5. Duck Lake, Kalamazoo County, Mich., is a eutrophic kettle lake with a maximum depth of 3.8 m and a mean depth of 2.0 m [M. C. Miller, thesis, Michigan State University (1972)]. During the summer of 1977, 52 percent of the surface area was covered by water lilies at densities of 10 to 20 leaves per square meter.
6. G. E. Hutchinson, *A Treatise on Limnology*, vol. 3, *Limnological Botany* (Wiley, New York, 1975); H. S. Conard, *The Waterlilies* (Publication 4, Carnegie Institution of Washington, Washington, D.C., 1905); H. E. Laing [*Am. J. Bot.* **27**, 861 (1940)] analyzed the distribution of gases in *Nuphar* sp. but did not report the presence of CH_4, probably because of analytical problems.
7. Bubbles were collected in a funnel held immediately above the sediment surface, and the gas composition was determined by gas chromatography.
8. R. T. Hartman and D. L. Brown, *Limnol. Oceanogr.* **11**, 109 (1966); R. S. Oremland and B. F. Taylor, *ibid.* **22**, 566 (1977). We have also found CH_4 in *Nymphaea odorata*, *Brasenia schreberi*, *Ceratophyllum demersum*, *Polygonum* sp., and *Typha* sp. We sampled the gases by syringe directly from plants in situ or immediately after they had been uprooted. Samples were analyzed by gas chromatography.
9. A low-permeability Saran bag (Anspec Company, Ann Arbor, Mich.) measuring 30 cm by 60 cm was tied closed around the petiole of the leaf. The gas in the bag was sampled through a serum stopper, and the CH_4 concentration was determined by gas chromatography. The volume of the bag was determined at the end of each measurement by the addition of a CH_4 internal standard. The bags are transparent and did not appear to influence leaf behavior. The CH_4 entered the bags within the first few minutes after attachment to the leaves at rates comparable to the rates observed over longer time intervals. Moreover, there was no significant divergence in the petiole gas composition of bagged leaves and adjacent nonbagged leaves.
10. The report by J. Kozuchowski and D. L. Johnson [*Nature (London)* **274**, 468 (1978)] is the first we know of that shows that gases originating in the sediment move through plants to the atmosphere. The rates of efflux they report are very much smaller ($\sim 10^{-5}$) than ours; the difference can be accounted for largely on the basis of the difference in the vapor pressures of Hg and CH_4 in the respective sediments. They suggest that the diurnal pattern of efflux from the plants results from variation in the transpiration rate.
11. The rates were determined with surface gas traps sampled at roughly 6-hour intervals. The insides of Styrofoam cartons (used for shipping acid bottles) were coated with a polyurethane sealant and floated on the lake surface, forming four-chambered surface traps. Any CH_4 entering the traps was diluted in the 1.8-liter atmosphere of the coated chamber. Such a coated chamber lost less than 0.7 percent of its CH_4 per hour. Experiments in which oil was used to slow surface exchange within the floats has revealed that most of the CH_4 accumulating in the traps is the result of ebullition of sediment gas.
12. L. E. Barber, thesis, University of Wisconsin (1974).
13. The leaf efflux value for the littoral zone (19.7 ± 1.6 mmole m^{-2} day^{-1}) is the mean for 18 leaves weighted according to the aerial density of the leaves on the lake. Surface efflux values (littoral zone, 6.7 ± 0.7; limnetic zone, 17.7 ± 2.2 mmole m^{-2} day^{-1}) are derived from extensive data collected over several weeks by gas traps placed on the lake surface (not over emergent leaves). The efflux rate for the littoral zone is therefore the sum of the leaf and surface fluxes; this combined flux is greater than that observed for the open water of the limnetic zone.
14. The total contribution of plants to this efflux in Duck Lake is probably higher than indicated. *Nymphaea odorata*, a white water lily, is fairly abundant in the deeper regions of the littoral zone; from preliminary data on these plants it appears that the flux rates per leaf are comparable to those of *Nuphar*.
15. We thank K. E. Hogg, J. J. Molongoski, E. D. Goodman, D. J. Hall, B. Laughlin, and collaborators in our laboratory. The work was supported by National Science Foundation grant DEB-76-06884 to M.J.K. and J. M. Tiedje and by Environmental Protection Agency grant R803859 to E. D. Goodman. Kellogg Biological Station publication 369; Michigan Agricultural Experiment Station journal article 8407.

