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Azospirillum spp. participation in dry matter partitioning in grasses at the whole plant level

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Abstract Plant growth-promoting rhizobacteria, particularly those from the genus *Azospirillum* spp., may affect root functions such as growth and nutrient/water uptake, which in turn may affect shoot growth. Calculations based on data from literature on shoot and root mass of crop grasses (79 plant/bacteria associations were analyzed) revealed that inoculation with *Azospirillum* spp. increased the shoot-to-root (S/R) ratio in about half of reported cases and decreased the S/R ratio in the other half. In 11 of 35 cases, the S/R ratio increased when the shoot mass increased more than the root mass. In 23 of 35 cases, the root mass did not increase, yet the S/R ratio still increased. Thus, the increase in the S/R ratio indicated that shoot growth responds to inoculation more than root growth. A decrease in the S/R ratio occurred when (a) root growth dominated shoot growth even though both increased (16 of 36 cases), or (b) root growth either increased or remained unchanged, and shoot growth was either unaffected or even decreased (19 of 36 cases). This analysis suggests that: (a) *Azospirillum* spp. participates in the partitioning of dry matter (both carbon compounds and minerals) at the whole plant level . by affecting root functions, and (b) the bacteria affect crop grass through multiple mechanisms operating during plant development.

Key words *Azospirillum* spp. · Crop plants · Plant growth-promoting rhizobacteria · Plant inoculation · Rhizosphere · Shoot-to-root ratio

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Introduction

Shoot-to-root ratio in plants is affected by the balance between shoot-specific (carbon supply) and root-specific (mineral and water uptake) activities (Davidson 1969; Thornley 1972; Agren and Ingestad 1987; Johnson and Thornley 1987). Various abiotic vehicles and biotic factors in the rhizosphere can affect root functioning (Peterson 1992) and in turn the S/R ratio. For example, temperature can significantly affect the Slit ratio (Davidson 1969; Larigauderie et al. 1991), and mycorrhizal fungi can increase the S/R ratio through increased .phosphorus uptake (Hall et al. 1984; Saif 1987).

Azospirillum is a rhizosphere bacterium that nonspecifically increases plant growth and yield (Jagnow 1987; Bashan and Levanony 1990; Kennedy and Tchan 1992), and several modes of action have been proposed (for a recent review see Bashan 1993). Most proposed mechanisms attributed the bacterial effect to a change in a single factor such as a specific hormone, mineral or water uptake, or specific enzymatic activity. One proposed mechanism involves cumulative, multiple mechanisms which combine to produce the observed effects (Bashan and Levanony 1990); however, to date there has been little consideration of the plant as a whole, e.g., major postinoculation changes that occur in the important functions of the entire plant and which can be measured by changes in the root-to-shoot ratio. Evaluation of the changes in root or shoot mass without considering their ratio is not adequate to clarify the effects of the inoculation at the whole plant level. Simultaneous data on the S/R ratio (or the R/S ratio) and on changes in the root and shoot mass for inoculated plants are relatively rare (Ferreira et al. 1987; Morgersten and Okon 1987; Kucey 1988), but when combined together they contain information on the prevalence of shoot or root growth after inoculation.

The aims of this study were to: (a) analyze data from the literature to determine whether the effect of inoculation by *Azospirillum* spp. is a whole plant phenomenon rather than a root-site phenomenon, and (b) to see whether these

data support any of the proposed mechanisms suggested for the effect of *Azospirillum* spp. inoculation on plants. An abstract of this study has been presented elsewhere (Dubrovsky and Bashan 1993).

Methods

In the literature, the question of how *Azospirillum* spp. affects the S/R ratio has not been addressed specifically. However, data concerning root and shoot dry weights are available in papers dealing with the effects of inoculation on various parameters of plant growth and development. The S/R calculations presented here are based on data from the international scientific literature. It should be noted that the increase or decrease in shoot-to-root ratio in inoculated plants may have occurred when both shoot mass and root mass increased (or decreased) even though each plant part changed its weight. Thus it is necessary for this type of analysis to simultaneously consider changes in dry mass partitioning with changes in the S/R ratio. Our calculations were made strictly from data which met the following criteria: (a) shoot and root mass data were obtained from the same plant species and from experiments in which both parameters were measured, (b) noninoculated and inoculated plants of the same age were maintained under similar environmental conditions, and (c) changes in root and shoot masses after inoculation were analyzed statistically by the original authors. Many references were not considered because they did not meet these exact criteria even though some of them contained data on dry mass partitioning.

