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Rhizobium-Linked Nutritional and Phytochemical Changes Under Multitrophic Functional Contexts in Sustainable Food Systems

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Rhizobia are bacteria that exhibit both endophytic and free-living lifestyles. Endophytic rhizobial strains are widely known to infect leguminous host plants, while some do infect non-legumes. Infection of leguminous roots often results in the formation of root nodules. Associations between rhizobia and host plants may result in beneficial or non-beneficial effects. Such effects are linked to various biochemical changes that have far-reaching implications on relationships between host plants and the dependent multitrophic biodiversity. This paper explores relationships that exist between rhizobia and various plant species. Emphasis is on nutritional and phytochemical changes that occur in rhizobial host plants, and how such changes affect diverse consumers at different trophic levels. The purpose of this paper is to bring into context various aspects of such interactions that could improve knowledge on the application of rhizobia in different fields. The relevance of rhizobia in sustainable food systems is addressed in context.

Keywords: multitrophic interactions, phytochemicals, *Rhizobium*, nitrogen, carbon, plant tolerance

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INTRODUCTION

Rhizobium is a group of bacteria that were first described in the year 1889 by the German botanist Dr. Albert Bernhard Frank (1839-1900) (Hassen et al., 2020). Such bacteria are part of complex microbiomes that exist endophytically in root nodules of leguminous plants (Martínez-Hidalgo and Hirsch, 2017; Hansen et al., 2020). With the advent of modern molecular identification tools (Young and Haukka, 1996; Deng et al., 2011), root nodulating rhizobia have currently been sub-classified into at least 15 genera including the alphaproteobacteria *Rhizobium*, *Ensifer* (syn. *Sinorhizobium*), *Allorhizobium*, *Pararhizobium*, *Neorhizobium*, *Shinella* (Rhizobiaceae), *Mesorhizobium*, *Aminobacter*, *Phyllobacterium* (Phyllobacteriaceae), *Ochrobactrum* (Brucellaceae), *Methylobacterium*, *Microvirga* (Methylobacteriaceae), *Bradyrhizobium* (Bradyrhizobiaceae), *Azorhizobium* (Xanthobacteraceae), and *Devosia* (Hyphomicrobiaceae), as well as the betaproteobacterial genera *Paraburkholderia*, *Cupriavidus,* and *Trinickia* (Burkholderiaceae)

(De Lajudie et al., 2019; Hassen et al., 2020). The term "*Rhizobium*" has mostly been retained for general reference and as a common name for these genera. However, apart from these root nodulating rhizobia, diverse strains of non-nodulating rhizobia do exist endophytically and in the rhizospheres of various leguminous plants (Wu et al., 2011; Gano-Cohen et al., 2016; Martínez-Hidalgo and Hirsch, 2017).

Symbiotic *Rhizobium* species associated within root nodule symbiosomes of leguminous plants endophytically fix molecular nitrogen (N_2) through reactions catalyzed by nitrogenase enzyme (Flores-Tinoco et al., 2020; Jangir et al., 2020). The biologically fixed nitrogen is assimilated by legumes to meet the nutritional demands especially under N-limited conditions (Basu and Kumar, 2020). In return, the autotroph legumes (macrosymbionts) provide the heterotrophic *Rhizobium* bacteroids (microsymbionts) with organic carbon for respiration derived from photosynthetic reactions (Mitsch et al., 2018; Flores-Tinoco et al., 2020). Therefore, the root nodule is the point of convergence of two very important reactions namely, biological nitrogen fixation through nitrogenase machinery (Lindström and Mousavi, 2019; Signorelli et al., 2020), and carbon fixation in the photosynthetic machinery (Pinnola and Bassi, 2018; Vanlerberghe et al., 2020) (**Figure 1**). The union of *Rhizobium* and leguminous plants through nitrogen-fixing root nodules is an efficient nutrient cycling component in biogeochemical cycles of various ecosystems.

The rhizobium-legume symbiosis supports aboveground and belowground networks of consumers at various trophic levels (Grunseich et al., 2020; Karoney et al., 2020). By fixing nitrogen, *Rhizobium* redefines autotrophy in leguminous plants and their interactions with various consumers. This is because root infection by rhizobia triggers variations in chemical composition of host plants that may be expressed in gaseous forms such as volatile organic compounds (VOCs) (Ballhorn et al., 2013), aqueous form including cellular fluids and root exudates (Karoney et al., 2020; Tian et al., 2020), as well as solid forms like cell walls (Fournier et al., 2015; Gigli-Bisceglia et al., 2020). Such chemical changes are linked with suitability of legumes as host plants in terms of nutrient content that promotes tolerance (Karoney et al., 2020), or expression of defensive compounds in terms of antibiosis and antixenosis (Cai et al., 2017). *Rhizobium*-legume symbiosis therefore determines biodiversity and the function of various ecosystems including drylands, wetlands, savannahs, tropical rain forests, and the human-managed agroecosystems.

Currently, the world is struggling to meet food demand for a fast-growing human population projected to reach 9.7 billion by the year 2050 (UN DESA, 2017). Global demand for protein-rich food sources including legumes for human food and animal feed will continue rising (Foyer et al., 2016). Intensification of food production to meet the rising food demand is associated with depletion of soil fertility (Kopittke et al., 2019), which results in the misuse of fertilizers and pesticides (Warra and Prasad, 2020), that serves the unsustainable goal of eliminating competition from pests and pathogens (Karoney et al., 2020), while trying to attain dominance in food markets (Gonzalez, 1999; Chalam et al., 2020). The result of such unsustainable practices is increased costs of production (Adolph et al., 2020), amidst a resource depleted and polluted agroecosystem that is toxic to human health and biodiversity (Mahmud et al., 2020; Warra and Prasad, 2020). These are among the reasons behind the constitution of the United Nations Sustainable Development Goals (SDGs), and in particular, to end hunger, achieve food security and improved nutrition, and promote sustainable agriculture (SDG2) (ICSU, 2017).

Rhizobia and their leguminous host plants are crucial components in attaining the SDGs through nitrogen and carbon dioxide fixation in agroecosystems (Saha and Bauddh, 2020). In-depth understanding of rhizobium-legume symbioses, especially the phytochemical mechanisms and changes associated with the nitrogenase-photosynthesis reactions, lays better ground for addressing some important issues regarding Sustainable Food Systems in agroecosystems. The present article focuses on symbiotic relationships between root nodulating *Rhizobium* species and leguminous plants in biological nitrogen fixation. Phytochemical changes associated with root infection by rhizobia, and how such changes affect various microbial and invertebrate consumers have been addressed in multitrophic contexts. Such interactions have been put into the perspective of Sustainable Food Systems in agroecosystems.

CARBON AND NITROGEN ACQUISITION BY PLANTS

Photosynthetic Machinery and Carbon Fixation in Host Plants

Plants are autotrophs equipped with two photosynthetic machineries in the thylakoid membrane inside the chloroplasts (Nelson and Junge, 2015), with the light reaction occurring in the grana of chloroplasts producing energy molecules (Mullineaux, 2005), and the dark reaction located in the stroma of chloroplasts (Poolman et al., 2003). The light reaction in the grana has two systems known as Photosystem II (PSII) (water-plastoquinone oxidoreductase) (Wydrzynski and Satoh, 2005; Freeman, 2006) and Photosystem I (PSI) (plastocyanin-ferredoxin oxidoreductase) (Golbeck, 2006). Photosystem I is located on the outer surface of the thylakoid membrane with a reaction center called P700 that absorbs light at 700 nm to reduce $NADP^+$ to NADPH (Webber and Lubitz, 2001). Photosystem II (PSII) is located on the inner surface of the thylakoid membrane with a reaction center called P680 that absorbs light energy at 680 nm to provide energy for photo-splitting of water molecules into protons (H^+) and oxygen gas (O_2) (Renger and Renger, 2008; Herbstová et al., 2012). Electrons produced in PSII are used to replace those donated by PSI to reduce $NADP^+$ into NADPH (Haldrup et al., 2001; Roach and Krieger-Liszkay, 2014). During photosynthetic reactions, ATP is synthesized from ADP and inorganic P through the process of phosphorylation (Jagendorf, 2002), which can either be cyclic phosphorylation involving only PSI (Allen, 2003; Johnson, 2011), or non-cyclic photophosphorylation involving both PSI and PSII that reduces $NADP^+$ and O^{2-} to NADPH and O_2, respectively (Shimazaki and Zeiger, 1985; Allen, 2003).