13 November 1978

Hydrogenase in *Rhizobium japonicum* Increases Nitrogen Fixation by Nodulated Soybeans

Abstract. *Some* Rhizobium *strains synthesize a unidirectional hydrogenase system in legume nodule bacteroids; this system participates in the recycling of hydrogen that otherwise would be lost as a by-product of the nitrogen fixation process. Soybeans inoculated with* Rhizobium japonicum *strains that synthesized the hydrogenase system fixed significantly more nitrogen and produced greater yields than plants inoculated with strains lacking hydrogen-uptake capacity.* Rhizobium *strains used as inocula for legumes should have the capability to synthesize the hydrogenase system as one of their desirable characteristics.*

The increasing demand for protein and the high cost of producing nitrogen fertilizer pose problems that may be solved in part by more extensive use of biological nitrogen fixation. Soybeans and most leguminous plants form root nodules whose associated bacteria can convert N_2 to ammonia. However, the enzyme that catalyzes the reduction of N_2 to ammonia also produces H_2 as a by-product (*1*), and H_2 production represents a loss of energy that otherwise would be available for N_2 fixation. We now show how this H_2 can be recycled with an accompanying increase in the dry weight and nitrogen content of plants.

Hoch *et al.* (*2*) were the first to observe H_2 evolution from nodules of soybeans. Dixon (*3*) reported that nodules of *Pisum sativum* formed by strain ONA 311 of *Rhizobium leguminosarum* evolved no H_2 but utilized H_2 from an external supply. We observed consistent O_2-dependent H_2 consumption by nodules from several legumes that evolved little or no H_2 under aerobic conditions. A survey (*4*) has revealed that the N_2-fixing potential of many legume-rhizobial associations may be decreased through H_2 losses. Estimates of losses from many agricultural legumes has ranged between 20 to 40 percent of the electron flow through nitrogenase (*5*). Dixon (*3*) concluded that the extent of H_2 loss was influenced by the host legume, but Carter *et al.* (*6*) observed no consistent effect of several different soybean cultivars on H_2 losses from nodules formed by selected strains of *R. japonicum*. There is evidence (*7, 8*) that environmental conditions influence the magnitude of H_2 evolution from nodules of *Pisum sativum*.

Some rhizobial bacteroids possess two enzyme-catalyzed reactions that participate in H_2 metabolism. These include the adenosine triphosphate (ATP)-dependent H_2 evolution reaction of nitrogenase and unidirectional hydrogenase which catalyzes H_2 oxidation in presence of an appropriate acceptor (*5*). Emerich *et al.* (*9*) have shown that H_2 oxidation by bacteroid suspensions increased the ATP content of bacteroids and protected nitrogenase from O_2 damage. Our objective, therefore, was to determine whether the observed physiological benefits of the hydrogenase system could be measured by increased N_2 fixation and growth of nodulated soybeans. We describe greenhouse and growth chamber experiments that compare yields and total N contents of soybean plants inoculated with H_2-uptake positive and H_2-uptake negative strains of *R. japonicum*.

In the first experiment we used five H_2-uptake positive strains and five H_2-uptake negative strains as inocula for soybeans in growth chambers. The strains included in the groups of positive and negative strains were selected on the basis of their capacities to produce reasonably comparable nodule weights and nitrogenase activities in previous experiments where 32 strains were surveyed (*6*) (legend of Table 1). We assumed random distribution of unknown genetic variability among all strains of the two groups that were compared. Capacities to form the hydrogenase system in nodules by the two groups, however, were strikingly different (Table 1).