Plant response to *Azospirillum* spp. inoculation varied greatly between plant species. To decrease this variability, only data from crop grasses were considered. A total of 79 individual cases of plant/bacteria association met the above criteria.

Results

The S/R ratios of noninoculated and inoculated plants were calculated (Table 1). The number of changes in shoot mass, root mass and the S/R ratio are presented in Table 2. These data demonstrate that *Azospirillum* spp. inoculation increased the S/R ratio in about half of reported cases and decreased the S/R ratio in the other half. The S/R ratio was unchanged in about 3% of the cases. The general distribution. pattern of the data of the 79 cases did not show a normal distribution. Further general analysis by the nonparametric Mann-Whitney test showed no difference between the S/R ratio of inoculated and noninoculated plants.

In 11 of 35 cases, the S/R ratio increased when the shoot mass increased more than the root mass. In 23 of 35 cases, the root mass did not increase, but the S/R ratio still increased (Table 2). An increase in the S/R ratio indicates that shoot growth responds to inoculation more than root growth, suggesting increased efficiency of the root as an absorbing organ when colonized by *Azospirillum* spp.

A decrease in the S/R ratio occurred when (a) root growth dominated shoot growth, even though both increased (16 of 36 cases) or (b) when root growth either increased or remained unchanged, and shoot growth was either unaffected or even decreased (19 of 36 cases) (Table 2). The decrease in the S/R ratio suggests that *Azospirillum* spp. affects root functions by increasing root mass, which indirectly leads to an increase in shoot growth.

The ratios presented in Table 1 were further analyzed by dividing the S/R ratio of inoculated plants by the SIR ratio of noninoculated plants originating from the same experiments. For the 79 cases analyzed in this study, the new ratio (R/R, the ratio of the ratios) fits a normal distribution pattern and was 1 ± 0.3 (mean ± SD, $n = 79$) (Fig. 1).

Discussion

The idea that the proportions of leaf, stem, shoot and root mass in most terrestrial plants should maintain a functional equilibrium is decades old (White 1937). Thus, factors participating in the partitioning of dry matter between the shoots and the roots are highly significant to the well being of the plant (Dewar 1993). The simplest equilibrium is between the shoot and the root material, expressed as the shoot:root ratio (S/R). Thornley's various models (Thornley 1972; Reynolds and Thornley 1982; Brugge and Thornley 1984) for dry matter partitioning between shoots and roots are currently the most acceptable theoretical models that explain and predict the responses of S/R to deficits of water, major nutrients, light and carbon dioxide, and to defoliation and root pruning. These models, however, cannot explain changes in S/R as a response to minor 'nutrients, nutrient toxicity or temperature differences (Wilson 1988). To the best of our knowledge, no current model explains the effect of inoculation with plant growth promoting rhizobacteria (PGPR) on the whole plant. Our lack of knowledge on the mechanisms governing dry mass partitioning for plants in general is one of the main limitations in developing models to understand the function of the whole plant (Landsberg et al. 1991; Dewar 1993). The main obstacle is that dry matter partitioning is the result of numerous large and small processes at different organizational levels operating over a large period of time (such as assimilation and translocation of substances, respiration and substrate storage). These functions involve practically all of the internal, environmental and genetic factors controlling plant growth (Dewar 1993).

Inoculation of plants with *Azospirillum* spp. may involve all or part of the above factors. The proposed modes of action of this bacterium over the last 2 decades point up the possibility that perhaps there is no major mechanism involved. Bashan and Levanony (1990) suggested that perhaps more than one mechanism is involved at the same time, and that perhaps individual mechanisms are less significant when evaluated separately. For example, N_2-fixation contributes less than 5% of the observed effect of these bacteria on the plant (Lin et al. 1983), yet when combined with other factors, this may be a significant contribution. Only the combined activities of all the involved mechanisms may be responsible for the measured effects of *Azospirillum* spp. inoculation on plants. When the exact mechanism is unknown, it would be more practical to look at the effect of *Azospirillum* spp. on the whole plant rather than only at organ, tissue, cellular or subcellular levels. The literature analysis presented in this study pointed

Table 1 Changes in shoot-to-root ratio in plants inoculated withshoot and root dry weight; *S*- or *R*- statistically proven no change in *Azospirillum* spp. *S* shoot. *R* root, *i and d* statistically significant in-shoot and root dry mass, * statistically proven no change in the S/R crease and decrease in dry mass of root or shoot after inoculation,ratio compared to control, (*i*) *and* (*d*) statistically insignificant increase in