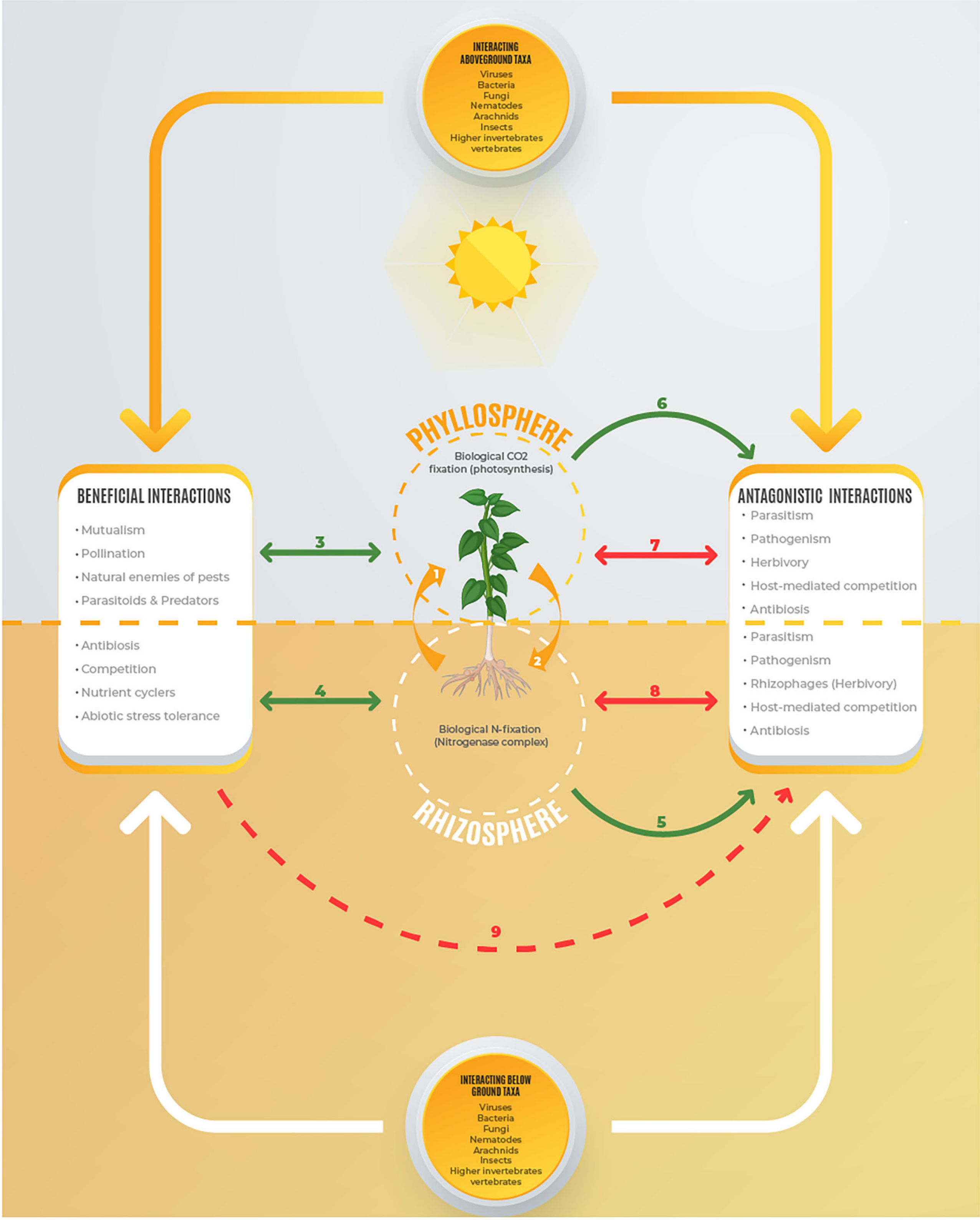

FIGURE 1 | Leguminous plant with *Rhizobium*-nodulated roots. (1) The aboveground foliar system obtains gaseous CO_2 from the phyllosphere and fixes it into organic compounds through photosynthetic machinery and translocate them to the heterotrophic rhizobia in the root nodules; (2) Rhizobium obtains nitrogen from the

(Continued)

FIGURE 1 | rhizosphere and fixes it into amino acids that are transmitted to the leguminous leaves for protein and chlorophyll synthesis; (3, 4) Beneficial mutualistic interactions between rhizobial plants with aboveground and belowground taxa with the autotroph providing organic carbon derived from photosynthesis and nitrogen fixation. (5, 6) The rhizobia plants providing food to antagonistic organisms under a situation of warfare (7, 8) and (9) beneficial biota help the rhizobial plant to suppress the antagonistic organisms.

The ATP and NADPH produced in the light reaction provide energy for the dark (carbon) reaction in the stroma that involves biofixation of carbon dioxide (Hopkins and Hüner, 2009; Buchanan, 2016). Carbon dioxide fixation can either be via the Calvin cycle in C_3 plants (Raines, 2011), which includes leguminous hosts of *Rhizobium* species (Archimède et al., 2011), or the Hatch-Slack pathway for carbon dioxide fixation found in C_4 plants (Osborne and Beerling, 2006). Crassulacean acid metabolism (CAM) functions in CAM plants (Males and Griffiths, 2017).

In the carbon reaction of C_3 plants (Calvin cycle) that includes leguminous hosts of *Rhizobium*, CO_2 that gets into plants cells via stomata is fixed into ribulose-1,5-diphosphate (RuBP) ($C_5H_{12}O_{11}P_2$) under the catalyzing effect of ribulose bisphosphate carboxylase (rubisco) to form two molecules of glyceric acid-3-phosphate (Wang and Lan, 2010). Glyceric acid-3-phosphate reacts with ATP to form two molecules of glyceraldehyde-3-phosphate while releasing ADP (Raines, 2003; Wang and Lan, 2010). Glyceraldehyde-3-phosphate can be synthesized into ribulose-1,5-biphosphate (RuBP) for continuation of the CO_2 biofixation in the Calvin cycle (Raines, 2003; Wang and Lan, 2010), or converted into fructose-1,6-bisphosphate as a precursor for biosynthesis of glucose, sucrose, starch, or other energy-rich carbohydrates (Strand et al., 2000; Lv et al., 2017). The carbohydrates are used for generation of energy through the respiratory TCA cycle in the mitochondria (Raghavendra et al., 1994; Plaxton and Podestá, 2006). Besides foliar acquisition of carbon in the form of CO_2 for photosynthesis, plants also do acquire carbon in the forms like CO_2, carbonate and organic compounds through their roots (Raven et al., 1988; Farrar and Jones, 2000).

Nitrogen Acquisition in Host Plants

Plants require nitrogen to synthesize proteins and other complex compounds that are very important for their growth and reproduction. Nitrogen is key for the synthesis of chlorophyll and the function of photosystem I and II (Lu et al., 2001; Bassi et al., 2018). For instance, glutamate ($C_5H_9NO_4$) is a nitrogenous compound that is a precursor for chlorophyll synthesis in developing leaves (Forde and Lea, 2007). Glutamate is the key compound involved in the acquisition of nitrogen by plants (Temple et al., 1998). This compound is primarily biosynthesized from pyruvate generated from the glycolytic pathway (Chesworth et al., 1998), through the breakdown of photosynthates arising from the Calvin cycle (Michelet et al., 2013). Pyruvate ($C_3H_4O_3$) is converted to 2-oxoglutarate (α-ketoglutarate) through the action of glutamate dehydrogenase (GDH) in the tricarboxylic acid (TCA) cycle (Qiu et al., 2019). Glutamate is also synthesized through the proline (Pro)/pyrroline 5-carboxylate (P5C) cycle in the plant cytoplasm (Miller et al., 2009; Qiu et al., 2019). Glutamate is then used in nitrogen acquisition systems.

Plants have two nitrogen acquisition systems, the root low-affinity transport system that functions when soil N is adequate, and a high-affinity transport system that functions when N is low (Kraiser et al., 2011; Kiba and Krapp, 2016). Nitrogen is mainly acquired in the form of ammonium (NH_4^+) in plants growing under low pH conditions and as nitrate (NO_3^-) adapted to high pH conditions (Masclaux-Daubresse et al., 2010). Whereas ammonium is assimilated directly into amino acids, nitrate has to first be reduced to ammonium in a reaction catalyzed by nitrate reductase and nitrite reductase (Chamizo-Ampudia et al., 2017). Nitrogen in the form of ammonium (NH_4^+) is assimilated via the glutamate synthase (GS)/glutamine oxoglutarate aminotransferase (GOGAT) synthetase pathway (Masclaux-Daubresse et al., 2006; Zhang Z. et al., 2017). In this pathway, ammonium from soil reacts with glutamate to form glutamine ($C_5H_{10}N_2O_3$) (Forde and Lea, 2007). Glutamate dehydrogenase (GDH) is another enzyme that catalyzes the incorporation of ammonium into glutamate just like glutamate synthase (Grabowska et al., 2012). However, glutamate dehydrogenase has lower affinity for ammonium than glutamate synthase (Zhang Z. et al., 2017).