In the first experiment (Table 1) the nodule weights of plants inoculated with the H_2-uptake negative strains were greater than those inoculated with the H_2-uptake positive strains. Relative efficiency values, which are estimates of the proportion of electron flow through nitrogenase that is utilized for N_2 reduction (*4, 5*) ranged from 0.97 to 1.00 for nodules formed by H_2-uptake positive strains and from 0.66 to 0.84 for nodules formed by the H_2-uptake negative strains. Nodules formed by the H_2-uptake negative strains (Table 1) reduced acetylene at high rates and all evolved H_2. In contrast, nodules formed by the group of H_2-uptake positive strains (Table 1) evolved little or no H_2 and thus showed relative efficiencies near 1.0. Acetylene reduction rates for the two groups of strains, however, were not appreciably different. In comparison with

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plants inoculated with the group of H_2-uptake negative strains, the percentage increases from inoculation with the H_2-uptake positive rhizobia were: dry weight, 15.7; nitrogen percentage, 10.3; total nitrogen in plants, 26.2 (Table 1).

The second trial compared three H_2-uptake negative mutant strains of *R. japonicum* with their antibiotic marked H_2-uptake positive parent (*10*) as inocula for 'Wilkin' soybeans (Table 2). The nodule masses and dry weights of plants in-

Table 1. Comparison of five H_2-uptake positive with five H_2-uptake negative strains of *Rhizobium japonicum* as inocula for soybeans. Soybeans [*Glycine max* (L.) Merr. cultivar 'Wilkin'] were maintained in a growth chamber with a 16-hour light and 8-hour dark cycle, at temperatures of 30°C and 20°C, respectively. Light intensity was 500 μE/m^2 · sec. Relative humidity was maintained at 65 ± 10 percent. Plants were grown in a mixture of sand and vermiculite (1:1) in autoclaved Leonard jar assemblies (*16*). Nitrogen-free Jensen's solution at one-fifth strength (*16*) was added as required. Seeds were surface-disinfected and germinated on 1 percent agar at 30°C. Seedlings for each treatment were inoculated with each of five H_2-uptake positive strains (USDA 136, USDA 110, USDA 122, 3I1b-143, and 3I1b-6), and each of five H_2-uptake negative strains (USDA 16, USDA 135, USDA 120, USDA 117, and USDA 3) of *R. japonicum*. In previous experiments (*6*) with the H_2-uptake positive strains (*6*), ranges in fresh weights of nodules and micromoles of acetylene reduced per hour per gram of fresh nodules were: 2.7 to 3.4, and 13 to 20, respectively. Comparable values for the five H_2-uptake negative strains were: 2.8 to 3.5, and 18 to 24, respectively. An uninoculated control was included. The *R. japonicum* strains used for inocula were cultured with shaking for 7 days at 30°C on a medium containing vitamins, glutamate, and mineral salts (*17*). Leonard jar assemblies were arranged in a completely randomized block design in two growth chambers. After 44 days, a sample of nodules was removed from each culture and tested for H_2 evolution. Two days prior to sampling, the plants were transferred to a controlled environment chamber with photoperiod and temperature regimes that were the same as those used in the growth chambers. Nodule samples (about 0.5 g, attached to root segments) from each pot culture were assayed for H_2 evolution in air, by an amperometric method (*4*). Acetylene reduction assays were performed with a gas chromatograph (*4*). Plants were harvested after 70 days and dried to a constant weight at 70°C; total nitrogen was determined by Kjeldahl digestion (*18*). Relative efficiencies were determined by the method of Schubert and Evans (*4*). Relative efficiency is equal to 1 − (rate of H_2 evolution in air/rate of acetylene reduction), with the rate of acetylene reduction used to estimate nitrogenase electron flux. For the assays of bacteroid H_2 uptake, the amperometric cuvette contained 2.8 ml of bacteroid suspension (*12*). Data are means of six replicate cultures (±S.E.M.) for each strain tested. Analyses of variance showed that differences in means of relative efficiencies, dry weights, percentage nitrogen, and total nitrogen contents of plants inoculated with H_2-uptake postive and H_2-uptake negative strains were significant at 1 percent probability.

