# Effect of Localized Nitrogen Availability to Soybean Half-Root Systems on Photosynthate Partitioning to Roots and Nodules'

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#### ABSTRACT

Soybean (Glycine max [L.] Merr. cv Davis) was grown in a split-root growth system designed to maintain control of the root atmosphere. Two experiments were conducted to examine how 80% Ar:20% O2(Ar:O2) and air (Air) atmospheres affected N assimilation (NH4N0 $_3$  and N $_2$  fixation) and the partitioning of photosynthate to roots and nodules. Application of NH<sub>4</sub>N0<sub>3</sub> to nonnodulated half-root systems enhanced root growth and root has been suggested that selective partitioning of photosynthate to respiration at the site of application. A second experiment applied Ar:0<sub>2</sub> or air to the two sides of nodulated soybean half-root systems for 11 days in soybean plant that is nodulated by strains of varying effectiveness to the following combinations: (a) Air to both sides (Air/Air); (b) Air to one side, Ar:0<sub>2</sub> to the other (Air/Ar:0<sub>2</sub>), and (c) Ar:O<sub>2</sub> to both sides (Ar:O<sub>2</sub>/Ar:O<sub>2</sub>). Results indicated that dry matter and current photosynthate ('°C) were selectively partitioned to nodules and roots where N<sub>2</sub> was available. Both root and nodule growth on the Air side of Air/Ar:O<sub>2</sub> plants was significantly greater than the Ar:O<sub>2</sub> side. The relative partitioning of carbon and current photosynthate between roots and nodules on a half-root system was also affected by N2 availability. The Ar:O<sub>z</sub> sides partitioned relatively more current photosynthate to roots (57%) than nodules (43%), while N<sub>2</sub>-fxing root systems partitioned 36 and 64% of the carbon to roots and nodules, respectively. The Ar:O<sub>2</sub> atmosphere decreased root and nodule respiration by 80% and nitrogenase activity by 85% compared to halfroot systems in Air while specific nitrogenase activity of nodules in Ar:O<sub>2</sub> was 50% of nodules supplied Air. Results indicated that nitrogen assimilation, whether from N<sub>2</sub> fixation or inorganic sources, had a localized effect on root development. Nodule development accounted for the major decrease in total photosynthate partitioning to non-N2-fixing nodules. Soybean compensates for ineffective nodulation by controlling the flux of carbon to ineffective nodules and their associated roots.

Legumes may be nodulated by many different strains of Rhizobium within a cross-inoculation group (8). Strains of Bradyrhizobium japonicum commonly found in soil vary in their symbiotic effectiveness (15) with soybean. Studies in which a native population of *Rhizobium* was overcome with an inoculant strain did not always result in increased N2 fixation (5, 16, 17) even when the inoculant proved to be a superior symbiont compared to native soil strains (16).

While investigations have been conducted concerning competition between strains for nodule sites (6, 10), little effort has been directed toward understanding host control of nodule development and function when a root system is nodulated by

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strains of varving effectiveness. It seems unlikely that the host can discriminate, on the basis of a nonfunctioning nitrogenase system, against invasive but ineffective symbionts during the infection process. Reports have indicated that substantial ineffective nodulation (25-35% of total) could be present without a proportional decrease in N<sub>2</sub> fixation by Trifolium subterraneum (12) and Glycine max (14). It effective nodules for development is a mechanism which allows a maintain N<sub>2</sub> fixation rates similar to plants nodulated with a single effective strain (14).

Pate et al. (11) and Atkins et al. (1) removed N2 from the rooting environment to determine how inhibition of N<sub>2</sub> fixation affected the partitioning of carbon and metabolic activities of Vigna unguiculata and Lupinus albus. Although N<sub>2</sub> fixation ceased when nodules were exposed to 80% Ar:20% O<sub>2</sub> (v:v) atmospheres, the evolution of CO<sub>2</sub> from the nodulated non-N<sub>2</sub>fixing root systems remained at 67% of air controls (11), and the partitioning of dry matter to nodules and roots (1, 11) was unaffected. Using populations of Medicago sativa with a recessive gene for ineffective nodulation, Cralle and Heichel (4) demonstrated that relative partitioning of dry matter and current photosynthate to nodules was not related to nodule bacteroid effectiveness. These results indicate that nodule development is not related to N2 fixation and the export of ammonium-N products from nodules. If this is the case, legumes could exercise little regulatory control over which nodules are developed on a root system infected by strains of Rhizobium which vary in their degree of effectiveness with the host.

