cycle is driving the insulin (and glucagon) oscillation. It seems reasonable to postulate that the glucose cycle itself reflects cyclic output of glucose by the liver in these fasting animals, a conclusion supported by reported measurements of hepatic glucose production (*13*), although cyclic changes in peripheral glucose utilization have not been excluded. The interval of 0.9 minute between the glucose cycle and insulin cycle is sufficient to encompass recirculation of glucose from the hepatic veins to the pancreatic artery plus time for delays in stimulus-secretion coupling in the islets (*14*). The phase relationships between cycles are appropriate for a linear feedback system with time delay, involving glucose and the endocrine pancreas. However, as Ookhtens *et al.* (*8*) point out, such a simple linear oscillator is inherently unlikely, and a nonlinear system is the better possibility.

The cells of origin of all three components displaying oscillatory behavior (the liver, and the beta and alpha cells of the islets) possess autonomic neural connections and are, at least in part, controlled by the central nervous system (*15*). Accordingly, cyclic stimulation of any or all components can be transmitted from an oscillator in the central nervous system. Since the cycles are not interrupted by atropine, neural transmission would not appear to depend upon parasympathetic innervation.

Another possibility is suggested by the recent demonstration of gap junctions between adjacent islet cells (*16*), the islet cells probable embryonic origin from neural crest, and the observation of spontaneous electrical activity in islet cells (*17*). These observations have suggested the hypothesis that the cells within the islets of Langerhans may function as an integrated unit under certain physiologic circumstances. This hypothesis has been extended to include a role for the D cells in the islets of Langerhans shown recently to contain the secretory inhibitor, somatostatin (*18*). All of these considerations taken together suggest that the observed oscillations in insulin and glucagon could originate with spontaneous fluctuations in activity within the islet complex; however, such a mechanism would require interislet communication.

A central nervous system origin for the oscillations would be greatly supported by finding other oscillations of the autonomic nervous system with which the observed oscillations were entrained. However, examinations of recordings made in rhesus monkeys of heart rate, blood pressure, respiration, skin temperature, and gastric motility failed to uncover cyclic phenomenon of comparable frequency. Further study will be necessary to place these observations in proper physiologic perspective. Our studies indicate that the rhesus monkey is particularly suited for study of this phenomenon, but it seems unlikely that the cyclic behavior of glucose, insulin, and glucagon will prove to be unique to this species.

CHARLES J. GOODNER
BARBARA C. WALIKE
DONNA J. KOERKER, JOHN W. ENSINCK
ARTHUR C. BROWN
ELLIOTT W. CHIDECKEL
JERRY PALMER, LYNNE KALNASY
Regional Primate Research Center, Diabetes Center, and *Departments of Physiology and Biophysics, Medicine,* and *Physiologic Nursing, University of Washington, Seattle 98195*

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21 July 1976; revised 13 September 1976

Interaction of *Beggiatoa* and Rice Plant: Detoxification of Hydrogen Sulfide in the Rice Rhizosphere

Abstract. Beggiatoa *was obtained from six habitats, including four water-saturated soils from rice fields. The isolate of* Beggiatoa *from Bernard clay, when reinoculated into soil treatments from pure culture, significantly reduced hydrogen sulfide levels in soils and increased oxygen release from rice plants. Rice plants significantly increased* Beggiatoa *survival in flooded soils. Some hydrogen sulfide was necessary for survival of the Bernard clay isolate; high concentrations of hydrogen sulfide killed the Bernard clay isolate but were tolerated by a Crowley silt loam isolate from Eagle Lake, Texas. The results suggest that* Beggiatoa *may be an element of wetlands plant ecosystems.*

Pitts *et al.* (*1*) suggested a mutually favorable interaction between the filamentous (gliding) bacterium *Beggiatoa* (*2*) and rice plant. A more general aspect of the physiology and nutrition of the genus *Beggiatoa* and its distribution in soil and water has arisen from studies by Pringsheim and co-workers (*3*). We have shown: (i) that hydrogen sulfide (H_2S) inhibits oxygen release from, and nutrient uptake by, rice plants; and (ii) a correlation between responses of rice cultivars to H_2S and sulfide diseases (*4*, *5*). In this report we describe the mutual interdependence of *Beggiatoa* and rice seedlings exposed to H_2S, as well as specific instances of protection of rice seedlings from H_2S by *Beggiatoa*.

Three types of soil obtained from a greenhouse (GH), the Eagle Lake area in Texas (Crowley silt loam, CSL), and south Louisiana (Bernard clay, BC) were air-dried to kill any indigenous *Beggiatoa*. We placed 300 g of each soil (moist weight) separately into 21 Mason jars (capacity, 946 ml each). These jars were then grouped into seven sets of three jars each. The jars in sets 1, 2, 3, and 4 received sufficient sterile tap water to produce a layer 3.5 cm thick on the soil surface; jars in sets 2, 4, 5, and 7 received approximately 700 trichomes per gram of soil of a pure culture isolate of *Beggiatoa* obtained originally from BC and maintained on agar medium. All jars were then sealed with their lids and placed

Table 1. Survival of *Beggiatoa*, concentrations of H_2S, and oxygen release from 2-week-old rice seedlings in three soils under different treatments for 5 weeks. Rice was planted 3 weeks after starting treatments. Percent survival of *Beggiatoa* was determined by inoculating four soil samples (1 g) from each of three replicate jars into glass tubes that contained enrichment medium. Values for H_2S represent means of three replicate jars with two subsamples per replicate. Oxygen release values are the means of nine seedlings; three per replicate. In both columns and rows, means not followed by the same symbol are significantly different; (P = .05) as determined by Duncan's new multiple range test. Abbreviations: FS, flooded soil; NFS, nonflooded soil; GH, greenhouse soil; BC, Bernard clay; CSL, Crowley silt loam; B, *Beggiatoa*.

