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Cooperation is a no-brainer for symbiotic bacteria

Humans may learn cooperation in kindergarten, but what about bacteria, whose behavior is preprogrammed by their DNA?

Some legume plants, which rely on beneficial soil bacteria called rhizobia that infect their roots and provide nitrogen, seem to promote cooperation by exacting a toll on those bacterial strains that don't hold up their end of the symbiotic bargain, according to a team of researchers at the University of California, Davis.

"In the case of soybeans, it appears that the plant applies sanctions against rhizobia that don't provide nitrogen. The plant does this by decreasing the oxygen supply to the rhizobia," said R. Ford Denison, a crop ecologist in the UC Davis Department of Agronomy and Range Science. "In this way, the host plant can control the environment of the symbiotic bacteria to favor the evolution of cooperation by ensuring that bacterial 'cheaters' reproduce less."

Findings from this study, to be reported in a letter in the Sept. 4 issue of the journal *Nature*, may one day lead to crops that selectively favor the most productive, beneficial strains of rhizobia, thus making optimal use of naturally available nitrogen.

Scientists have long been intrigued by the cooperative relationships between certain legumes -- peas, soybeans and alfalfa -- and the soil bacteria that "fix," or convert, nitrogen from the air into a form that can be used by the plant. While the rhizobia produce nitrogen for the plant, the plant returns the favor by providing nutrients necessary for the growth and reproduction of the bacteria.

Such mutually beneficial relationships are common in nature and would be easier to understand if there were only one bacterial strain associated with the plant. But there are often several competing strains interacting with the plant, and not all of those strains fix nitrogen at the same rate.

Why wouldn't the bacteria that don't expend energy and resources on fixing nitrogen for the plant be fitter because they have more resources available for their own growth and reproduction? Wouldn't the bacterial species that dutifully provide the plant with nitrogen eventually lose out to their goldbricking cousins that aren't doing so?

Denison and colleagues suspected that the plants were somehow penalizing rhizobial species that "cheat" on the symbiotic relationship by fixing little or no nitrogen for the plant. To test that hypothesis, they altered the atmospheric conditions surrounding soybean root nodules containing the rhizobia. By replacing the air with a nitrogen-free argon-and-oxygen mixture, they reduced the rhizobia's ability to fix nitrogen to just 1 percent of normal -- forcing the bacteria to shirk their nitrogen-fixing duties.

The researchers observed the impact of this simulated rhizobial cheating on whole soybean plants, on root systems split in half and grown in different atmospheres, and on individual root nodules.

They discovered that the plants appeared to retaliate by decreasing the supply of oxygen to the root nodules inhabited by the rhizobial species that failed to fix nitrogen. They also found that nitrogen-fixing populations consistently grew to larger numbers over time, perhaps because they had access to more oxygen. The root nodules inhabited by nitrogen-fixing rhizobia grew more, so they cost the plant more but not relative to the benefits they provided to the plant.

"The data illustrate that the soybean plants selectively reward or punish their symbiotic bacteria, based on the amount of nitrogen they provide to the plant hosts," Denison said. "This mechanism helps explain why this ancient cooperation between the plant and various rhizobial strains hasn't already broken down."

He noted that such breakdown in cooperation between species can have serious consequences, as in the case of coral bleaching that results when algae leave or are expelled from the coral.

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Collaborating with Denison on this study were E. Toby Kiers and Robert A. Rousseau of UC Davis' Department of Agronomy and Range Science, and Stuart A. West of the Institute of Cell, Animal & Population Biology at the University of Edinburgh.

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