S and R response	Plant/bacteria pairs	S/R ratio		References
		Control	Inoculation	
S/R increase				
SiRi	*Sorghum bicolor* x *S. sudanense* cv. Vidan/ *A. brasilense*	0.46	0.78	Kapulnik et al. 1981b ('Table 1)
SiRi	*Panicum miliaceum/A. brasilense* (mixed strains)	0.81	1.16	Kapulnik et al. 1981b (Table 1)
SiRi	*Triticum aestivum* cv. Deganit/ *A. brasilense* Cd	0.94	1.13	Bashan et al. 1990 (Fig. 2)
SiRi	*Triticum aestivum* cv. Deganit/ *A. brasilense* 245	0.94	1.03	Bashan et al. 1990 (Fig. 2)
SiRi	*Triticum aestivum* cv. Tikal/*A. brasilense* 245	0.87	1.11	Bashan et al. 1990 (Fig. 2)
SiRi	*Triticum aestivum* cv. Tikal/*A. brasilense* Cd	0.87	1.18	Bashan et al. 1990 (Fig. 2)
SiRi	*Triticum aestivum* cv. Tikal/*A. brasilense* 246	0.87	1.18	Bashan et al. 1990 (Fig. 2)
SiRi	Tridcum *aestivum* cv. Tikal/*A. brasilense* 67	0.87	0.95	Bashan et al. 1990 (Fig. 2)
SiRi	*Triticum* aestivurn cv. Cadet, line R2A/ *A. brasilense* ATCC 29145	2.21	2.94	Rennie and Larson 1979 (Table 1)
SiRi	*Triticum aestivum* cv. Cadet, line R5D/ *A. brasilense* ATCC 29145	2.58	2.85	Rennie and Larson 1979 (Table 1)
S(i)R(i)	*Sorghum bicolor* x *S. sudanense* cv. Hazera 697/ *A. brasilense* Cd	1.45	2.20	Morgersten and Okon 1987 (Table 2)
SiR-	*Triticum aestivum* cv. Cadet, line R2A/ *A. brasilense* ATCC 29145	2.55	5.50	Rennie and Larson 1979 (Table 1)
SiR-	Oryza sativa cv. IR421 *A. lipoferum* 34 H	1.42	1.50	Murty and Ladh 1988 (Table 2)
SiR-	*Pennisetum americanum* cv. Gahi 3/ *A. brasilense* Sp 13t SR2	4.39	6.18	Tier et al. 1979 (Table 2; 32 days)
SiR-	*Pennisetum americanum* cv. Gahi 3/ *A. brasilense* Sp 13t SR2	4.31	4.82	Tien et al. 1979 (Table 2; 12 days)
SiR-	*Zea mays* cv. Dea/*A. lipoferum* CRTI	3.07	3.55	Arsac et al. 1990 (Table 4, trial 2; 10^8 cfu ml^{-1})
SiR-	*Zea mays* cv. Dea/*A. lipoferum* CRT	3.07	3.31	Arsac et al. 1990 (Table 4, trial 2; 10^7 cfu ml^{-1})
SiR-	*Zea mays* cv. Dea/*A. lipoferum* CRT	3.07	3.85	Arsac et al. 1990 (Table 4. trial 2; 10^6 cfu ml^{-1})
SiR-	*Zea mays* cv. Eva/*A. lipoferum* CRTl	1.86	2.08	Arsac et al. 1990 (Table 5)
SiR-	*Sorghum bicolor* cv. Hazera 226/*A. brasilense* (mixed strains)	*1*.41	2.31	Kapulnik et al. 1981b (Table 3)
SiR-	*Setaria italica/A. brasilense* Sp-7	3.50	3.75	Nur et al. 1980 (Table 2)
SiR-	*Triticum aestivum* cv. Rescue, line C2D/ *A. brasilense* ATCC 29145	2.15	4.86	Rennie and Larson 1979 (Table 1)
S-R-	*Triticum aestivum*/*A. brasilense* Sp-7	1.26	1.32	Rennie and Larson 1979 (Table 1)
S-R-	*Setaria italica*/*A. brasilense* Cd-3	3.50	3.89	Nur et al. 1980 (Table 2)
S-R-	*Sorghum bicolor* cv. Funk's G 522/ *A*: *brasilense* JM 125	3.80	4.21	Lee and Gaskins 1982 (Table 2)
S-R-	*Sorghum bicolor* cv. Funk's G 522/ *A. brasilense* JM 125	3.36	3.57	Lee and Gaskins 1982 ('Fable 3)
S-R-	*Sorghum bicolor* cv. Funk's G 522/ *A. brasilense* JM 125	2.96	3.39	Lee and Gaskins 1982 (Table 3)
S-R-	*Zea mays*, H-708/*A. brasilense*, strain 1774	3.00	3.45	Stancheva and Dinev 1992 (Table 2)
S-R-	*Triticum dicoccum*, AB genome/ *A. brasilense*, strain 1774.	3.17	3.97	Stancheva and Dinev 1992 (Table 2)
S-R-	*Festuca arundinacea* cv. El Palenque/ strains of *A. brasilense* *ATCC* 29145 and *A. lipoferum* Sp G	3.23	3.57	Perotti et al. 1987 (Table 1; experiment 1)
S-R-	*Festuca arundinacea* cv. El Palenque/ strains of *A. brasilense* ATCC 29145 and *A. lipoferum* Sp G	2.33	2.70	Perotti et al. 1987 (Table 1; experiment 2)
S-R-	*Zea mays* cv. Marina /*A. lipoferum* CRTI	3.08	3.12	Arsac et al. 1990 (Table 5)
S-R-	*Zea mays* cv. Sirena /*A. lipoferum* CRT I	3.75	3.78	Arsac et al. 1990 (Table 5).
S-R-	*Triticum aestivum* cv. Carasinho/ *A. brasilense* Wa5	1.56	1.61	Christiansen-Weniger and Van Veen 1991 (Table 5)
SdRd	*Triticum aestivum*/*A. brasilense* Sp 107	1.44	1.52	Ferreira et al. 1987 (Table 3, $N0_3^-$ l m*M*, experiment 1)