When soil nitrogen supply is limited, the biosynthesis and function of PS I and PS II compounds is constrained (Nunes et al., 1993; Bassi et al., 2018), and hence the provision of energy for CO_2 fixation into glutamate and other products (Bascuñán-Godoy et al., 2018). Such conditions require alternative ways of acquiring nitrogen. This is whereby diazotrophic *Rhizobium* species become of significance to the plants by symbiotic nitrogen fixation through nitrogenase-catalyzed reactions.

ACQUISITION OF CARBON AND NITROGEN BY RHIZOBIUM

Being heterotrophs, free-living rhizobia saprophytically acquire organic carbon and nitrogen in the rhizosphere (Poole et al., 2018). When soil fertility is low and the supply of organic carbon and nitrogen are limited, chances of survival of rhizobia diminish amidst intensifying competition and predation in the rhizosphere (Gabasawa, 2020) (**Figure 1**). Saprophytic processes that require more investment in breaking down organic compounds are weakened amidst scarcity of substrates. Scarcity of organic carbon and nitrogen in the rhizosphere favor the establishment of endophytic populations of symbiotic rhizobia in root nodules of host plants (Coba de la Peña et al., 2018). Besides providing shelter for rhizobia, root nodules also supply the symbiotic bacteria with organic carbon and other nutrients (Brewin, 2010). *Rhizobium* in the root nodules fix atmospheric N_2 with the help of nitrogenase enzyme. Root nodules are facilitated with leghemoglobin and mitochondria that scavenge for oxygen to provide microaerobic conditions that protect nitrogenase from inhibition by O_2 (Bergersen, 1997).

Carbon Acquisition by Endophytic Rhizobium Species

Rhizobia require organic carbon to generate energy in the form of ATP within the bacteroid Tricarboxylic acid cycle (TCA cycle) (Lodwig and Poole, 2003). The TCA cycle of the host plant is the source of organic carbon to rhizobia in root nodules (Andersen, 2020). Endophytic rhizobia acquire carbon from host plants in the form of C_4-dicarboxylates (fumarate, malate, and succinate), which can easily penetrate peribacteroid membranes of root nodules (Mitsch et al., 2018). Specifically, L-malate ($C_4H_6O_5$) is the key C_4-dicarboxylate that supplies carbon to symbiotic rhizobia in root nodules (Haaker et al., 1996; Poole and Allaway, 2000; Mitsch et al., 2018). Rhizobial TCA cycle functions aerobically in free-living cells (Maier, 2004), and microaerobically involving anaplerotic enzymatic pathways in endophytic bacteroids (Dunn, 1998). The ATP produced is utilized as the energy molecule for nitrogen fixation by rhizobia (Duval et al., 2013). However, there is growing information on the existence of some photosynthetic rhizobia that colonize nitrogen fixing-stem nodules (Fleischman et al., 1995; Zhang et al., 2019).

Nitrogen Acquisition by Endophytic Rhizobium Species

Endophytic rhizobia acquire dinitrogen molecules (N_2) through the gas diffusion pathway in the intercellular air spaces of root nodule cortical cells (Zeng et al., 1989; Hunt and Layzell, 1993). Nitrogen fixation reaction is catalyzed by a group of enzymes known as "nitrogenase" (Hoffman et al., 2009, 2014), which comprises of three main genetically distinct types namely Nif, Vnf, and Anf that either have molybdenum (Mo), vanadium (V), or iron (Fe) as their respective active-site central metals (Zhao et al., 2006; McGlynn et al., 2013). Mo-nitrogenase is found in all N_2 fixing bacteria besides being the most widely studied (Newton, 1997; Garcia et al., 2020). Nitrogen is fixed via two distinct biochemical pathways arising from Janus reactions (Harris et al., 2018), with the "distal" (D) pathway being associated with the Chatt-Schrock cycle (Husch and Reiher, 2017), and the "alternating" (A) pathway (Hoffman et al., 2014). In the diazotrophic reaction, nitrogen gas (N_2) is reduced to ammonium (NH_3) with the supply of energy from ATP and catalyzed by nitrogenase ($N_2 + 8e^- + 16ATP\ 8H^+ \rightarrow\ 2NH_3 + H_2 + 16ADP + 16P_i$) (Hoffman et al., 2014; Ghebreamlak and Mansoorabadi, 2020). The resulting ammonium (NH_4^+) diffuses into root cells (Patriarca et al., 2002), and assimilated through the glutamate synthetase (GS)/glutamine oxoglutarate aminotransferase (GOGAT) pathway (Zhang Z. et al., 2017; Lea and Miflin, 2018). Other rhizobia infect non-leguminous plants to provide plant growth promoting services through processes that do not rely on nitrogenase-catalyzed reactions (Mehboob et al., 2009).

PHYTOCHEMICALS IN RHIZOBIUM-LEGUME SYMBIOSIS AND THEIR INFLUENCE ON CONSUMERS

The photosynthesis-nitrogen fixation machinery of leguminous plants supports complex rhizosphere (belowground) and phyllosphere (aboveground) food webs comprising of organisms from various taxonomic groups (Kempel et al., 2009; Katayama et al., 2011a,b; Zhao et al., 2014; Wu et al., 2017; Karoney et al., 2020) (**Figure 1**). Such trophic interactions primarily relate to the demand for nutrients, shelter, and reproductive space. Underlying such relationships is energy flow from the sun through complex biochemical reactions that have far-reaching effects, including the formation of subsequent generations of the organisms. Phytochemical composition of leguminous host plants exhibits variations, right from the process of rhizobial infection, multiplication into bacteroids, nitrogen fixation to senescence (Irmer et al., 2015). Such chemical compounds include chlorophylls, enzymes, photosynthates and their nutritional derivatives, plant secondary metabolites, hormones, and other signaling molecules as well as inorganic compounds (Wink, 2013; Sánchez-Chino et al., 2015; Šibul et al., 2016; Karoney et al., 2020). Various published works have linked rhizobium infection to nutritional and phytochemical changes that affect consumers in multitrophic systems (**Tables 1**, **2**). Nutritional suitability of host plants is therefore influenced by rhizobium infection (Naluyange et al., 2014, 2016; Karoney et al., 2020), while prevention of overexploitation by the consumers depends on the expression of such compounds in terms of host plant resistance and tolerance (Enneking and Wink, 2000; Joosten and van Veen, 2011; Goyal et al., 2012; Goyal, 2013; Karoney et al., 2020).

Leguminous root nodules are microecosystems that host unique microbiomes consisting of consumers that benefit from resources provided by the photosynthesis-nitrogen fixation machinery. Success of root nodule symbiosis depends on how abiotic and biotic factors that determine compatibility between host plants and rhizobia take prominence over those related to antagonism. Leguminous host plants provide conducive environment that is characterized by production of resistance factors that are not harmful to mutualistic rhizobia. The leguminous root nodule also accommodates other microbes that benefit the host plant and cooperate with rhizobia. Together, the host plant, rhizobia, and other beneficial microbes within the root nodule microbiome promote their fitness over other endophytic and exophytic organisms that interact negatively through processes such as parasitism, pathogenism, predation, and competition. Organic carbon and nitrogen produced by the photosynthesis-nitrogen fixation machinery of legumes and rhizobia supports consumers at various trophic levels. Consumers are affected by compatible relationships between host plants and *Rhizobium* species (Dean et al., 2014; Naluyange et al., 2014, 2016; Pulido et al., 2019; Karoney et al., 2020; Xu et al., 2020). Consumers are also affected by antagonisms arising from incompatible relationship between host plants and rhizobium species (Gourion et al., 2015; Clúa et al., 2018;

TABLE 1 | Phytochemical variations associated with *Rhizobium* species and their effects on host plants and herbivorous consumers.

