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MINIREVIEW

Gut and Root Microbiota Commonalities

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Animal guts and plant roots have absorption roles for nutrient uptake and converge in harboring large, complex, and dynamic groups of microbes that participate in degradation or modification of nutrients and other substances. Gut and root bacteria regulate host gene expression, provide metabolic capabilities, essential nutrients, and protection against pathogens, and seem to share evolutionary trends.

Guts and roots are inhabited by many different bacteria (1–5), archaea (6–12), and viruses (13–16), as well as by eukaryotes (17–20), with some of them containing bacteria of their own (21–24). Variations in gut microbiota respond to age (25–28), diet (29–31), or species (32). Most insects have dozens of microbial species in their guts, while mammalian guts may contain thousands. Herbivores exhibit the largest diversity (32, 33), including probably plant-associated bacteria, especially endophytes (34) that, by being inside plant tissues, may survive stomach digestion. Transiting diet-borne bacteria may contribute to gut metabolic capacities. Different soil types, moisture (35), plant genotypes (36), age (37), and root lysates, secretions, or exudates (38) are determinants of root microbiotas. Factors that determine root exudates, such as availability of inorganic nutrients, temperature, light intensity, O_2/CO_2 level, or root damage, may indirectly affect root microbiotas (39). The presence of pathogens induces changes in microbiota composition in roots and guts (40, 41).

Guts and roots have large surface areas, with microvilli and folds or root hairs in some parts. Both roots and guts are structured, nonhomogenous habitats with pH, nutrient, water, and oxygen differential levels or gradients. Gradients would favor colonization by distinct bacteria that are more successful in some root or gut regions. In consequence, the multiple microhabitats that exist in roots and guts contribute to high species richness (42, 43). Different conditions are found in the cecum and distal colon in humans, with cecal and colon microbiotas containing a larger proportion of facultative anaerobes (44). Colon mucosal folds exhibit particular bacteria adapted to colonic conditions and maybe to mucin degradation (45). Some insects have specialized structures in their gut, such as midgut sacs and tubular outgrowths called ceca or crypts, in which they harbor specific bacteria (46), and others with less-complex guts also have pH and oxygen gradients in their guts (47). A steep oxygen gradient including an anaerobic root environment in water-saturated roots parallels the gut oxygen gradient and anaerobic gut systems. Clostridia, and especially members of the family *Ruminococcaceae*, are more prevalent than other anaerobes and methanogens, a trend which is similar in the different gut systems (48). These communities take care of the degradation of the complex organic matter in the outer root layers. Some gut and root acid-tolerant bacteria can modify their environment by lowering the pH when producing diverse acids (49, 50). Along the roots, there are physiological differences, and their exudates are secreted differentially at the apical meristem, root cap, or root hairs (42), creating different microhabitats. A single *Burkholderia* strain colonizes only discrete root regions (51), and different burkholderias were found at different soil depths (37).

"*Arabidopsis thaliana* root microbiome might assemble by core ecological principles similar to those shaping the mammalian microbiome in which core phylum level enterotypes provide broad metabolic potential combined with modest levels of host genotype-dependent associations" (35). Metacommunity theory may be applied to root microbiotas, as has been used to explain the assembly of the gut microbial community (52). Metacommunity theory is based on the concept of discontinuous patches and interactions that can satisfactorily describe bacterial patchy colonization of roots. Future applications of these concepts will assert their usefulness.

Remarkably, there are individual-to-individual variations in bacterial composition of the gut (2, 53) and roots (54). Individual differences may be due to genetic differences and stochastic colonization processes (52). Limited patterns (enterotypes) in relation to stratified variation were distinguished in human and insect gut microbiotas (2, 55); however, it is controversial if there are only a few enterotypes in humans or gradients of diversity (28). In plants, similar bacterial genera are recurrently isolated from rhizospheres (soil surrounding roots affected by plants) or roots (34, 56). In roots, *Rhizobium* strain diversity with functional differentiation is high (57). Strain variability in vitamin production has been detected among gut bifidobacteria (reviewed in reference 58). Similarly, lactobacilli (reviewed in reference 59) are a heterogeneous group of bacteria with partly probiotic character which have considerable variation in terms of molecular characteristics and preferred natural habitats.

With few exceptions (see below), the gut microbiota is different from that of other host organs, and similarly, the root microbiota shares only some bacteria with those of other plant organs.