Table 1 (continued)

S and R response	Plant/bacteria pairs	SIR ratio		References
		Control	Inoculation	
SIR decrease				
SiRi	*Triticum aestivum* cv. Cadet /*A. brasilense* ATCC 29145	2.84	2.53	Rennie and Larson 1979 (Table 1)
SiRi	*Triticum aestivum* cv. Rescue, line C5B/ *A. brasilense* ATCC 29145	4.37	2.70	Rennie and Larson 1979 (Table 1)
SiRi	*Triticum aestivum* cv. Rescue, line C5D/ *A. brasilense* ATCC 29145	2.06	0.97	Rennie and Larson 1979 (Table I)
SiRi	*Triticum* aestivun cv. Iafit/*A. brasilense* (mixed strains)	1.07	0.83	Kapulnik et al. 1981b (Table 2)
SiRi	*Triticum aestivum*/*A. brasilense* Sp 245	1.26	1.19	Ferreira et al. 1987 (Table 3, NO_3^- 10 m*M*, experiment 1)
SiRi	*Sorghum bicolor* x *S. sudanense* cv. Hazera 697/ *A. brasilense* Cd	2.12	2.07	Morgersten and Okon 1987 (Table 2, 12 days)
SiRi	*Triticum aestivum* ev. Deganit/*A. brasilense* 28	0.94	0.85	Bashan et al. 1990 (Fig. 2)
SiRi	*Setaria italica*/*A. brasilense* Cd	3.50	2.82	Nur et al. 1980 (Table 2)
SiRi	*Triticum aestivum* cv. Fidel/*A. brasilense S*p Br 14	3.40	2.33	Warembourg et al. 1987 (Table 1)
SiRi	*Triticum aestivum* cv. Miriam/*A. brasilense* (mixed strains)	4.0	3.45	Kapulnik et al. 1985 (Table 3)
SiRi	*Triticum aestivum* cv. Carasinho/*A.brasilense* C3	1.56	1.29	Christiansen-Weniger and Van Veen 1991 (Table 5)
SiRi	*Triticum aestivum* cv. Carasinho/*A.brasilense* C5	1.56	1.19	repeat
S(i)R(i)	*Setaria italica*/*A. brasilense* ATCC 29279	4.12	2.73	Kapulnik et al. 1981a (Fig. 4, 10 mg 1^{-1} NH_4N0_3)
SiRi	*Setaria italica*/*A. brasilense ATCC* 29279	8.30	3.00	repeat, 40 mg 1^{-1} NH_4NO_3
S(i)R(i)	*Setaria italica*/*A. brasilense* ATCC 29279	2.94	2.74	repeat, 100 mg 1^{-1} NH_4NO_3
S(i)R(i)	*Setaria italica*/*A. brasilense* ATCC 29279	7.13	5.29	repeat, 200 mg 1^{-1} NH_4NO_3
S(i)R(i)	*Festuca arundinacea* cv. El Palenque/mixed strains of *A. brasilense* ATCC 29145 and *A. lipoferum* sp G	3.33	2.77	Perotti et al. 1987 (Table 2, experiment 4)
S-Ri	*Triticum aestivum* cv. Miriam/*A. brasilense* (mixed strains)	2.24	1.84	Kapulnik et al. 1985 (Table 2)