***Rhizobium* species**	**Phytochemical variations**	**Ecological effects**		**References**
		Effects on host plants	**Effects on consumers**	
Rhizobium leguminosarum bv. viceae	Increased lipids (Jasmonic acid) and flavonoids (quercetin, kaempferol) concentration	Enhances *Pisum sativum* yield through increased seed fresh and dry weights based on better seed filling	Reduced seed infection level by *Didymella pinodes*	Ranjbar Sistani et al., 2017
Bradyrhizobium japonica	Increased rhizobiotoxine production in cowpea (*Vigna unguiculata*)	Increased cowpea growth	Reduced seed infection level by *Macrophomina phaseolina*	Deshwal et al., 2003b
Rhizobium leguminosarum	Induces pterocarpan production in pea plant (*Pisum sativum)*	Enhances *Pisum sativum* growth	Increased resistance to *Fusarium solani*	Patel et al., 1988
Rhizobium tropici	Reduced production of C-based compounds (Flavonoids, phenols, and Tannins); increased production of N-based compounds (Peroxidase, ascorbate peroxidase, and lipid peroxidases in *Phaseolus vulgaris)*	Improved *Phaseolus vulgaris* tolerance to *Colletotrichum lindemuthianum*	Increased *Colletotrichum infection* in *Phaseolus vulgaris*	Karoney et al., 2020
Rhizobium leguminosarum	Increased nitrogen	Increased growth of *Phaseolus vulgaris*	Increased *Colletotrichum* infection and aphid attack on *Phaseolus vulgaris*	Naluyange et al., 2014, 2016
Bradyrhizobium japonica	Increased nitrogen levels in Soybean *(Glycine max)*	Increased plant biomass (size and leaf number)	Increased susceptibility to spider mites (*Tetranycus urticae*) and other arthropods	Katayama et al., 2010, 2011a
Rhizobium ensifer medicae	Enhances saponins production in *Medicago truncatula*	Improves plant resistance against Pythopathogens	Deterrence of *Spodoptera exigua*	Cai et al., 2017
Bradyrhizobium arachis	Increased IAA and rhibotoxines production in *Pisum sativum*	Increased plant growth and biomass	Reduce infection by *Macrophomina phaseolina* on *Pisum sativum*	Deshwal et al., 2003b
Bradyrhizobium spp.	Enhanced Pyrrolizidine alkaloid production in *Crotolaria spectabilis*	Improves plant resistance against herbivores	Enhances plant defensive mechanisms against herbivores e.g., grazing livestock	Irmer et al., 2015
Mesorhizobium spp.	Increased Indolizidine alkaloids (swainsonine) production in *Astragalus* spp and *Oxytropis sericea*	Boost plant resistance against insect herbivores	Increases swainsonine production, serve as deterrent factor to *Frankliniella occidentalis* and *Heliothis virescens*	Laguerre et al., 1997; Liu et al., 2017
Bradyrhizobium liaoningense	Enhances production of imidaoles, pyrimidines, indoles and trigonellines in soybean,	Increased nodulation, nitrogenase activity and plant growth	Improved plant defense against fungal pathogens e.g., *Fusarium spp*	Gao et al., 2015; Shen et al., 2018
Rhizobium sp. (Cicer)	Increased total protein in chickpea (*Cicer arietinum*)	Increased seed weight, yield, and total protein content	Improves plant resistance against *F. oxysporumf. sp. ciceris (Foc)*	Volpiano et al., 2019
Rhizobium tropici CIAT899	Enhanced production of peroxidase, catalase, and ascorbate peroxidase in *Phaseolus vulgaris*	Increase nutritive suitability to *Colletotrichum lindemuthianum*	Improve plant tolerance to *Colletotrichum lindemuthianum*	Karoney et al., 2020
Rhizobium leguminosarum bv. viceae	Increased production of jasmonic acid, kaempferol, and Quercetin in *Pisum sativum*	Improves plant resistance to pathogens	Inhibits the growth and development of *Didymella pinodes*	Ranjbar Sistani et al., 2017
Rhizobium tropici CIAT899	Reduced production of flavonoids, phenol, and tannins in common bean *Phaseolus vulgaris*	Increased plant susceptibility to *Colletotrichum lindemuthianum*	Increased *Colletotrichum lindemuthianum* infection on *Phaseolus vulgaris*	Karoney et al., 2020
Rhizbozium leguminosarum bv. viceae (Rlv)	Triggers flavanone and chalcones production in *Vicia sativa*	Enhances the expression of nod genes increasing nodulation	Reduces the incidences of damping off caused by *Pythium* spp.	Huang and Erickson, 2007
Rhizobium ensifer medicae	Enhances saponins production in *Medicago truncatula*	Improved plant resistance to herbivores	Increased saponin production resulting into deterrence of *Spodoptera exigua* herbivory	Cai et al., 2017

(Continued)

TABLE 1 | Continued

***Rhizobium* species**	**Phytochemical variations**	**Ecological effects**		**References**
		Effects on host plants	**Effects on consumers**	
Rhizobium leguminosarum	Increased daidzein and coumetrol production in *legumes*	Induced transcription of *nod C* and *lac z* genes responsible for nodulation	Protects the plant against arthropod herbivores	Khanna et al., 1999; Karowe and Radi, 2011
Bradyrhizobium japonica	Increased rhizobiotoxine, citrate, and catechol production	Increased iron chelation leading to increased nodulation and improved soybean resistance against pathogen	Inhibits plant infection by *Macrophomina phaseolina*	Modi et al., 1985; Guerinot et al., 1990; Deshwal et al., 2003a
Rhizobium strains 116,133	Increased auxins, nitrogen, and chlorophyll content in *Phaseolus vulgaris.*	Enhanced vegetative growth and plant biomass	Increased plant protection by influencing cellulase, protease, lipase and β-1,3 glucanase productions and enhance plant defense to pytopathogens e.g., *Macrophomina phaseolina*, *Rhizoctonia solani* and *Fusarium solani*	Sara et al., 2013; Gopalakrishnan et al., 2015
Rhizobium leguminosarum	Increased athranilate, vicibactin and phytoalexins production in *Phaseolus vulgaris*	Enhances iron chelation, nodulation, and nitrogen fixation.	Induced plant resistance to soil pathogens e.g., *Fusarium* spp.	Rioux et al., 1986; Dilworth et al., 1998; Deshwal et al., 2003a

Benezech et al., 2020a). The function of both compatible and non-compatible relationships between host plants and rhizobia may still be affected by other beneficial or antagonistic biota and abiotic factors (Pugashetti et al., 1982; Parker, 2001; Mehboob et al., 2013; Haldar and Sengupta, 2015; Han et al., 2020). The photosynthesis-nitrogen fixation linkage of leguminous host plants and rhizobium, shapes the chemical profile and hence the community structures of both endophytic and exophytic organisms in the rhizosphere and phyllosphere, respectively. Therefore, a functional leguminous root nodule could be equated to stable and self-sufficient institution that provisions for its diverse citizens and protects its interests.

COMPATIBILITY OF RHIZOBIUM WITH HOST PLANTS

The term "symbiosis" was coined in the year 1879 by the Father of Plant Pathology, the German botanist and mycologist Professor Heinrich Anton de Bary (1831-1888), to imply "the living together of unlike organisms" (Oulhen et al., 2016). Relationships between rhizobia and leguminous plants are among the most widely known examples of symbiosis. Compatibility of rhizobium with host plants is genetically determined and highly specific (Mergaert et al., 1997; Clúa et al., 2018; Sachs et al., 2018). The key determinants of specificity in rhizobium-legume relationships are lipo-chitooligosaccharide compounds known as Nod factors secreted by rhizobium strains (Mergaert et al., 1997; Geurts and Bisseling, 2002; Soto et al., 2006), in response to flavonoid signaling compounds in root exudates (Clúa et al., 2018). Flavonoid compounds such as the flavonoid aglycones (apigenin, daidzein, kaempferol, luteolin, myricetin, and quercetin) and the flavonoid glycosides (daidzin, genistin, hesperidin, hyperoside, kaempferol-7-O-glucoside, naringin, and rutin) have been detected in root exudates of the leguminous plants *Melilotus indicus*, *Trifolium alexandrinum,* and *T. resupinatum* (Gomaa et al., 2015). Compatible interactions based on plant flavonoids and rhizobial Nod factors trigger a series of events that lead to successful infection and development of nodules that can fix nitrogen (Wang et al., 2018). Such nodules can be determinate (nodules with determinate meristematic activity) or indeterminate (nodules with indeterminate meristematic activity) (Prell and Poole, 2006; Terpolilli et al., 2012; Mao et al., 2013).

Incompatible interactions between plants and *Rhizobium* may either result in non-formation of nodules (Wu et al., 2011; Gano-Cohen et al., 2016), or if formed, the nodules cannot fix nitrogen (Oono et al., 2009; Wang et al., 2018). Such groups of "freeloaders who do not pay rent" cannot be considered to be mutualistic, but they are parasitic *Rhizobium* species (Lewin, 1982; Taha, 1993; Denison and Kiers, 2004; Oono et al., 2009; Ballhorn et al., 2016). The main factors underlying incompatible interactions between plants and *Rhizobium* are genetically expressed in the form of non-complementary Nod factors (Mergaert et al., 1997; Geurts and Bisseling, 2002; Wang et al., 2018). *Rhizobium* species having genetic symbiotic defects are incompatible with host plants (Long, 1989; Nadler et al., 1990). Besides this, the legume

TABLE 2 | Leguminous root exudates and their role in rhizosphere interactions with *Rhizobium* and other organisms.

