizer [94]. The nifH gene encodes the nitrogenase reductase subunit, the enzyme responsible for N fixation, and is therefore used as a marker gene for identification of N-fixing populations were higher [96]. Although the effect of fertilization on sorghum soil microbiology is not linked to the GR, the trend of N-fixing microbial community growth being inversely related to N fertilization is comparable to other cereal crops.

3.5. Barley

Unlike other cereal crops, barley (*Hordeum vulgare* L.) is morphologically similar to the wild progenitor, *H. spontaneum* C. Koch [97]. Barley domestication occurred 8000 BCE, and traits such as a non-brittle rachis and naked caryopsis were selected [98,99]. Further improvements were made during the GR in which photoperiod insensitivity and semi-dwarfism were emphasized. The *Ppd-H1* gene in barley is homologous to the wheat photoperiod insensitivity gene *PPD1* [100]. Development of this trait was important because it allowed barley to be cultivated in different altitudes while producing acceptable agronomic output [101]. Further, introduction of the semi-dwarfing gene, *sdw1*, led to greater barley production, especially for feed barley. The *sdw1* gene is an ortholog of the *sd1*

gene in rice. Barley *sdw1* mutants have a loss-of-function of GA200x, and would therefore result in reduced shoot lengtH (Figure 3). This gene results in higher yield, better lodging resistance, and more efficient N use from the environment [89,101].

Semi-dwarf barley has larger root system sizes than taller varieties of barley [102]. This change in root phenotype may impact the root and rhizosphere microbiome. Perez-Jaramillo et al. [59], for instance, identified that *Bacteroidetes* members were in greater abundance in roots with greater specific length than plants with smaller roots. Further, Albertyn et al. [103] found that the rhizosphere microbiome of wild barley compared to modern varieties of barley harbored more microbial community diversity. They found large communities of Proteobacteria that are associated with N fixation. Similarly, modern and traditional barley have been found to vary in their rhizosphere microbiome community composition. Modern varieties of barley have a higher abundance of *Actinobacteria* than in landraces, and *Rhizobiaceae* and *Oxalobactereceae* have been found in higher abundance in the rhizosphere of modern varieties [104].

4. Conclusions

The GR brought about changes in agronomic outputs of staple crops including wheat, rice, maize, sorghum, and barley. Because of both introgression of genes from wild germplasm and selection of beneficial aboveground traits, post-GR revolution cultivars have healthy root systems that can establish high diversity of rhizosphere microbes [56,62]. The GR increased food production because of development of high-yielding cultivars and efficient farming technologies, and high fertilization regimes [1].

Although the GR resulted in high-yielding varieties, it also necessitated greater fertilizer use. Excessive use of inorganic chemical fertilizers disrupts soil health and reduces the efficiency of natural symbiosis with N-fixing diazotrophs and P-solubilizing microbes [24,25,74]. Further, mineral reserves of fertilizer resources, especially P, are finite and have an unequal global geographic distribution that have led, in part, to high fertilizer prices [105,106]. Thus, there is still a need to enhance nutrient use efficiency in agroecosystems. Strategies that emphasize enhancing soil health while reducing reliance of inorganic fertilizers may be beneficial. Use of organic amendments, such as biochar and manure, reduce N loss from soil while also increasing soil microbial biomass pools [107,108]. Therefore, incorporating use of these organic amendments may help growers optimize the benefits of the high yielding GR varieties while ameliorating some of the negative effects of high inorganic fertilizer applications. Finally, developing new varieties with enhanced abilities to promote beneficial microbial symbiosis in the rhizosphere will further enhance these sustainability goals.

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