S-Ri	*Sorghum bicolor* x *S. sudanense* cv. Hazera 697/ *A. brasilense* Cd	2.15	1.86	Morgersten and Okon 1987 (Table 2, 20 days)
S-Ri	*Triticum aestivum*/*A. brasilense S*p 245	1.44	1.16	Ferreira et al. 1987 (Table 3, $N0_3^-$ 1 m*M*, experiment 1)
S-Ri	*Triticum aestivum* cv. Fielder/*A. brasilense Cd*	1.89	1.42	Kucey 1988 (Table 1)
SdRi	*Triticum aestivum* cv. Chester/*A. brasilense* Cd	2.45	1.71	repeat
S(d)R(i)	*Festuca arundinacea* cv. El Palenque/mixed strains of *A. brasilense* ATCC 29145 and *A. lipoferum* sp G	2.33	2.08	Perotti et al. 1987 (Table 2; experiment 3)
S(d)R(i)	*Festuca arundinacea* cv. EI Palenque/ndxed strains of *A. brasilense* ATCC 29145 and *A. lipoferum* sp G	3.33	2.50	Perotti et al. 1987 (Table 2; experiment 5)
S-R-	*Sorghum bicolor* cv. Funk's G 522/*A. brasilense* JM 125	4.14	4.07	Lee and Gaskins 1982 (Table 2; 105 mg $1^{-1}NO_3^-$)
S-R-	*Zea mays*/*A. brasilense*	3.68	3.14	Albrecht et al. 1981 (Table 2, +N)
S-R-	*Zea mays*/*A. brasilense*	4.92	3.08	Albrecht et al. 1981 (Table 2, -N)
S-R-	*Setaria italica*/*A. brasilense* Cd-1	3.50	2.82	Nur et al. 1980 (Table 2)
S-R-	*Triticum aestivum* cv. Cadet, line R5B/*A. brasilense* ATCC 29145	5.05	4.21	Rennie and Larson 1979 (Table 1)
S-R-	*Triticum aestivum* cv. Rescue/A. *brasilense* ATCC 29145	2.78	2.24	Rennie and Larson 1979 (Table 1)
S-R-	*Triticum aestivum* cv. Rescue, line C2A/*A. brasilense* ATCC 29145	6.28	2.94	Rennie and Larson 1979 (Table 1)
S-R-	*Triticum boeticum* Boiss/*A. brasilense*, strain 1774	2.93	1.59	Stancheva and Dinev 1992 (Table 2)
S-R-	*Aegilops speltoides* Tausch/*A. brasilense, strain* 1774	9.53	5.33	Stancheva and Dinev 1992 (Table 2)
*S-R-*_.	*Triticum timopheevi* Zhuk/*A. brasilense*, strain 1774	3.42	2.37	Stancheva and Dinev 1992 (Table 2)
S-R-	*Dazypyrum villosum* Candargi/*A. brasilense*, strain 1774	3.71	3.08	Stancheva and Dinev 1992 (Table 2)
S-R-	*Triticum aestivum* cv. Chinese Spring/*A. brasilense*, strain 1774	3.80	3.19	Stancheva and Dinev 1992 (Table 2)
SdRd	*Triticum aestivum*/*A. brasilense* Sp 7	1.44	1.27	Ferreira et al. 1987 (Table 3, $N0_3^-$ 1 m*M*, experiment 1)

Table 1 (continued)