Our experiments were designed to determine whether soybean selectively partitions photosynthate and controls development of nodules and roots where the assimilation of N occurs. We employed a split-root technique in two experiments and controlled either inorganic N assimilation (NH<sub>4</sub>NO<sub>3</sub>) with localized applications to nonnodulated roots or controlled N2 fixation by controlling the availability of N2 to half-root systems. In the latter experiment, both half-root systems were nodulated with the same strain of B. japonicum.

By utilizing the same strain of *B. japonicum* on both sides of a split-root system and controlling the availability of N2 to nodules, we effectively eliminated genetic differences (strain virulence, for example) as a potentially confounding variable affecting carbon partitioning to roots and nodules.

## MATERIALS AND METHODS

Split-Root Assembly. A split-root assembly (Fig. 1) was constructed from PVC pipe and fittings. The two rooting chambers of the system were 5.1 cm diameter (i.d.) x 24.5 cm long PVC pipe (ASTM schedule 40) stoppered (No. 11) at bottom and top. A modification of a planting elbow (13) was made by drilling a 0.95 cm diameter hole in the elbow of a 2.20 cm diameter (i.d.)



FIG. 1. Design of a split-root growth system to control the rooting atmosphere of soybean half-root systems.

90° PVC elbow (slip x slip). A 2.50 cm length of 1.91 cm diameter (i.d.) PVC pipe was glued into each side of the planting elbow such that it extended beyond the end of the elbow by 0.8 cm. This sleeve served as an insert fitting to a 2.20 cm diameter (i.d.) 45° PVC elbow which was fitted to a hole (2.7 cm diameter) in the side of the rooting chamber. A wax seal was formed at the rooting chamber end of each 45° elbow by melting toilet bowl gasket wax (Longhorn Wax Bowl Gasket, Kirkhill, Inc. Downey, CA 90241),' standing one end of the 45° elbow on a piece of weighing paper and pipetting in 3.0 ml of wax. After cooling, the paper was removed. We have found with other types of splitroot assemblies that this wax does not harm roots and also prevents any movement of rhizobia between connected rooting chambers. The 45° elbows were either glued into the rooting chambers with Oatly grey PVC glue (no primer) in experiment 1 or sealed in place with toilet bowl wax in experiment 2. The glue is recommended, without primer the elbows can be removed for reuse and form a seal more resistant to pressure than the wax. Under pressures developed in these experiments there was no flushing of gases through the seals. The 90° elbows and 45° elbows were packed with wet horticultural vermiculite. The vermiculite below the planting hole in the 90° elbow was packed firmly. The 90° elbow was fit into the 45° elbows and the joint was secured with tape. Movement of elbows after root penetration of seals must be prevented to maintain a gas tight seal. Rooting chambers were filled with a layer (3 cm) of coarse gravel then to the top of the  $45^{\circ}$  elbow with silica sand (No. 20). The assemblies were secured firmly into holes drilled in a length of 4.45 cm x 9.53 cm board which served as a base.

Three plastic aquarium tubing connectors (1.0 mm i.d., 3.0 mm o.d., Plen Plax miniature connectors) were glued into each

<sup>2</sup> Neither conclusions of this paper nor mention of a product name constitute an endorsement by the granting agencies.

rooting chamber. Two adjacent connectors were fitted 2.3 cm from the top of the chamber. One received a flexible plastic tube (Plen Plax Miniature air line tubing) connected to an irrigation system, and the second served as a gas outlet. Nitrogen-free nutrient solution (13) was pumped from a reservoir through a PVC manifold. A check valve was installed in the main line so that the lateral lines serving each rooting chamber remained full between irrigations. Gases therefore could not be exchanged between tubes. A drainage hole 1.3 cm diameter and 2.5 cm from the bottom of each tube remained stoppered except to drain excess nutrient solution after irrigation.