ENVIRONMENTAL AND MATERNAL ACQUISITION

Root and gut microorganisms are usually acquired from the environment. Roots are colonized by bulk soil microorganisms at-

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tracted by chemotaxis and enriched by nutrients secreted by the roots in the rhizosphere. Animals also acquire their gut microbiota from their environment after they are born (60). In a few cases, microorganisms can be transferred vertically from mother to progenies. Endophytes present in plant seeds may subsequently colonize the roots and the rhizosphere. *Enterobacter asburiae*, found in maize kernels, is able to exit the roots and colonize the rhizosphere after the plant has established (61). Other seed bacteria do the same (54, 62). Animals can also acquire their gut microbiota from their mothers after being born, but there are cases of paternal transmission of symbionts, as in malaria vectors (63). Maternal transmission may occur before birth (64–66). When mammals are breast-fed, they acquire microorganisms that are present in the milk or on the mother's skin (67–69). Some stinkbug larvae acquire their mother's gut bacteria from contaminated eggs, by coprophagy, or by capsule-mediated transmission just after they have hatched (46). In view of the vertical and environmental transmission of root and gut microbes, gnotobiotic animals or plants are needed to clearly evaluate the effects of selected strains on hosts.

FUNCTIONAL REDUNDANCY AND ROLE OF MINORITIES

It seems that different microbiota composition may lead to the same and stable function. This may apply to gut and root bacteria and has been found to be true in methanogenic reactors (70). Similar degrading capacities are found in different gut bacteria (reviewed in reference 71). In roots, many different bacterial genera and species produce hormones, auxins, cytokinins, or gibberellins (reviewed in references 56 and 72). Our research group found that riboflavin is produced and excreted by different strains from several species of *Methylobacterium*, *Rhizobium*, *Sinorhizobium*, and *Bacillus*, both in rice and alfalfa root exudates and in pure cultures in minimal medium (our unpublished data). *In vitro* excretion of riboflavin by a large diversity of bacteria, including *Chromobacterium violaceum* and *Pantoea agglomerans*, was reported earlier (73), and both riboflavin and lumichrome (which is derived from riboflavin) stimulate root respiration (74). Additionally, many different plant-associated bacteria inhibit pathogenic fungi or bacteria (reviewed in reference 56).

Minority species present in the microbiota may help cover some of the host-specific needs. Methanogens, methylotrophs, and nitrogen-fixing bacteria are minor components in guts and rhizospheres (11, 75–78); however, they have important ecological roles. In some roots and guts, nitrogen fixation provides nitrogen to plants (79) and insects (80–82).

GUT AND ROOT BACTERIA ENHANCE THE METABOLIC CAPACITIES OF THEIR HOSTS

It is remarkable that gut bacteria are rich in sugar hydrolases (83) and other catabolic genes, such as those for tannin (84), cholesterol (85), or mucin (gut glycosylated proteins) (86). Similarly, capacities to degrade polyphenols, polysaccharides, protocatechuate, and proteins and to solubilize phosphate and weather rocks (50, 54, 87, 88) are prevalent among different rhizospheric bacteria. Mimosine-degrading bacteria are found in mimosa plants that produce mimosine (89), and cows that have such bacteria in their rumen are capable of degrading it (90). Alginate-degrading bacteria are found in abalone and human guts of algae consumers in Japan (91). The outstanding degrading capacities of root bacteria are the basis of rhizoremediation of polluting substances (92, 93) and are also evidenced in medical drug transformation or degradation in the human gut (94–96). Interestingly, in bioremediation, the abilities of bacteria to degrade soil pollutants may be triggered by flavonoids (97).

Gut and rhizospheric bacteria produce vitamins as riboflavin, as stated above. Vitamin B_{12} is an exclusive product of prokaryotes (98), and it is produced by plant root and gut bacteria (99–102). Essential amino acids and vitamins B and K are produced by gut bacteria (reviewed in reference 58). An alcohol dehydrogenase from the commensal bacterium *Acetobacter pomorum* modulates *Drosophila* developmental and metabolic homeostasis via insulin signaling (103). While root bacteria produce plant hormones that have effects on plant growth (reviewed in reference 56), gut bacteria seem to regulate animal behavior (104, 105).