R. japonicum strain	Nodule mass (g/culture)*	Acetylene reduction (μmole/g · hour)†	Bacteroid hydrogenase protein (μmole/mg · hour)‡	Relative efficiency	Plant dry weight (g/culture)	Nitrogen (% dry weight)	Total nitrogen (mg/culture)
			H_2-uptake positive strains				
USDA 136	5.1 ± 0.4	15.1 ± 1.6		1.00 ± 0.03	30.8 ± 1.4	3.1 ± 0.1	955 ± 52
USDA 110	4.9 ± 0.5	16.4 ± 1.8	2.3 ± 1.2	0.97 ± 0.09	28.5 ± 1.2	3.2 ± 0.1	912 ± 33
USDA 122	5.3 ± 0.2	18.6 ± 0.4	2.2 ± 0.9	1.00 ± 0.07	30.3 ± 1.2	3.2 ± 0.2	970 ± 38
3I1b-143	5.6 ± 0.2	14.9 ± 2.2	4.7 ± 2.2	0.98 ± 0.01	31.0 ± 1.5	3.2 ± 0.1	992 ± 22
3Ilb-6	5.2 ± 0.3	14.4 ± 2.8	3.6 ± 1.8	0.98 ± 0.03	27.0 ± 1.3	3.2 ± 0.1	864 ± 21
Means	5.2	15.9	3.2	0.99	29.5	3.2	939
			H_2-uptake negative strains				
USDA 16	5.3 ± 0.2	15.8 ± 1.3	<0.05	0.66 ± 0.05	26.8 ± 1.5	2.9 ± 0.1	777 ± 16
USDA 135	6.4 ± 0.2	14.9 ± 2.1	<0.05	0.70 ± 0.05	26.7 ± 1.8	2.9 ± 0.1	774 ± 42
USDA 120	6.4 ± 0.3	12.5 ± 3.5	<0.05	0.67 ± 0.19	27.5 ± 0.9	2.8 ± 0.1	770 ± 29
USDA 117	6.3 ± 0.2	15.0 ± 1.1	<0.05	0.71 ± 0.07	25.2 ± 1.3	3.0 ± 0.1	756 ± 29
USDA 3	5.3 ± 0.4	16.2 ± 4.3	<0.05	0.73 ± 0.04	21.5 ± 1.5	3.0 ± 0.1	645 ± 45
Means	5.9	14.9	<0.05	0.69	25.5	2.9	744
			Uninoculated control				
	0.1 ± 0.1				4.0 ± 0.5	1.7 ± 0.2	5

*Fresh weight. †Per gram of fresh nodule. ‡Per milligram of protein.

Table 2. Comparison of H_2-uptake negative mutants with the parental *Rhizobium japonicum* strains as inocula for soybeans. Soybeans (*Glycine max* (L.) Merr. cultivar 'Wilkin') were grown in autoclaved Leonard jar assemblies (*16*) in the greenhouse in a randomized complete block design under supplemental lighting with a 16-hour light (750 μE/m^2 · sec) period at 30°C, and an 8-hour dark period at 20°C. Leonard jars were provided with one-fifth strength nitrogen-free Jensen's nutrient solution (*16*). Relative humidity was maintained at 60 ± 10 percent. Seeds were disinfected and inoculated with parental H_2-uptake positive strains USDA 122 DES and SR, and H_2-uptake negative mutant strains SR1, SR2, SR3 of *R. japonicum* (*10, 13*). Strain USDA 122 DES is a small-colony derivative of USDA 122. Strain SR is a streptomycin- and kanamycin-resistant mutant of USDA 122 DES. Mutants SR1, SR2, and SR3 were derived from strain SR (*13*). Analyses were made as described (legend of Table 1). Data are means (±S.E.M.) of eight replicate plant cultures for each *R. japonicum* strain tested. Each culture contained five plants, and these were harvested after a growth period of 50 days. Analyses of variance revealed that mean differences in relative efficiencies, plant dry weights, percentage nitrogen, and total nitrogen content of plants inoculated with H_2-uptake positive and H_2-uptake negative strains were significant at the 1 percent probability level.