Root exudates	Function in the rhizosphere	References
Sugars (monosaccharides, disaccharides, polysaccharides)	Act as chemo-attractants of rhizobia in the rhizosphere to colonize the leguminous plant roots	Igiehon and Babalola, 2018
Amino acids		
Arginine	Act as chemo-attractants of rhizobia in the rhizosphere to colonize the leguminous plant roots	Rasmann and Turlings, 2016
Benzoic acids	Act as chemo-attractants of rhizobia in the rhizosphere to colonize the leguminous plant roots	Rasmann and Turlings, 2016
Proline, Aspartic acids and Valine	Produced by Sesame (*Sesamum orientale*) inhibit egg hatching of plant parasitic nematodes thus controlling of *Meloidogyne* spp.	Bajaj et al., 1989; Ansari et al., 2019
Phenylalanine ammonia-lyase	Leads to high production of phytoalexins and glyceollins which induce *Glycine max* resistance) to *Pytopthora sojae*	Zhang C. et al., 2017
High molecular weight compounds		
Tannins	Chemo-attractants of rhizobia in the soil and enhance microbial interaction especially for *Rhizobacteria* and Arbuscular Mycorrhizal Fungi	Igiehon and Babalola, 2018
Luteolin	Act as chemo-attractants and increase *Pseudomonas putida* and *Rhizobium meliloti* growth rates	Maj et al., 2010; Spini et al., 2016
Qutercetin	Stimulate *Rhizobium meliloti* growth and interaction with vesicular-arbuscular mycorrhizal symbioses	Spini et al., 2016
Flavonoids	Act as chemo-attractants of rhizobia stimulating their growth and nodulation in *Medicago truncuIata*	Mathesius, 2019
Phytoalexins	High phytoalexins production inhibits the growth of *Phytopthora megasperma* in soybean	Ebel and Grisebach, 1988
Genistein	Signaling molecule of *Bradyrhizobium japonicum* in soy bean triggering expression of Nod genes (Nodulin) which stimulate nodulation. Increases competitiveness and symbiotic activity of *Rhizobium leguminosarum bv. trifolii* in red clover	Kosslak et al., 1987; Bolaños-Vásquez and Werner, 1997; Sugiyama et al., 2008
Daidzein	Signaling molecule of *Bradyrhizobium japonicum* in soy bean and stimulate the release of nod gene for nodulation process. Increases competitiveness and symbiotic activity of *Rhizobium leguminosarum bv. trifolii* in red clover.	Kosslak et al., 1987; Bolaños-Vásquez and Werner, 1997; Sugiyama et al., 2008
Apigenin	Signaling molecule of *Bradyrhizobium japonicum* in soy bean triggering the release of nod genes which stimulate nodulation.	Kosslak et al., 1987; Sugiyama et al., 2008
Afrormosin	Signaling molecule of *Bradyrhizobium japonicum* in soy bean which stimulate nodulation.	Kosslak et al., 1987; Sugiyama et al., 2008
Coumestrol	Signaling molecule of *Bradyrhizobium japonicum* in soy bean to release the nod genes and stimulate nodulation. Increases competitiveness and symbiotic activity of *R. leguminosarum bv. trifolin* in red clover.	Kosslak et al., 1987; Bolaños-Vásquez and Werner, 1997; Sugiyama et al., 2008
Liquiritigenin, Naringenin and Hesperitin	Signaling molecules released by *Vicia sativa* and red clover to attract *Rhizobium leguminosarum and* trigger nod genes production boosting their competitiveness and symbiotic activities	Maj et al., 2010

host plant may produce defensive compounds including reactive oxygen species (ROS) that may inhibit *Rhizobium* nodulation (Gourion et al., 2015; Tóth and Stacey, 2015), or even the plant may be genetically non-nodulating (Matthews and Davis, 1990; Ali et al., 2014).

ANTAGONISTIC AND BENEFICIAL RHIZOSPHERE BIOTA TO RHIZOBIUM-LEGUME SYMBIOSIS

Antagonistic Rhizosphere Biota to Rhizobium-Legume Symbiosis

The leguminous rhizosphere is characterized by root exudation of organic compounds, enzymes, and ion exchange (Kidd et al., 2018; Preece and Peñuelas, 2020), supporting complex food webs of heterotrophic biota from various taxa (Bonkowski et al., 2009; De-la-Peña and Loyola-Vargas, 2014; Taylor et al., 2020) (**Table 2**). *Rhizobium* has to survive both in the rhizosphere and host tissues where they still encounter diverse endophytic biota inside the root nodule microbiome (Taha, 1993; Omar and Abd-Alla, 2000; Sharaf et al., 2019; Taylor et al., 2020). Such rhizosphere and endophytic biota have different influences on *Rhizobium*-legume symbiosis (Checcucci et al., 2017).

Competitors of Rhizobium Symbiosis

Competition is the contentious interaction for limited resources between organisms that is characterized by efficient resource consumption (exploitation) or harmful effects to the adversary (interference) (Ghoul and Mitri, 2016). Competition for nutrients and space is a key form of antagonistic interaction that affects rhizobia and host plants (Postma et al., 1990; Poole et al., 2018), in both independent and symbiotic states of the two organisms (Mendoza et al., 2016; Hortal et al., 2017; Lardi et al., 2017). Non-nodulating strains of *Rhizobium leguminosarum* compete with the nodulating types for infection sites, causing delay in development and function of root nodules (Lie et al., 1988), which reduces the performance of leguminous host plants (Gano-Cohen et al., 2016). In the root nodule microbiome of *Medicago sativa*, endophytic non-rhizobium bacteria engage in competitive interactions, with *Brevibacillus brevis* to diminish the benefits of cooperation between *Sinorhizobium meliloti* with the non-rhizobial *Pseudomonas* sp. and *Paenibacillus* sp. (Hansen et al., 2020). Apart from competing for infection sites on leguminous roots (Spaink, 1995; Mendoza-Suárez et al., 2020), free-living rhizobia, and other rhizosphere microbes compete for organic carbon in root exudates (Olanrewaju et al., 2019). Sources of organic carbon in root exudates include simple and complex sugars (e.g., fructose, mannose, glucose, maltose, arabinose, and oligosaccharides), amino acids (e.g., aspartate, asparagine, glutamine, arginine, and cysteine), organic acids (e.g., ascorbic, acetic, benzoic, ferulic, and malic acids), phenolic compounds, flavonoids, enzymes, fatty acids, auxins, gibberellins, nucleotides, tannins, steroids, terpenoids, alkaloids, polyacetylenes, and vitamins (Gunina and Kuzyakov, 2015; Hayat et al., 2017; Olanrewaju et al., 2019) (**Table 2**). Exudation of carbon-rich compounds by leguminous plants becomes more intense under conditions of phosphorus and nitrogen deficiency in the soil (Yoneyama et al., 2012; Tawaraya et al., 2014). Such nutrient-deficient conditions instigate intensive competition for N and P between leguminous roots and rhizosphere biota (Kuzyakov and Xu, 2013). Besides helping plants fix limited nitrogen (Liu et al., 2018), rhizobia are phosphate solubilizing microbes capable of enhancing phosphorus acquisition by leguminous host plants in P-deficient rhizospheres (Qin et al., 2011; Verma et al., 2020). As endophytes, the multiplying *Rhizobium* bacteroids require organic compounds in forms such as fumarate ($C_4H_4O_4$), malate ($C_4H_6O_5$), and succinate ($C_4H_6O_4$) (Mitsch et al., 2018), as well as various mineral elements especially molybdenum (Mo), vanadium (V), iron (Fe), and phosphorus (P) that are required for nitrogenase synthesis within the O_2 limited endonodular space (Rüttimann-Johnson et al., 1999; O'Hara, 2001; Rubio and Ludden, 2008; Brear et al., 2013; Hu and Ribbe, 2016). Whether intraspecific or interspecific, *in planta* competition for such nutrients is expected to occur under nutrient-deficient conditions (Oono et al., 2009).