**Planting and Plant Culture.** Seeds of soybean (*Glycine max* [L.] Merr. cv Davis) were surface sterilized in 2% NaOCI for 2 min, rinsed, and planted hilum down in wet, sterile vermiculite. Forty-eight h later uniform seedlings were selected (radicle length 2 cm), the root tip cut off, and the cut radicle inserted into a 3 mm diameter hole made in the wet vermiculite at the top of the 90° elbow. Sterile water was applied (2-3 ml) to the vermiculite to ensure contact between the media and the radicle. Plants were shaded for 1 d then placed in the greenhouse at Hamakuapoko, Maui. Assemblies were oriented on an East to West axis because differential temperature between sides of the planting elbow at the time of planting caused an uneven split of roots.

Plant roots emerged through the wax seals 5 DAP.<sup>3</sup> Plants, grown in unstoppered, open assemblies until gas treatment started, were irrigated every other day until solution was at the level of the drainage hole (experiment 1) or excess allowed to drain (experiment 2).

**Experiment 1.** Assemblies were connected to a gas delivery manifold 12 DAP. One tube of each assembly was supplied with C0<sub>2</sub>-free air (gases passed through NaOH and silica gel) at the rate of 66 ml min-', and the other tube was supplied with a mixture (v:v) of 80% argon:20% oxygen (Ar:O<sub>2</sub>) at 66 ml min-'. A total of 60 mg N as NH<sub>4</sub>NO<sub>3</sub> was applied to the half-root systems in three equal applications at 13, 17, and 27 DAP. Nitrogen was applied to the half-root systems in three combinations: (a) Air (60 mg N), Ar:O<sub>2</sub> (0 mg N); (b) Air (0 mg N), Ar:O<sub>2</sub> (60 mg N); and (c) Air (30 mg N), Ar:O<sub>2</sub> (30 mg N). Applications were made with stock NH<sub>4</sub>NO<sub>3</sub> diluted in 20 ml of plant nutrient solution. Four plants were harvested at treatment initiation; final harvest was at 28 DAP. Additions of nutrient solution were made without drainage through the system. Assemblies were arranged in a completely randomized block design with four replications.

**Experiment 2.** Both sides of each assembly were inoculated 6 DAP with 106 cells of *Bradyrhizobium japonicum* strain USDA 110 (USDA, Beltsville, Md.) suspended in 20 ml of plant nutrient solution. Plants were grown with the assemblies unstoppered for an additional 25 d. Five plants were harvested at treatment initiation (31 DAP) when rooting chambers of the remaining plants were supplied with CO<sub>2</sub>-free air or a 80% Ar:20% O<sub>2</sub> gas mixture delivery manifold in the following combinations: (a) Air, Air; (b) Air, Ar:O<sub>2</sub>; and (c) Ar:O<sub>2</sub>, Ar:O<sub>2</sub>. Flow rates were 66 ml min-'. Plants were arranged in a completely randomized block design with five replications and harvested 42 DAP.

**Harvest.** Plants were harvested by block between 0930 and 1430 h. Assemblies from one block were disconnected from the gas and irrigation systems, the plastic connectors sealed with serum stoppers, and all assemblies of a block placed in a sealed clear plastic chamber. The  ${}^{14}CO_2$  (1 .1 x 10<sup>7</sup> Bq) was generated by injecting 10 ml of 3.0 N lactic acid through a serum stopper in the side of the chamber into a vessel containing [ ${}^{14}C$ ]NaHCO<sub>3</sub> in 10 ml 0.1 N NaOH. A fan within the chamber was used to circulate the  ${}^{14}CO_2$ . Plants were allowed to assimilate  ${}^{14}CO_2$  for 45 min then removed from the chamber. PAR ranged from 450 to 560 ìE M<sup>-2</sup> s-' and temperature from 27 to 30°C within the

<sup>3</sup> Abbreviation: DAP, days after planting.

chamber during harvest. The top rubber stopper was removed from the rooting chamber, a small plastic dish was placed on top of the sand, and 10 ml of  $0.1 \ N$  NaOH was pipetted into the dish. The tops of tubes were then quickly sealed with parafilm. Assemblies without plants were also incubated as controls. The shoot of the plant was cut at the planting elbow after a 90-min chase period, and the NaOH trap was removed to a stoppered calibrated tube and brought to a final volume of 25 ml with CO<sub>2</sub> free deionized H<sub>2</sub>O. Roots were cut at the wax seals and removed from the chambers to a 1.0 L plastic container, which was then injected with 50 ml acetylene and incubated for 15 min. Gas samples were taken with 10 ml evacuated tubes (Vacutainers). Roots were washed free of sand and placed on ice. Shoots and roots were dried at 65°C, and nodules were then removed from roots, counted, and weighed.