R. japonicum strain	Nodule mass (g/culture)*	Acetylene reduction (μmole/g · hour)†	Bacteroid hydrogenase (μmole/mg · hour)‡	Relative efficiency	Plant dry weight (g/culture)	Nitrogen (% dry weight)	Total nitrogen (mg/culture)
			H_2-uptake positive parental strains				
USDA 122 (DES)	3.8 ± 0.3	9.8 ± 1.1	4.0 ± 0.3	0.99 ± 0.03	13.3 ± 0.8	3.3 ± 0.1	442 ± 34
SR	3.8 ± 0.3	12.5 ± 0.9	3.9 ± 0.3	1.00 ± 0.04	14.0 ± 0.5	3.3 ± 0.1	459 ± 21
Means	3.8	11.2	4.0	0.99	13.6	3.3	450.5
			H_2-uptake negative mutant strains				
SR1	3.7 ± 0.1	15.9 ± 1.2	<0.05	0.79 ± 0.04	11.4 ± 0.5	3.1 ± 0.1	349 ± 9
SR2	3.3 ± 0.2	14.1 ± 0.6	<0.05	0.84 ± 0.06	10.4 ± 0.5	3.0 ± 0.1	305 ± 11
SR3	3.1 ± 0.2	15.4 ± 1.1	<0.05	0.80 ± 0.05	9.1 ± 0.4	2.8 ± 0.1	251 ± 14
Means	3.4	15.1	<0.05	0.81	10.3	3.0	302
			Uninoculated control				
	0				4.0 ± 0.2	1.0 ± 0.1	40 ± 5

*Fresh weight. †Fresh nodule. ‡Hydrogen oxidized per milligram of protein as measured by the amperometric procedure (*4*).

oculated with the mutants were less than those of plants inoculated with the parental strains (Table 2). The ratios of nodule mass to dry weight for plants nodulated with the H_2-uptake negative mutants were greater than comparable ratios for plants inoculated with the H_2-uptake positive parental strains (Table 2). The increase in dry weight and nitrogen contents of plants nodulated by the H_2-uptake positive strains cannot be accounted for by differences in nodule weight.

In agreement with previous reports (*3–5, 11*) all H_2-uptake positive strains produced nodule bacteroids with hydrogenase activity (Table 2), but no activity was detected in the nodule cytosol (soluble nonbacteroid part of the nodule). In contrast, no measurable hydrogenase activity could be detected in bacteroids from nodules that evolved H_2, and these observations agree with the other reports (*6, 12*). The acetylene reduction rates of nodules formed by the H_2-uptake negative mutant strains were somewhat less than acetylene reduction rates of nodules formed by the H_2-uptake positive parental strains. In comparison with the plants inoculated with the H_2-uptake negative mutants, the percentage increases from inoculation with the H_2-uptake positive parental strains were: dry weight, 32; nitrogen, 13; and total nitrogen in plants, 49 (Table 2). Although all three of the H_2-uptake negative mutants behaved similarly in previous studies (*13*) in this experiment, the mean total nitrogen content of plants inoculated with SR3 was less than that of plants inoculated with mutants of SR1 or SR2. The mutants were selected on the basis of their inability to take up H_2, and further characterization of them is required and is in progress.