Treatment	Percent *Beggiatoa* survival			H_2S concentration (μg/g)			O_2 release (μl/min per seedling)		
	GH	BC	CSL	GH	BC	CSL	GH	BC	CSL
FS	0▲	0▲	0▲	0.27■	0.46▲	0.33●△			
FS + B	58.0●	50.0●	25.0□	0.01○	0.32△□	0.31△□			
FS + rice	0▲	0▲	0▲	0.26■	0.35◍	0.30□	0.42▲	0.39▲	0.39▲
FS + B + rice	91.0△	100.0△	100.0△	0.01○	0.25▩	0.27▩	0.58●	0.55●	0.50●
NFS + B	8.0▲	0▲	0▲						
NFS + rice	0▲	0▲	0▲				0.52●	0.49●	0.49●
NFS + B + rice	25.0□	8.3▲	0▲				0.53●	0.52●	0.50●

in the dark at 25°C. After a 3-week incubation period for H_2S production, each jar in sets 3, 4, 6, and 7 was planted with three sprouted seeds of the rice cultivar Dawn. Soils in the jars of sets 5, 6, and 7 were saturated with sterile tap water. Jars in sets 1 through 4 did not receive additional water. All jars were incubated for two more weeks to allow for the growth of rice plants. Seven treatments were created in which each set of jars represented one treatment (Table 1).

At the end of 5 weeks, H_2S was determined in treatments 1, 2, 3, and 4 by both methylene blue (*6*) and iodine methods (*7*). Oxygen release from the 2-week-old rice seedlings was measured by the method of Joshi *et al.* (*4*).

Four soil samples (1 g) were collected from each of the three jars of a treatment and inoculated into glass tubes (20 by 2.5 cm) containing 40 ml of enrichment medium (*8*). The tubes were covered with Parafilm and incubated at 28°C for 7 days. At the end of this period, each tube was examined and the number of tubes that contained *Beggiatoa* was recorded for each replicate jar. The survival data are shown as the percentages of samples that yielded *Beggiatoa*. Statistical significance of the data was determined by analysis of variance with randomized complete-block or factorial designs and by use of Duncan's new multiple range test.

Interactions between *Beggiatoa*, rice, and H_2S are indicated in Table 1. Flooding resulted in H_2S generation and inhibited oxygen release from rice in all three soils. The presence of *Beggiatoa* in flooded soils significantly increased oxygen release from rice seedlings. Oxygen release from rice seedlings growing in nonflooded soil was unaffected by *Beggiatoa* addition.

Beggiatoa caused significant reductions in H_2S accumulation in GH and BC; however, this reduction was not significant for CSL. Rice alone significantly reduced H_2S concentrations in BC and CSL. Rice and *Beggiatoa* together caused a further reduction in H_2S concentrations in BC and CSL.

Beggiatoa did not survive in nonflooded soils; rice had little or no effect on the survival rate. This may be attributed to the lack of H_2S. Hydrogen sulfide buildup as a result of flooding increased the survival rate of *Beggiatoa* in all soils. A further increase in survival of *Beggiatoa* was observed in the presence of both rice and H_2S.

The isolate of *Beggiatoa* used in these experiments did not survive in any of the three soils when H_2S concentrations were greater than 3 μg/g. However, one strain of *Beggiatoa* was enriched from CSL that contained H_2S in the range of 13.7 to 14.0 μg/g, indicating that some strains may tolerate or require higher levels of H_2S than others.

We have obtained *Beggiatoa* from six habitats. Only the BC isolate could be purified in agar culture by repeated transfer; other isolates were associated in culture with genera of the Pseudomonadales and Eubacteriales. We were unsuccessful in our repeated attempts at enrichment from Eagle Lake, Texas, soils (Crowley very fine sandy, Clodine, and Gessner loams), which are susceptible to straighthead disease of rice (*5*), and from CSL of the Habetz and Hardee sites. This could be a result of the uniformly high concentration of H_2S in the Eagle Lake soils (*9*) or of low *p*H manifested by soils from the three areas (Habetz, 5.2 to 6.0; Hardee, 4.9 to 5.6; Eagle Lake, 5.05 to 5.65). Distribution and concentration of *Beggiatoa* in soils may be important in determining the distribution of sulfide diseases of rice. We have suggested that H_2S is the most prevalent cause of straighthead disease of rice (*5*), although arsenic has been implicated in isolated instances on old cotton land.

Beggiatoa apparently plays an important role in rice paddies, where H_2S accumulation can cause physiological disorders of the rice plant. Oxidation of H_2S by *Beggiatoa* is probably significant not only in rice soils but also in wetlands such as swamps, coastal marshes, and estuaries that sustain plant species which check soil erosion, provide food for aquatic animals, and remove pollutants. High levels of H_2S (30 to 200 μg/g) have been measured in coastal marsh soils (*10*), and *Beggiatoa* has also been associated with the roots of *Spartina* (*11*). The use of *Beggiatoa* for detoxification of H_2S in cultivated and natural ecosystems will hinge on increased knowledge of its activity and survival in soils over extended periods of time.

M. M. Joshi*
J. P. Hollis
Department of Plant Pathology, Louisiana State University, Baton Rouge 70803

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* Present address: Kalo Laboratories, Inc., 525 Kentucky Street, Quincy, Illinois 62301.

15 September 1975; revised 7 June 1976