Pathogenic and Non-pathogenic Parasites of Rhizobium Symbiosis

Pathogenic interactions are those that involve parasitic microbes that infect and reduce the performance of their hosts (Ochieno, 2020). *Rhizobium* symbioses exist within a situation of exploitation by various forms of parasites that can either be pathogenic or non-pathogenic (Brader et al., 2017). The main pathogens that directly affect *Rhizobium* cells are bacteriophage viruses (Werquin et al., 1988; Santamaría et al., 2014; Cubo et al., 2020). Phytopathogenic viruses infect leguminous shoots and root nodules resulting in reduced nodule biomass, premature nodule decay, low leghemoglobin content, and hence impaired nitrogen fixation (Orellana and Fan, 1978; Taha, 1993; Ismail and Atef, 1998; Huang, 2001; Mangeni et al., 2020). Other phytopathogens that infect root nodules include diverse bacterial species such as *Ralstonia solanacearum* in *Medicago truncatula* and *Mimosa pudica* (Benezech et al., 2020b; Moura et al., 2020). Fungal species such as *Cladosporium cladosporioides*, *Fusarium moniliforme*, *Fusarium oxysporum*, *Fusarium solani*, *Macrophominia phaseolina*, and *Rhizoctonia solani* are known plant pathogens (Walker et al., 2016; Batnini et al., 2020; Chen et al., 2020; Lakhran and Ahir, 2020; Poveda et al., 2020). However, non-pathogenic strains of the previously mentioned fungi with plant growth promoting effects have been isolated from leguminous root nodules of faba bean *(Vicia faba)* (Omar and Abd-Alla, 2000). While currently there is scarcity of published works on pathogenic endophytic fungi infection of leguminous root nodules, establishment of host range, and non-pathogenicity of some endophytic fungi remains a contentious subject (Ochieno, 2010, 2020; Avedi et al., 2014; Zarafi et al., 2015; Oula et al., 2020).

Root endoparasitic nematodes are pathogenic microinvertebrates that exploit resources from rhizobium-legume symbioses (Taha, 1993; Weerasinghe et al., 2005). Root knot nematodes of *Meloidogyne* spp. are examples of plant parasitic nematodes that cause galls on leguminous roots that affect rhizobial nodulation (El-Bahrawy and Salem, 1989; Wood et al., 2018; Yergaliyev et al., 2020). *Meloidogyne incognita* produces chemical factors that elicit signal transduction events that result in root knots, in a similar manner that roots nodules are formed through *Rhizobium* Nod factors (Weerasinghe et al., 2005).

Non-pathogenic parasites of *Rhizobium*-legume symbioses comprise a wide range of microbes that draw resources from symbiotic systems without causing disease to rhizobia or the host plant. These include non-pathogenic non-symbiotic bacteria and fungi that live endophytically in root nodules and other plant tissues without causing disease (Omar and Abd-Alla, 2000; Mrabet et al., 2006; Selvakumar et al., 2013; De Meyer et al., 2015; Martínez-Hidalgo and Hirsch, 2017; Hassen et al., 2018; Muresu et al., 2019). Besides the non-pathogenic bacteria, root nodules of leguminous plants such as *Hedysarum* species and *Vicia faba* host human pathogens such as *Enterobacter cloacae*, *Enterobacter kobei*, *Escherichia vuneris*, *Pantoea agglomerans,* and *Leclercia adecarboxylata* (Muresu et al., 2010; Saïdi et al., 2013; Selvakumar et al., 2013). These are non-pathogenic parasites to rhizobial host plants.

Predation of Rhizobium-Legume Symbiosis

Predation is a form of biointeraction in which one organism (predator) eats all or part of another organisms (prey). Herbivory is a form of predation in which the prey is a plant such as legumes, while microbivory is where the prey is a microbe like *Rhizobium*. Predation of the *Rhizobium*-plant symbiosis comes both in the form of microbivory and herbivory (Ramirez and Alexander, 1980). Direct predation on *Rhizobium* cells occurs in the rhizosphere by microbivore protozoans and nematodes (Ramirez and Alexander, 1980; Postma et al., 1990; Verhagen et al., 1993; Trap et al., 2016; Jiang et al., 2017). When ingested, *Rhizobium* induces DNA damage in the intestinal cells of the bacterivorous nematode *Caenorhabditis elegans* (Kniazeva and Ruvkun, 2019). Herbivory by rhizophages belonging to various taxa that feed on leguminous roots determines the establishment and function of *Rhizobium*-legume symbiosis within the root nodule microbiome. These include nematodes, arthropods, molluscs, and vertebrates that feed on roots of various leguminous plants (Brooks et al., 1988; Douglas and Tooker, 2012; Pereira et al., 2018; Gilarte et al., 2020). Herbivory on *Rhizobium*-plant symbiosis involves damage to root nodules and adjacent tissues by mandibulate coleopterous insects such as larval *Cerotoma arcuata* (Chrysomelidae) and *Sitona lepidus* (Curculionidae) that feed on root nodules of leguminous crops (Teixeira et al., 1996; Johnson et al., 2005; Evenden, 2018; Pereira et al., 2018). Sap-sucking organisms such as the root parasitic nematode *Meloidogyne incognita* and bean root aphid *Smynthurodes betae* (Aphididae) also fall into this category of belowground herbivores (Stevenson et al., 2007; Sikora et al., 2018). Molluscs such as slugs engage in rhizophagy through feeding by scraping of leguminous roots of *medicago sativa* among other plants (Douglas and Tooker, 2012). Rhizophagy extends to vertebrate species that interfere with leguminous roots while accessing edible belowground structures (Brooks et al., 1988).

Allelopathy and Rhizobium-Legume Symbiosis

Allelopathy (Greek: allelon=mutual, pathos=harm) is a biointeraction concept that was conceived by Professor Hans Molisch (1856-1937) around the year 1935 (Chou, 2006). Allelopathy is a mutual relationship between organisms that involves the release of secondary metabolites known as allelochemicals (Vokou et al., 2006; Farooq et al., 2020). Allelochemicals may have stimulatory (positive allelopathy) or inhibitive (negative allelopathy) effects among plants, microbes, invertebrates, and other interacting organisms (Cheng and Cheng, 2015; Mahdhi et al., 2018; Schandry and Becker, 2020). Positive allelopathy can also be referred to as "probiosis" while negative allelopathy is termed as "antibiosis" (Yunes, 2019). Allelochemicals produced by the interacting organisms are referred to as "probiotics" and "antibiotics," respectively (Selleck, 1972; Yunes, 2019; Schandry and Becker, 2020).

Release of allelochemicals by leguminous plants can increase their vulnerability to antagonists thereby interfering with nitrogen fixing symbiosis with *Rhizobium*. For instance, cowpea *Vigna unguiculata* and faba bean *Vicia faba* are leguminous hosts of *Rhizobium* that release strigolactone allelochemicals via the carotenoid biosynthetic pathway (Matusova et al., 2005; Miyakawa et al., 2020), which stimulate germination and infection by the parasitic weeds *Striga gesnerioides* and Broomrapes *Orobanche* spp. (Bouraoui et al., 2016; Miyakawa et al., 2020). Flavonoids and strigolactones stimulate the germination of fungal pathogen spores and attraction of parasitic nematodes increasing chances of root infection (Steinkellner et al., 2007; Chin et al., 2018). Antagonistic plants can also release allelochemicals that interfere with leguminous host plants and symbiotic *Rhizobium* species in the rhizosphere (Rice, 1992; Kluson, 1995). For instance, the weed *Sonchus oleraceus* (Asteraceae) produces allelochemicals that inhibit the production of flavonoid compounds and root nodulation in the leguminous weeds *Melilotus indicus* and *Trifolium resupinatum* (Gomaa et al., 2015).

Leguminous host plants and rhizobia also produce allelochemicals that have detrimental effects on other plants, microbes, and herbivores through negative allelopathy (antibiosis). For instance, velvetbean (*Mucuna deeringiana*), jackbean (*Canavalia ensiformis*), jumbiebean (*Leucaena leucocephala*), and wild tamarind (*Lysiloma latisiliquum*) produce phytotoxic allelochemicals that are suppressive to weeds (Caamal-Maldonado et al., 2001). The leguminous weeds *Trigonella polycerata*, *Vicia sativa*, *Lathyrus aphaca,* and *Medicago polymorpha* produce allelochemicals that are suppressive to the growth of rice (*Oryza sativa*) (Zohaib et al., 2017). Forage legumes of the genus *Desmodium* release allelochemicals that are suppressive to the parasitic weeds *Striga* spp. (Pickett et al., 2013). Furthermore, *M. deeringiana* and *C. ensiformis* allelochemicals were found to be inhibitive to plant parasitic nematodes (Caamal-Maldonado et al., 2001). Leguminous plants also release antimicrobial allelochemicals including quercetin, luteolin and other substituted flavones that inhibit pathogens in the rhizosphere (Weston and Mathesius, 2013). Rhizobia on the other hand release allelochemicals that inhibit the activities of other organisms. Such allelochemicals include anti-rhizobial peptides produced by strains of *Rhizobium*, *Mesorhizobium,* and *Sinorhizobium* associated with their enhanced nodulation capacity and competitiveness (Triplett, 1999; Naamala et al., 2016).