**Analysis.** The evolution of  $CO_2$  from root systems was determined by titration. Ten ml subsamples of the diluted NaOH trap were titrated with 0.09 N HCl after treatment with 5 ml 3 N BaCl<sub>2</sub>.

Ethylene production was determined by GC.

Dried nodules were ground with a mortar and pestle. Roots were cut into 1 to 3 mm sections. Subsamples of roots and nodules were weighed (12-15 mg), placed in scintillation vials, rehydrated with 0.5 ml  $H_2O$ , and then suspended in 10 ml of scintillation cocktail (Scintiverse II, Fisher Scientific). Radioactivity in the NaOH traps was determined by adding 10 ml of cocktail to 1.0 ml samples of the trap.

#### **RESULTS AND DISCUSSION**

Localized applications of inorganic nitrogen affect root development at the point of application (7). Mineral nitrogen also affects the distribution of dry weight between shoots and roots of soybean (3). Our experiments examine how inorganic N and N<sub>2</sub> fixation affect the partitioning of both current photosynthate and dry matter to roots and nodules of soybean. Our approach simulates the carbon partitioning of soybean nodulated in the field by a native population of rhizobia consisting of both effective and ineffective strains of *Bradyrhizobium japonicum*.

Experiment 1 demonstrated that the Ar:O<sub>2</sub> atmosphere (80% air:20% O2, v:v) did not affect total root development and shoot growth (Table I). All plants received 60 mg N during the 15-d treatment period. Nitrogen application doubled root weights of half-root systems receiving N compared to those receiving no N regardless of the atmosphere in the rooting media. There was balanced root growth when N was applied equally to both sides of the root. Root respiration of half-root systems followed a similar pattern as dry matter partitioning to half-root systems. Respiration of "CO<sub>2</sub> (Table I) by +N roots was 10 times that of roots receiving no nitrogen compared to only a doubling in total CO<sub>2</sub> evolution by +N half-root systems. Specific radioactivity of root systems (data not shown) was not significantly affected by nitrogen application to root systems. Current photosynthate is preferentially translocated to roots assimilating nitrogen. The flux of current photosynthate from shoot to +N roots is many times faster than to -N roots and is due to the greater size of the root sink rather than greater respiratory output per unit root weight.

Soybean can derive N from both mineral or symbiotic sources. Symbiotic N can be derived from many different nodules formed by a variety of strains of *B. japonicum*. Each nodule, usually induced by a single strain of rhizobia, forms a discrete metabolic interaction with the host in terms of supply of photosynthate and output of fixation products. Which strain of rhizobia forms nodules on the root is a function of ecological factors, strain competitiveness, and strain interaction with the host (2), and probably has little to do with their degree of effectiveness for fixing  $N_2$  (10). Controlling development of individual nodules

may therefore be one mechanism available to the host to counter the effects of infection by ineffective or lesser effective strains. Earlier work which removed N<sub>2</sub> from the rooting medium indicated that N<sub>2</sub> fixation had only a minor effect on nodule development even though root and nodule respiration was severely decreased (1, 11).

The partitioning of dry matter between shoots, roots, and nodules of soybean with nodulated half-root systems supplied with either  $CO_2$ -free air (Air) or Ar:O\_2 is displayed in Table II. Relative partitioning of dry matter to below ground parts was identical for plants receiving Air on both sides (Air/Air) and plants with one-half the root system in Ar:O\_2 (Air/Ar:O\_2). Dry matter gains were similar for roots and nodules and accounted for 7 and 8% of total dry matter gain, respectively. Relatively more dry matter was allocated below ground of plants with both root halves in Ar:O\_2 (Ar:O\_2/Ar:O\_2) compared to plants supplied with N\_2. Roots and nodules of Ar:O\_2/Ar:O\_2 plants accounted for 15 and 4% of dry matter gain, respectively.

Soybean selectively partitions dry matter to the source of  $N_2$  fixation (Table II). Growth of nodules and roots on the Air side of Air/Ar:O<sub>2</sub> plants was significantly greater than on the Ar:O<sub>2</sub> side and significantly greater than root and nodule growth of Air/Air plants. Root growth of Ar:O<sub>2</sub>/Ar:O<sub>2</sub> plants was greater than on the ArO<sub>2</sub> side of Air/Ar:O<sub>2</sub> plants. Respiratory output followed a similar pattern. Results indicate that host dry matter partitioning to below ground parts is controlled by nitrogen assimilation whether the N source is inorganic or from N<sub>2</sub> fixation. Localized stimulation of soybean root growth by effective nodulation has been reported (13). Our data indicate that root stimulation is the result not of genetic interaction between rhizobial strain and the host but is due to the products of N<sub>2</sub> fixation.