In both experiments a regression analysis revealed highly significant positive correlations between relative efficiency values and total nitrogen contents of plants ($r^2 = .92$ and $r^2 = .90$ for data in Tables 1 and 2, respectively). Also, in both experiments, analyses of variance revealed that dry weights, percentage nitrogen, and total nitrogen in plants inoculated with the H_2-uptake positive strains were significantly higher than comparable values for plants inoculated with the H_2-uptake negative strains (Tables 1 and 2). The data from the two different types of experiments are consistent, showing in both cases that plants with nodules containing the hydrogenase system fixed more N_2 and produced greater dry weights than plants that were nodulated with the H_2-uptake negative strains.

Any process that would decrease H_2 evolution by nitrogenase or contribute toward recycling of the evolved H_2 should increase nodule relative efficiency, as defined by Schubert and Evans (*4*), and should lead to increased N_2 fixation and plant growth, provided that N_2 fixation is limited by the energy provided by carbon substrates. Hardy and Havelka (*14*) have suggested that the supply of carbon substrates from photosynthesis is a major factor limiting N_2 fixation by legumes. The diversion of energy from nitrogenase by H_2 evolution would be expected to have a deleterious effect on N_2 fixation and plant growth. The maximum benefits of the hydrogenase system to N_2 fixation in the legume-*Rhizobium* symbiosis would be predicted when the energy supply for support of N_2 fixation is limiting.

The results of these greenhouse experiments are consistent with those obtained in a field trial (*11*). From the combined evidence we conclude that incorporation of the hydrogenase system into the gene pool of existing rhizobial inocula is desirable and may contribute toward increased productivity of soybeans. Beneficial effects of the hydrogenase system in a strain of cowpea *Rhizobium* also has been observed (*15*). It seems reasonable that use of H_2-uptake positive strains of *Rhizobium* species for the inoculation of other legumes may contribute to increased efficiency of the N_2-fixing process.

STEVE L. ALBRECHT, ROBERT J. MAIER
F. JOE HANUS, STERLING A. RUSSELL
DAVID W. EMERICH, HAROLD J. EVANS
Laboratory for Nitrogen Fixation Research, Oregon State University, Corvallis 97331

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19. Supported by grants from the Cooperative State Research Service (701-15-30), NSF (77-08784), and the Oregon Agricultural Experiment Station (Paper No. 4978). We thank N. T. Jennings, K. R. Carter, and Dr. T. Ruiz-Argüeso for technical help and discussions. Two of us (D.W.E. and R.J.M.) thank the Rockefeller Foundation for postdoctoral fellowships. We thank Dr. G. Ham of the University of Minnesota and Dr. D. Weber of the USDA for providing strains of *R. japonicum*.

20 October 1978; revised 19 December 1978

Ammonia Volatilization from Senescing Leaves of Maize

Abstract. *Ammonia release by plants growing in normal air is reported. Contrary to observations made at high ambient ammonia concentrations, corn plants did not absorb ammonia in normal air but released it as they senesced, even while photosynthesizing actively.*

Studies of the global ammonia cycle have either ignored living plants (*1*) or treated them solely as sinks (*2, 3*). Several workers have demonstrated that plants assimilate gaseous ammonia (*2, 4*), but they imposed external partial pressures of ammonia (30 to 20,000 nbar) that were much higher than those found in unpolluted areas (1 to 8 nbar) (*5*). Their results have been extrapolated to field conditions (*2*) on the assumption that the rate of absorption of ammonia is the product of the stomatal conductance to diffusion of ammonia and the concentration of ammonia in the surrounding air, the concentration in the leaf being assumed zero. The assumption that the internal concentration is negligible appeared to be borne out in experiments in which high external concentrations were used (*2, 4*), but these imposed concentrations were so high as to obscure the presence of a small internal partial pressure of a few nanobars. Meyer (*6*) showed that plants released ammonia into air from which the ammonia had been re-

0036-8075/79/0323-1257$00.50/0