GUT AND ROOT MICROBIOTAS COMPETE WITH PATHOGENS

Gut and root microbiotas suppress pathogens (reviewed in references 56 and 106). The human control of root bacteria has been envisaged as a manner to promote plant growth and health with benefits to agriculture (93, 107). Bacterial inoculants in agriculture and forestry are considered equivalent to probiotics (beneficial microbes provided as supplements) for animal health. Probiotics stimulate host defense systems and the competitive exclusion of pathogens, as plant growth-promoting rhizobacteria do (108). Seeds may harbor a reservoir of probiotics for their seedlings (54, 109). Prebiotics are added nutrients used to stimulate desirable bacteria in humans (110). We may even speculate that prebiotics were invented by roots, as some substances from their exudates stimulate bacterial growth selectively (89, 111, 112).

For over one hundred years, inoculants have been provided to plants in agricultural fields with variable success. Recently, a large number of commercial products whose effects are not always desirable have appeared to promote plant growth. Similarly, an increased number of probiotics and prebiotics whose effects have not been completely evaluated in different human populations are coming to the market. Gut gene expression in response to probiotics varies from person to person (113). In many cases, clinical benefits have been obtained in patients with specific probiotic strains (114).

Experience with plants has shown that appropriate use and regulation of probiotics (inoculants) is difficult to achieve. Undesirable genetic characteristics, such as denitrifying capacities, have been identified among inoculants (115). Strains used as probiotics should not contain glucosaminidase or glucuronidase genes that seem to have roles in producing toxic substances in the gut (reviewed in reference 116), but these recommendations may not be easily followed.

SIMILAR BACTERIUM-HOST INTERACTIONS IN GUTS AND ROOTS

Differential gene expression of bacteria in hosts. Bacterium-plant interactions have been studied for many years, and a molecular ping pong between rhizobia and plants that may serve as a model to analyze insect or human gut symbioses is known (reviewed in references 1 and 117). In rhizobium-plant molecular dialogue, *Rhizobium* NodD receptors, which bind root exudate molecules, function as transcriptional regulators that induce the expression of several genes, including *nod* genes and secretion systems (reviewed in references 117 and 118). Extrusion pumps are inducible by flavonoids that are present in root exudates but

do not require NodD genes (119). Many ABC transporter systems are induced by the respective substrate or other molecules from roots (111, 120).

In roots, bacteria have a differential gene expression that supposedly allows them to adapt to the root environment. Genes involved in root exudate usage, root attachment, and survival are induced in bacteria colonizing roots (120, 121). *In vitro* expression technology (IVET) (122), proteomic analysis, microarray and RNA Seq transcriptomics, and genetic analysis have revealed rhizobial (120, 121, 123), *Pseudomonas* (124, 125), *Streptomyces* (126), and other bacterial genes expressed on roots or rhizospheres. Similarly, bacteria may differentially express genes when in guts. Gut bacteria are exposed to bile salts that solubilize diet fat, have antimicrobial activities (127), and regulate bacterial gene expression. An efflux transporter of the multidrug resistance type (MDR) was induced in *Bifidobacterium* by bile (128). Different bile substances have been identified to control gene expression in bifidobacteria (129). Other bile-inducible genes have been found in *Lactobacillus plantarum* (130). Lastly, human gut bacteria transform bile salts (131). Gut bacteria can also modify dietary flavonoids (132) that have significant effects on animal physiology. Analogously, in roots, flavonoids produced by plants are signal molecules in bacteria (133) and are also transformed by bacteria *in vitro*, though this has not been shown *in vivo*. Plant phytoalexins are antimicrobials that are expelled from *Rhizobium etli*, *Bradyrhizobium japonicum*, and *Agrobacterium* by MDR efflux pumps that are inducible by root-exudated flavonoids (20, 119, 134).

Interestingly, gut and root microbiotas may follow the circadian cycles of their hosts. This was observed in nitrogen-fixing bacteria that fixed more during the daytime on rice roots (135). Epithelial cell proliferation, gastrointestinal motility, and other gut processes follow biological rhythms. In the gastrointestinal tract, there are large amounts of melatonin, which is a key hormone in the clock biological regulation (136). The Burmese python's microbiota is responsive to host cycles of feeding and fasting (137).

Host gene expression regulated by microbiotas. Outstandingly, gut and root bacteria modify gene expression in animal (138, 139) and plant (140) hosts, respectively. Gut gene expression is also modified by probiotics (113) that modify gut bacterial gene expression as well (141). Gut genes expressed in the presence of the gut bacterium *Bacteroides thetaiotaomicron* are involved in xenobiotic catabolism, in angiogenesis, in gut barrier epithelium maintenance, and in immunity development (139), with very complex host molecular responses (142).