Leguminous host plants and rhizobia engage in positive allelopathy (probiosis) in establishing root nodule symbiosis. Leguminous root exudates contain flavonoids that are the main allelochemical attractants for *Rhizobium* symbiosis (Hassan and Mathesius, 2012; Makoi and Ndakidemi, 2012). On the other side, *Rhizobium* secretes lipo-chitooligosaccharide compounds known as Nod factors that induce root nodulation in leguminous host plants (D'haeze and Holsters, 2002; Nandhini et al., 2018). Besides flavonoids, legumes also produce strigolactone allelochemicals that enhance *Rhizobium* activities on host roots (Peláez-Vico et al., 2016; McAdam et al., 2017), while stimulating the germination of arbuscular mycorrhizal fungi that facilitate phosphorus acquisition for improved nitrogen fixation (Püschel et al., 2017; Kafle et al., 2019). Positive allelopathy also exists in the leguminous crop *Trifolium alexandrinum*, which is induced to release high level of flavonoid compounds as a resistance response toward phytotoxic allelochemicals produced by the weed *Sonchus oleraceus* (Gomaa et al., 2015).

It is worth noting that the root words of the "allelopathy" terminology, denote harmful interactions. Therefore, "positive allelopathy" should be limited to situations whereby an organism releases allelochemicals that stimulate activities of the enemy. A good example is the stimulatory effect of plant allelochemicals to parasitic weeds and microbial pathogens. Cases whereby allelochemicals are harmful to other organisms should be considered as "negative allelopathy" or "antibiosis." Stimulatory effects of plant metabolites to symbiotic beneficial microbes such as rhizobium and arbuscular mycorrhizal fungi should not be considered to be any form of allelopathy. These should be termed as "probiosis," a term that would better be delinked from allelopathy.

Beneficial Rhizosphere Biota to *Rhizobium*-Legume Symbiosis

Rhizobium-legume symbioses are associated with rhizosphere organisms that favor their establishment and performance. The most common is the tripartite symbiotic relationship of *Rhizobium* and legumes with endophytic arbuscular mycorrhizal fungi such as *Glomus intraradices* (Scheublin et al., 2004; Scheublin and Van Der Heijden, 2006; Kaschuk et al., 2009, 2010), which enhance the acquisition of phosphorus (Tajini et al., 2012; Meng et al., 2015), while protecting the leguminous roots from attacks by microbial pathogens and root parasitic nematodes (Harrier and Watson, 2004; Wille et al., 2019). The rhizosphere also hosts a range of plant growth promoting microbes including non-nodulating bacterial species that provide services such as nitrogen fixation, nutrient cycling, growth hormone and siderophore production, and biological control while improving soil texture and water holding capacity (Martínez-Hidalgo and Hirsch, 2017; Mishra et al., 2017; Backer et al., 2018; Naik et al., 2019). For instance, apart from biological nitrogen fixation by endophytic rhizobia, other rhizosphere microbes play the roles of ammonification, nitrification, and denitrification that are part of the nitrogen cycle (Pajares and Bohannan, 2016; Kakraliya et al., 2018). Rhizosphere microbes involved in nitrification include the ammonia-oxidizing bacteria (e.g. *Nitrosomonas*, *Micrococcus*, *Europaea*, *Nitrosococcus*, *Nitrosospira*, *Briensis*, *Nitrosovibrio,* and *Nitrocystis*), nitrite-oxidizing bacteria (*Nitrobacter winogradskyi*, *Nitrosococcus mobilis*, *Nitrocystis*, *Nitrospina gracilis*), and nitrite-oxidizing fungi (e.g., *Penicillium*, *Aspergillus*) and actinomycetes (e.g., *Streptomyces*, *Nocardia*) (Paungfoo-Lonhienne et al., 2017; Kakraliya et al., 2018). Legume crops such as peanut (*Arachis hypogaea*) and soybean (*Glycine max*) increase the abundance of soil bacteria and archaea, but they suppress ammonia oxidizers dominated by archaea (Paungfoo-Lonhienne et al., 2017). This is probably due to competition for ammonium between plant roots and nitrifying bacteria (Verhagen et al., 1993). Mineral phosphate solubilizing microbes include bacteria in the genus *Bacillus* and *Pseudomonas* and the fungal genera *Aspergillus* and *Penicillium* (Khan et al., 2007). Biological control by beneficial rhizosphere microbes is offered through mechanisms such as antibiosis, competition for iron, parasitism, production of extracellular cell wall degrading enzymes, and induced resistance (Whipps, 2001). Furthermore, non-nodulating bacterial species that exist in root nodules help the nodulating rhizobia in extending their host range (Wu et al., 2011). *Rhizobium*-legume symbioses may also benefit from rhizosphere invertebrates through phoretic transfer of bacterial cells by nematodes like *Caenorhabditis elegans* that are attracted by plant volatiles to enhance root nodulation (Horiuchi et al., 2005).

RHIZOBIUM-LEGUME SYMBIOSIS AND ABOVEGROUND INTERACTIONS

Increase in Abundance of Aboveground Consumers

Indirect interactions exist between *Rhizobium* in root nodules and consumers in the phyllosphere through host-mediated processes (Kempel et al., 2009). *Rhizobium* infection of leguminous roots has been linked with increased colonization of common bean leaves by the fungal pathogen *Colletotrichum lindemuthianum* (Naluyange et al., 2014, 2016; Karoney et al., 2020). Also, the presence of *Rhizobium* in leguminous roots is associated with increased abundance of arthropods such as aphids and mites (Katayama et al., 2011a,b; Dean et al., 2014; Naluyange et al., 2014, 2016). Besides this, aboveground insects such as clover root weevil (*Sitona lepidus*) prefer ovipositing at the base of *Rhizobium*-infected white clover (*Trifolium repens*) to ensure food availability and hence survival of their larvae (Johnson et al., 2006). Increase in abundance of foliar consumers is due to improved nutritive suitability of rhizobial plants through symbiotic nitrogen fixation (Karoney et al., 2020). Plants infected with root nodulating nitrogen fixing rhizobia become tolerant to herbivory (Naluyange et al., 2014; Ballhorn et al., 2017; Karoney et al., 2020).

Decrease in Abundance of Aboveground Consumers

Rhizobium infection of roots has been associated with inhibition of aboveground consumers through induced resistance mechanisms. Leguminous plants may either exhibit an increase in production of toxic compounds (antibiosis) (Clement et al., 1994; Soundararajan et al., 2013), or may affect the behaviors of the consumers through less attractive volatile emissions and unpleasant tastes (antixenosis) (Clement et al., 1994; Soundararajan et al., 2013). *Rhizobium*-induced antibiosis has been reported in Lima bean (*Phaseolus lunatus*) inoculated with *Bradyrhizobium elkanii* characterized by enhanced cyanogenesis that inhibits the Mexican bean beetle *Epilachna varivestis* (Coccinellidae) (Thamer et al., 2011; Godschalx et al., 2017). Nodulation of *Crotalaria* roots by *Bradyrhizobium* induces the biosynthesis of pyrrolizidine alkaloids that are toxic to grazers (Irmer et al., 2015). *Rhizobium*-induced antixenosis has been reported in Lima bean (*P. lunatus*) inoculated with *B. elkanii* that exhibits reduction in attractiveness to *E. varivestis* (Ballhorn et al., 2013), while the extrafloral nectar is less preferred by the pavement ant *Tetramorium caespitum* (Formicidae) (Godschalx et al., 2015). Apart from resistance mechanisms, rhizobia may establish dense endophytic and rhizosphere populations that compete with host plants for nutrients, and hence interfering with food supply to aboveground consumers. Such a situation may occur in plants growing under nutrient-deficient conditions (Ochieno, 2010, 2020), or when light energy for photosynthesis is not sufficient (Ballhorn et al., 2016).

Suppression of *Rhizobium* by Aboveground Consumers

Aboveground organisms influence symbiotic activities of *Rhizobium* in leguminous roots. Infection of common bean leaves by the fungal pathogen *Colletotrichum gloeosporioides* induces plant defense responses that inhibit root nodulation by *Rhizobium* and colonization by arbuscular mycorrhizal fungi (Ballhorn et al., 2014). In this interaction, *C. gloeosporioides* in the leaves enhances root activity of polyphenol oxidase (PPO) (Ballhorn et al., 2014), an enzyme associated with plant resistance to microbial pathogens (Constabel and Barbehenn, 2008; Taranto et al., 2017). *Rhizobium* usually evades such plant defenses in successful infections to induce root nodulation (Tóth and Stacey, 2015; Cao et al., 2017). However, polyphenol oxidase may not be responsible for suppression of *Rhizobium* nodulation, because the enzyme improves the development, structure, and function of root nodules (Webb et al., 2014). *Rhizobium* inoculation results in high concentration of nitrogen-based compounds including polyphenol oxidase, while reducing the concentration of phenolic compounds and other carbon-based metabolites (Karoney et al., 2020). The absence of polyphenol oxidase results in the accumulation of phenolic compounds (Webb et al., 2014), which are not viable sources of organic carbon for *Rhizobium* development and function compared to the C_4 compounds (fumarate, malate and succinate) (Mitsch et al., 2018).

