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Rhizophagy Symbiosis in Cereals: Bacterial Transport of Nutrients to Roots/Oxidative Extraction of Nutrients from Bacteria in Roots

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Cereal grasses carry a small community of symbiotic bacteria on surfaces and interiors of seeds. These bacteria include species of *Bacillus*, *Enterobacter*, *Methylobacterium*, *Pseudomonas*, and *Pantoea*, among others. When the seed germinates the symbiotic bacteria colonize seedling root and shoot meristems and become distributed throughout the plant; simultaneously bacteria colonize the rhizosphere where they reduce growth of soil pathogens and suppress colonization of seedlings by pathogenic fungi. Bacteria also internally colonize cells of the plant—in roots colonizing root cells to establish the ‘rhizophagy symbiosis’. In rhizophagy symbiosis, or rhizophagy cycle (see diagram of rhizophagy cycle), plants obtain nutrients from bacteria that alternate between a root intracellular endophytic phase and a free-living soil phase. Bacteria acquire soil nutrients in the free-living soil phase; nutrients are extracted from bacteria oxidatively in the intracellular endophytic phase. We conducted experiments on seed-vectored bacterial endophytes in rice (*Oryza sativa*), brown-top millet (*Urochloa ramosa*), wheat (*Triticum aestivum*), corn (*Zea mays*), reed grass (*Phragmites australis*) and annual bluegrass (*Poa annua*). In these experiments we found that initially symbiotic bacteria grow on the rhizoplane in the exudate zone behind the root meristem. Bacteria enter root tip meristem cells—locating within the periplasmic space between cell wall and plasma membrane. In the periplasmic spaces of root cells bacteria convert to wall-less L-forms. As root cells mature, bacteria are exposed to reactive oxygen (superoxide) produced by NADPH oxidases on the root cell plasma membranes. Reactive oxygen degrades some of the intracellular bacteria—effectively extracting nutrients from them. Generally, surviving bacteria in root epidermal cells trigger root hair elongation, and as hairs elongate bacteria exit at the hair tips, reforming cell walls and rod shapes as they emerge into the rhizosphere where they may obtain additional nutrients. Later attraction of bacteria to the root exudate zone behind the root tip meristem again places bacteria in position to enter root meristem cells. Experiments involving grass seedlings with and without endophytic bacteria grown on ¹⁵N-labeled proteins suggest that rhizophagy symbiosis could account for as much as 30% of the nutrients absorbed by grass roots. Other experiments using bacteria that differed in resistance to oxidative degradation suggest that bacteria that participate in rhizophagy symbiosis with plants must be adapted to the host plant to the extent that bacteria are susceptible to oxidative degradation within plant root cells, but resistant enough for some bacterial cells to survive and trigger root hair elongation to exit into the rhizosphere. Bacteria resistant to oxidative degradation may enter cells but nutrients cannot be extracted from them and their intracellular numbers cannot be regulated, resulting in parasitisms where plant root growth is suppressed. Due to the

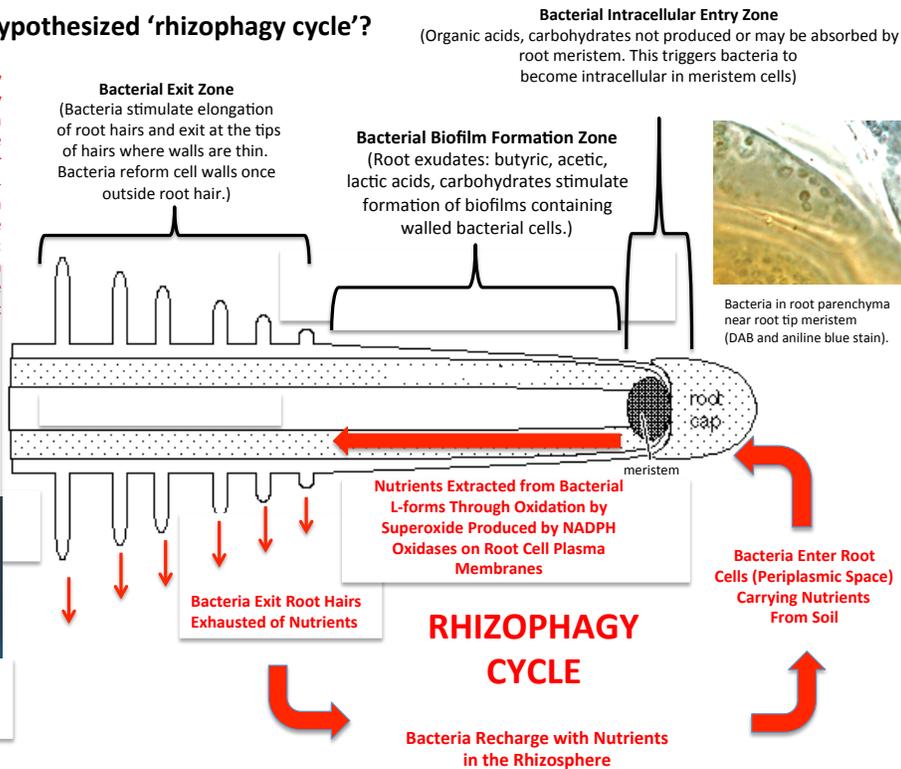
central role that root-tip meristems play in the rhizophagy symbiosis, it seems probable that grasses whose roots ramify prolifically, producing many root tips, may rely heavily on the rhizophagy symbiosis to obtain soil nutrients. Because the rhizophagy symbiosis involves oxidative interactions with intracellular bacteria one outcome of this nutritive symbiosis is increased resistance to oxidative stresses, both of biotic and abiotic origins.

What is the hypothesized 'rhizophagy cycle'?

Definition: The rhizophagy cycle is a process whereby plants obtain nutrients from bacteria that alternate between an intracellular endophytic phase and a free-living soil phase. Bacteria acquire soil nutrients in the free-living soil phase; nutrients are extracted from bacteria oxidatively in the intracellular endophytic phase.



Bacteria emerging from root hair tip of millet seedling.



Isotopic N tracking experiments using tall fescue grass suggest that 30% of the nutrients absorbed by roots could come from bacteria involved in the rhizophagy cycle (see White et al. 2015).

James White; Rutgers University (11/20/2017)