Plants and humans can sense bacterially produced acylhomoserine lactones (AHLs), different volatiles, microbe-associated molecular patterns (MAMPS) (72, 143), and other bacterial molecules unknown at present. Root gene expression is differently modified by acylhomoserine lactones from pathogenic or symbiotic bacteria (144). In turn, plant products may act like quorum-sensing signals in bacteria (145). In recent years, specific regulatory roles of *N*-acylhomoserine lactones have become apparent, because plants responded with either a systemic resistance response or a hormonal regulated growth response to the presence of AHL-producing bacteria colonizing the root surface. Also in the animal/human systems, a specific perception of AHL compounds, produced by Gram-negative, mostly pathogenic bacteria, was found in many tissues, including the gut system, leading to immunomodulatory effects (146). In plants, root genes induced by rhizospheric bacteria are involved in oxidative and defense responses, in plant secondary metabolism, or in signaling (140). Plants may detect bacterial cyclopeptides through auxin sensing pathways (147). In a more specialized symbiosis, a cascade of signaling processes occurs inside root cells in the presence of rhizobia or Nod factors (148).

Control of microbiotas. A *Drosophila* mutant with increased levels of antimicrobial peptides showed deregulated balances of gut populations (149), with smaller numbers of *Commensalibacter intestini* (an acetic acid bacterium present in normal gut) bacteria (150) and increased numbers of *Gluconobacter morbifer* cells that caused gut cell apoptosis and early insect death (149). It is interesting to note that *C. intestini* antagonizes *G. morbifer*, which is a normal gut member, but with detrimental effects when present in large numbers; thus, *C. intestini* contributes to gut homeostasis and host fitness (151). Similarly, among root microbiotas, there are plant-pathogenic bacteria that normally would not affect the plants when kept in low numbers by other plant community strains or plant antimicrobials. Lipopolysaccharide *Rhizobium* mutants that were more sensitive to maize antimicrobial benzoxazinones had reduced rhizospheric colonization (152). Antimicrobial peptides constitute a line of defense in plants as effectors of innate immunity and regulate not only bacteria but also methanogenic archaea in guts (153). Gut immunity determines bacterial composition; reciprocally, bacteria modulate host immunity in guts (154, 155). Carbohydrate binding proteins (lectins) from guts and roots bind bacteria, form aggregates, and may have antibacterial effects (156, 157).

In addition to bacterium-host interactions, bacterium-bacterium interactions may determine community composition and its function (158). Those that occur in the mouth (159) may guide research in gut and root symbioses. In *Rhizobium*, mutants in quorum sensing are affected in rhizosphere colonization (160). Acylhomoserine lactones may be degraded by rhizospheric bacteria causing interference with quorum signals that regulate gene expression in other bacteria (161). This may have a role in protecting plants from pathogens but may also affect mutualistic interactions.

EVOLUTIONARY PATHWAYS

Lateral gene transfer in guts and roots. In roots, root nodules, and guts, lateral transfer of genetic material between different bacteria has been evidenced (2, 162, 163), seemingly promoted by close contacts in high-density populations. The presence of similar catabolic or antibiotic resistance genes in various gut bacterial genera has been explained as acquisitions by lateral gene transfers (91). It has been suggested that starch catabolism genes have been transferred from gut to bacteria (164).

There are many more phages than bacteria in the gut (13), and some may be involved in lateral gene transfer among gut bacteria (165). Lateral transfer of genetic material is mediated by plasmids or genomic island mobilization in rhizobia and other rhizospheric bacteria (54, 166), but phages may have a role as well.

Specialized symbiont evolution from root and gut bacteria. It has been suggested that gut bacteria gave rise to endosymbiotic bacteria in insects (167) based on similarities of gut bacteria and insect endosymbionts (168). Correspondingly, rhizospheric bacteria may have preceded nodule and endophytic bacteria in plants (169). Insect endosymbionts and nodule rhizobia are selected

symbionts that occupy intracellularly host-specialized structures and attain high numbers with a determined functional role. However, transmission modes of plant- and insect-specialized symbionts (reviewed in reference 46) and their genome sizes (rhizobial genome sizes reviewed in references 121 and 170) are different.

CONCLUSIONS

The comparison of plant and gut microbial ecologies may help to guide research toward the understanding of such complex symbioses. Literature on the subject is so extensive that only a few references were used to illustrate the commonalities of gut and root microbiotas. Interested readers are referred to recent literature (171–175). Plants use their "guts" (roots) outwards, and this simplifies their study in comparison to study of animal guts. Gut and root microbiotas significantly impact health, development, and fitness of their respective hosts.

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