Current photosynthate is selectively partitioned to the source of fixed N<sub>2</sub> (Table III). The evolution of "CO<sub>2</sub> from roots and nodules supplied with Air was more than 10 times that of Ar:O<sub>2</sub> root systems during the 90-min chase period. Treatment differences in "CO<sub>2</sub> evolution were relatively greater than differences in total CO<sub>2</sub> evolution (Table II). This indicates that the flux of current photosynthate to N<sub>2</sub>-fixing nodules and their associated roots is greater than in non-N<sub>2</sub>-fixing root sections. Roots and nodules of half-root systems supplied with Air had twice the amount of "C label per mg tissue as Ar:O2 roots and nodules. Partitioning of "C-labeled photosynthate was a function of both the size and intensity of the below ground sink created by N<sub>2</sub> fixation. Relative treatment differences in specific nitrogenase activity (acetylene reduction) per unit weight of nodule tissue was similar to differences in specific radioactivity in the nodule (Table III). The decline in total nitrogenase activity by nodules supplied with Ar:02 was due mainly to a decrease in nodule development and only partially accounted for by decreased specific activity. The nitrogenase system remained active for 11 d despite the absence of N<sub>2</sub> substrate. Atkins et al. (1) returned nodulated Vigna unguiculata supplied with Ar:O2 to Air after 3 d and observed a rapid return to normal rates of nitrogenase activity. Our results indicate that host control of the nodule system when nodule N output is restricted is primarily one of restricted carbon allocation for further nodule development. Respiration by Ar:O<sub>2</sub> nodules may have been used for hydrogen evolution (11) and nodule maintenance. It may be that one role of hydrogen evolution by the nitrogenase enzyme complex is to maintain nodule integrity when normal N<sub>2</sub> fixation or demand for nodule products is limited.

The effect of  $N_2$  deficiency on the relative partitioning of current photosynthate to roots and nodules is displayed in Table IV. Half-root systems exposed to Ar:O<sub>2</sub> environments had relatively more "C label in roots than in nodules, while the opposite was true when nodules were fixing N<sub>2</sub>. Earlier reports indicated

Table I. Effect of NH<sub>4</sub>NO<sub>3</sub> and Ar:O<sub>2</sub> on Shoot and Root Weights and Root CO<sub>2</sub> Respiration of Split-Root Sovbeans

	Treatment*					
	Air +N	Ar:O <sub>2</sub> -N	Air -N	Ar:O <sub>2</sub> +N	Air ½N	Ar:O <sub>2</sub> ½N
	mg plant <sup>-1</sup>					
Shoot weight	736a <sup>b</sup>		606a		691a	
Weight of half root <sup>e</sup>	119ab	61c	56c	128a	87bc	103ab
Total root weight	180	Da	184a		190a	
CO2 respiration h <sup>-1</sup>	1.59a	0.74c	0.99c	1.59a	1.38ab	1.22b
			dps	× 10 <sup>-3</sup>		
14CO2 respiration h-1	3.10a	0.23c	0.38c	2.96a	1.36b	1.56b

<sup>a</sup> Air, Ar:O<sub>2</sub> (80% Ar:20%O<sub>2</sub>) indicates which atmosphere was supplied to each half-root system of a plant; 60 mg N to the half root system (+N); 0 mg N to the half root system (-N); 30 mg N to each half-root system ( $\frac{1}{2}$ N). Treatments initiated at 12 DAP and plants harvested at 28 DAP. <sup>b</sup> Data within a row not followed by the same letter are significantly different at P = 0.05 according to LSD. <sup>c</sup> Root weight of a half-root system at treatment initiation = 14 mg.

### Table II. Dry Matter Partitioning and CO2 Respiration of Roots and Nodules of Half-Root Systems of Soybean with Root Systems Exposed to Either Air or Ar:O2 Atmosphere for 11 d

Data are net increases in dry matter from treatment initiation to final harvest. Dry weight at treatment initiation: shoot, 360 mg; half-root system, 93 mg; nodules on half-root system, 20 mg.