S and R response	Plant/bacteria pairs	S/R ratio		References
		Control	Inoculation	
No change in SIR				
SiRi	*Sorghum bicolor* x S. *sudanense* cv. Hazera 697/ *A, brasilense Cd*	3.30	3.00	Morgersten and Okon 1987 (Table 1)*
SiRi	*Triticum aestivum* cv. Tikal/*A. brasilense* 28	0.87	0.88	Bashan et al. 1990 (Fig. 2)
SiRi	*Triticum aestivum* cv. Deganit/*A. brasilense 246*	0.94	0.93	Bashan et al. 1990 (Fig. 2)
SiRi	*Triticum aestivum* cv. Deganit/*A. brasilense* 67	0.94	0.91	Bashan et al. 1990 (Fig. 2)
SiR-	*Sorghum bicolor* x S. *sudanense* cv. Hu= 697/ *A. brasilense Cd*	2.13	2.18	Morgersten and Okon 1987 ('Table 2)
S-R-	*Sorghum bicolor* cv. Funk's G 522/*A. brasilense* JM 12	3.66	3.66	Lee and Gaskins 1982 (Table 2; 53 mg^{-1} NO_3^-)
S-R-	*Triticum aestivum*/*A. brasilense* Sp 107	1.26	1.27	Ferreira et al. 1987 (Table 3, NO_3^- 10 m*M*, experiment 1)
S-R-	*Zea mays* cv. Fulvia/*A. lipoferum* CRTI	2.70	2.66	Arsac et al. 1990 (Table 5)

Table 2 Various cases of shoot and root dry mass change at increased and decreased S/R ratio in plants inoculated with *Azospirillum*. From the analysis of Table 1. Abbreviations are the same as in Table 1

S/R ratio increased				S/R ratio decreased					No change		
SO	SiR-	S-R-	SdRd	SiRi	S-Ri	SdRi	S-R-	SdRd	SiRi	SiR-	S-R-
11	11	12	1	16	4	3	12	1	4	1	3

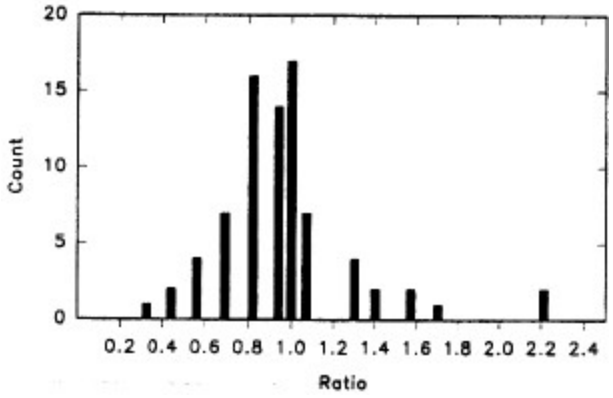

Fig. 1 Distribution of S/R ratio in inoculated plants vs noninoculated plants, calculated from data presented in Table 1. The calculation was made by dividing the S/R ratio of inoculated plants by the S/R ratio of noninoculated plants of the same experiment. Counts are the numbers of individual cases sharing the same ratio in different experiments

out that the general effect of *Azospirillum* spp. on the entire plant was largely overlooked. From the changes the bacteria produces in the S/R ratio, it appears that it also participates (in a mechanism as yet unknown) in the partitioning of carbon compounds within the plant, in addition to its experimentally proven ability to enhance water and mineral uptake by the plant (Murty and Lada 1988; Sarig et al. 1988; Bashan et al. 1990).

There are hundreds of reports on the effects of *Azospirillum* spp. on yield and plant parameters. However, most are presented from an agronomic (changes in the size of the plant part) or economic (yield per unit area) point of view (Jagnow 1987; Basher and Levanony 1990), rather than from a physiological point of view. This analysis revealed the possibility that when investigating a particular controlling mechanism (such as hormonal effects by the bacteria, a particular enzymatic activity or a new phenotype derived from genetic engineering), one should also consider evaluating these agronomic parameters as they are reflected by changes in the S/R ratios. An S/R ratio is easily and quickly measurable and provides information about whether the bacteria affect plant growth.

Thus, from the data presented in Tables 1 and 2 and Fig. 1, we believe that *Azospirillum* spp. may affect root functions in two major ways: (a) by increasing the efficiency of the root as an absorbing organ (increased S/R ratio in 23 out of 35 cases where there was no increase in root mass) and/or (b) by increasing root mass relative to shoot mass (decreased S/R ratio in 23 out of 36 cases where root mass increased). In both types of response, inoculation increased shoot growth.

In conclusion, this analysis of the literature (a) suggests that future physiological studies on *Azospirillum* spp. should look at the bacteria's effect at the whole plant level and (b) provides experimental data (although collected from many diverse studies) that the mode of action of *Azospirillum* spp. is probably composed of multiple, smaller mechanisms as previously suggested (Basher and Levanony 1990).

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