An alternative explanation is that, aboveground consumers destroy leaves and interfere with photosynthesis while consuming sugars and other nutrients that are required by *Rhizobium* leading to poor root nodulation (Katayama et al., 2014). This is similar to conditions of inadequate light for photosynthesis that constrains symbiosis transforming *Rhizobium* and other mutualists into parasites (Ballhorn et al., 2016). However, there is evidence that herbivory of red alder *Alnus rubra* (Betulaceae) seedlings induces compensatory growth with enhanced root nodulation by the nitrogen-fixing *Frankia* bacteria (Ballhorn et al., 2017). This is a form of *Rhizobium*-induced tolerance to consumers in host plants (Karoney et al., 2020).

RHIZOBIUM IN SUSTAINABLE FOOD SYSTEMS

Sustainable food systems (SFS) are currently being emphasized globally to improve food production in terms of quality and quantity in line with Sustainable Development Goals (SDGs) (ICSU, 2017). This can be achieved through methods and processes that ensure continuous profitability (economic sustainability), having broad-based benefits for society (social sustainability), with positive or neutral impacts on the natural environment (environmental sustainability) (FAO, 2018). Nitrogen-fixing *Rhizobium* species are part of plant growth promoting microbes being developed into bio-inoculants (Giller and Ronner, 2019), as part of Sustainable Food Systems (SFS) (FAO, 2018). The application of *Rhizobium* for biological nitrogen fixation (BNF) restores the function of the nitrogen and carbon cycles (Thornton et al., 2007), which are key nutrient deficiencies in human-disturbed agroecosystems (Morrow et al., 2016; Smith et al., 2016). Rhizobia symbiotically fix approximately 40 million tons of nitrogen in agroecosystems annually (Udvardi and Poole, 2013). Bio-inoculants based on symbiotic nitrogen fixing *Rhizobium* species could help minimize the misuse of synthetic nitrogenous fertilizers (Zahran, 1999), which have been linked to phytotoxicity (Naluyange et al., 2014; Delgado et al., 2016), soil acidification (Sha et al., 2020), and eutrophication of water bodies resulting in algal blooms and water hyacinth invasiveness (Naluyange et al., 2014; Onyango et al., 2020). Besides, the misuse of synthetic nitrogenous fertilizers is a public health concern (Wang and Lu, 2020), as the unassimilated salts in consumed plant tissues and the environment have been linked with health problems including respiratory ailments, cardiac diseases, and cancers (Townsend et al., 2003; Lu et al., 2015).

The coupling of rhizobial nitrogenase activity to leguminous photosynthesis improves carbon dioxide fixation and hence carbon sequestration (Kou-Giesbrecht and Menge, 2019). Nitrogen-fixing legume crops contribute to reduced emission of greenhouse gases associated with global warming and vulnerability to the effects of climate change (Stagnari et al., 2017). Mitigation of the negative effects of atmospheric carbon dioxide can be achieved through legume-based intercropping, agroforestry, conservation agriculture, and organic farming that integrate biological nitrogen fixation by various *Rhizobium* species (Khan et al., 2011; Stagnari et al., 2017). Furthermore, *Rhizobium* species are biological control agents in Integrated Pest Management systems (IPM) (Khan et al., 2011), which act directly on pests through processes such as antibiosis and competition (Deshwal et al., 2003b; Kawaguchi et al., 2012), and indirectly by enhancing tolerance of leguminous plants to pests (Naluyange et al., 2014; Karoney et al., 2020). Biological nitrogen fixation also improves food availability and hence species richness of beneficial organisms that provide ecosystem services such as parasitoids, predators, and pollinators (Mattson Jr, 1980; Barber and Soper Gorden, 2015; Tao et al., 2017).

FUTURE PROSPECTS

The world human population grew past 7.7 billion in the year 2019 and is expected to rise to 9.7 billion by the year 2050 (UN DESA, 2017). Feeding such a fast-growing population requires the intensification of food production systems (Corbeels et al., 2020). The Green Revolution started in the 1960s by Professor Norman E. Borlaug (1914-2009) was meant to ensure increased food production (Borlaug, 2002; Sumberg et al., 2012). However, this Green Revolution was characterized by excessive use of agrochemicals that polluted the environment besides being a threat to food security (van Emden and Peakall, 1996; Carson, 2002; Arora et al., 2020). The development of modern biotechnology industries and their marketing strategies (McCullum et al., 2003; Paarlberg, 2009), whose emphasis is perceived to require more focus on the importance of agroecological approaches (Herren et al., 2015; D'Annolfo et al., 2017), have brought up complex dimensions on the concept of Sustainable Food Systems (Zollitsch et al., 2007; Schütte et al., 2017; Ochieno, 2020). For instance, without adequate agroecological conceptualization, it may be a contentious matter to suggest that, destruction of leguminous biodiversity through herbicide-based weed management (Norsworthy et al., 2010; Corbeels et al., 2020), destroys nitrogen fixing and carbon-fixing machinery that sustain life on earth (Khan et al., 2006; Druille et al., 2015). This is because biodiversity of leguminous plants is associated with complexes of symbiotic nitrogen fixing *Rhizobium* species (Athar and Shabbir, 2008; Marwat et al., 2009).

There is need to establish agroecological management systems that support biological nitrogen fixation as part of the nitrogen cycle, as well as photosynthesis within the carbon cycle, in order to attain sustainable food systems (Tully and Ryals, 2017; Shah et al., 2020). In this case, *Rhizobium*-legume symbioses need to be an integral part of agroecosystems management strategies in the Next Green Revolution (Conway and Barbie, 1988; Arora et al., 2020). Integrated approaches that promote inflow and sufficient utilization of energy and nutrients while limiting the loss of such resources in agroecosystems need to be encouraged. This comprises Integrated Food Energy Systems (IFES) (Sachs and Silk, 1991; Bogdanski et al., 2011), especially those that include leguminous crops (Germaine et al., 2010; Bogdanski, 2012; Orr et al., 2015). Evidence already exists in yield improvement under mixed-cropping systems that include leguminous crops (Ofori and Stern, 1987; Duchene et al., 2017). For instance, agroecological technologies such as Push-Pull that rely on leguminous crops to promote cereal production while suppressing the parasitic weed *Striga hermonthica* and insect pests like the fall armyworm *Spodoptera frugiperda* and the stemborers *Chilo partellus* and *Busseola fusca* (Hailu et al., 2018). The use of organic matter such as compost and mulch to improve soil carbon, nitrogen and other soil properties that benefit *Rhizobium*-legume symbiosis need to be encouraged (Naluyange et al., 2014). Informed and better methods for the application of synthetic fertilizers and pesticides, such as those based on precision agriculture need to be developed for the promotion of *Rhizobium* symbioses (Thilakarathna and Raizada, 2018). There is need to re-examine IPM decision models such as Economic Threshold Levels (ETLs) (Capinera, 1981; Knight and Cammell, 1994), especially in situations whereby herbivore populations are boosted by *Rhizobium*-induced improved nutritive suitability and tolerance in leguminous host plants (Dean et al., 2014; Karoney et al., 2020). This will help in preventing the misuse of pest control products. This should be extended to other beneficial rhizobacteria whose interactions with herbivores have been associated with induced susceptibility in various host plants (Katayama et al., 2010, 2011a,b; Pineda et al., 2012). Resources need to be allocated toward research and innovation in microbial genetic resources (Sharma et al., 2018), so as to identify and develop competitive and efficient *Rhizobium strains* (Irisarri et al., 2019). This should follow guidelines that deliver endophytic plant growth promoting microbes and identifying non-beneficial ones for the bio-inoculant and biofertilizer industry (Avedi et al., 2014; Ochieno, 2020). This should be complemented with research on plant genetic resources to improve *Rhizobium*-legume symbiosis with nutrient use efficiency. Regardless of the technology used to develop such plants and microbes, their function as biotic factors in agroecosystems need to be well-integrated into Sustainable Food Systems conceptual frameworks (Hansen et al., 2017; Afzal et al., 2020). There is need to address disparities in research partnerships related to *Rhizobium*-legume symbioses and other similar plant and soil associated technologies (Giller, 2020; Minasny et al., 2020; Ochieno, 2020). Investment in research on various aspects of *Rhizobium*-legume interactions is necessary for the application of such plant growth promoting microbes for Sustainable Food Systems. Emphasis should be on the application of modern technologies in unraveling the composition and function of root nodule microbiomes in relation to rhizosphere microbiomes of various ecosystems.

AUTHOR CONTRIBUTIONS

DO conceptualization and drafting the manuscript. EK drafting the manuscript and tables. EM, EN, and VN drafting the manuscript and imaging. DB and SS drafting the manuscript. All authors contributed to the article and approved the submitted version.

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