		H	lalf-root Sys	tems Exposed	to	
	Air	Air	Air	Ar:O <sub>2</sub>	Ar:O <sub>2</sub>	Ar:O <sub>2</sub>
				mg		
Shoot weight	134	Oaª	10	40b	52	0c
Root weight	63b	61b	77a	23c	47Ь	48b
Nodule weight	69ab	59b	79a	8c	13c	15c
Total	157	la	12	26b	63	4c
CO2 respiration h <sup>-1</sup>	4.8ab	4.2b	5.3a	0.8c	1.0c	1.2c

<sup>a</sup> Data not followed by the same letter within a row are significantly different at P = 0.05 according to LSD.

 

 Table III. Effect of Air or Ar:O2 Atmospheres Applied to Nodulated Half-root Systems of Soybeans on the Respiration and Partitioning of Current <sup>14</sup>C-Labeled Photosynthate by Nodules and Roots and on Nodule Nitrogenase Activity

		Hal	f-Root Syster	n Exposed to	)	
	Air	Air	Air	Ar:O2	Ar:O <sub>2</sub>	Ar:O <sub>2</sub>
			$dps \times l$	0-2		
14CO2 respiration h <sup>-1</sup>	74.2a*	66.3a	78.3a	7.0b	2.7b	2.5b
<sup>14</sup> C mg <sup>-1</sup> nodule	0.72ab	0.77a	0.59b	0.34c	0.34c	0.28c
<sup>14</sup> C mg <sup>-1</sup> root	0.29ab	0.30a	0.25b	0.16c	0.16c	0.14c
			µmol C2H	I4 h <sup>-1</sup>		
Nitrogenase activity per						
half-root system	14a	10a	14a	2b	2b	2ь
Nitrogenase activity g-1						
nodule	158a	150a	145a	64b	61b	47Ь

<sup>a</sup> Data not followed by the same letter within a row are significantly different at P = 0.05 according to LSD.

Table IV. Percent of Below Ground <sup>14</sup>C-Labeled Photosynthate in Roots and Nodules of Soybean with Root Systems Exposed to Either Air or Ar:O<sub>2</sub> Atmospheres for 11 D

		Half-Root Systems Exposed to						
	Air	Air	Air	Ar:O <sub>2</sub>	Ar:O <sub>2</sub>	Ar:O <sub>2</sub>		
				%				
Roots	33a <sup>a</sup>	38a	36a	56b	59b	56b		
Nodules	67a	62a	64a	44b	41b	44b		

<sup>a</sup> Data within a row not followed by the same letter are significantly different at P = 0.05 according to LSD.

that nodules of *Medicago sativa* accounted for relatively little of below ground <sup>14</sup>C-labeled photosynthate (4). The chase period from <sup>14</sup>C labeling in that experiment was 24 h compared to the brief chase (90 min) we employed. It is likely that after a prolonged chase period most radioactivity in the nodule is associated with structural material (9), and the relative amount of total plant radioactivity found in the nodule does not measure the allocation of current photosynthate.

The "C partitioning to roots and nodules of  $Ar:O_2$  half-root systems was not affected by having Air on the opposite side. Although increased availability of photosynthate in Air/Ar:O<sub>2</sub> plants compared to  $Ar:O_2/Ar:O_2$  plants did alter the allocation of total dry matter increases to below-ground parts (Table II), there was no localized effect on the pattern of <sup>14</sup>C partitioning within a half-root system.

Our experiments indicate that N2 fixation creates a strong localized sink for photosynthate that affects both root and nodule development. The control of carbon flow to roots and nodules is affected by the output of N<sub>2</sub> fixation products from nodules. Selective carbon partitioning mainly affects the size of the below ground sink and only partially affects root and nodule function. The effects of nitrogen assimilation on carbon partitioning to roots are similar whether the source of N is inorganic or from N2 fixation. The selective partitioning of carbon to N2-fixing nodules may indicate how the host plant compensates for infection by invasive but ineffective strains of Rhizobium. The preferential development of effective nodules by the host indicates that this mechanism may even play a role in the dynamics of soil rhizobial populations. Upon nodule senescence larger effective nodules could release many more rhizobia into the soil than ineffective strains and could ultimately enrich the soil with effective strains.

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