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MiniReview

Lifestyle alternatives for rhizobia: mutualism, parasitism, and forgoing symbiosis

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Abstract

Strains of rhizobia within a single species can have three different genetically determined strategies. Mutualistic rhizobia provide their legume hosts with nitrogen. Parasitic rhizobia infect legumes, but fix little or no nitrogen. Nonsymbiotic strains are unable to infect legumes at all. Why have rhizobium strains with one of these three strategies not displaced the others? A symbiotic (mutualistic or parasitic) rhizobium that succeeds in founding a nodule may produce many millions of descendants. The chances of success can be so low, however, that nonsymbiotic rhizobia can have greater reproductive success. Legume sanctions against nodules that fix little or no nitrogen favor more mutualistic strains, but parasitic strains that use plant resources only for their own reproduction may do well when they share nodules with mutualistic strains.

Keywords: Rhizobium; Ineffective; Evolution; Sanction; Nitrogen-fixation; Symbiosis; Mutualism; Parasitism

1. Introduction

Rhizobia are soil bacteria best known for their symbiosis with legume plants. They are classified in various genera, including *Rhizobium*, *Bradyrhizobium*, *Mesorhizobium*, and *Sinorhizobium*. Rhizobia typically receive carbon fixed by the plant, while the plant receives nitrogen fixed by the rhizobia. Molecular aspects of infection of plant roots by rhizobia, and subsequent N_2 fixation by the bacteroid form of rhizobia inside root nodules, have received considerable attention. Our focus, however, is on why rhizobia that lack genes for infecting legumes are so common in the rhizosphere of some suitable host legumes [1]. Rhizobia that infect legumes but then fix little or no N_2 are also common in some soils [2]. Why have rhizobium strains that do fix N_2 in symbiosis not consistently outcompeted and displaced those of the same species that do not?

Infecting legumes and fixing N_2 in symbiosis is not the only viable life-history strategy for rhizobia, as proved by the numerical abundance of strains with alternative strategies. The strategies of bacteria and plants, however sophisticated, are genetically programmed, rather than learned or chosen. Therefore, the strategy of an individual rhizobium changes only through mutation. For example, an *R. leguminosarum* bv. *phaseoli* strain with the genetic capacity to fix N_2 in symbiosis is still considered a symbiotic strain when it is between hosts, in contrast to nonsymbiotic *R. leguminosarum* bv. *phaseoli* strains, which are unable to infect legumes [3].

Rhizobia genetically programmed to infect legume plants but then to fix little or no N_2 (perhaps due to a mutation in a nitrogenase gene) are less familiar than mutualistic N_2 fixers, but these "ineffective" strains are widespread [2,4,5]. Different strains of rhizobia infecting

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