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ROOT-MICROORGANISMS ASSOCIATIONS IN ARID AND SEMI-ARID AREAS TO BENEFIT PLANT GROWTH

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Semi-arid tropics have been defined approximately as those regions where evapotranspiration exceeds precipitation for 5 to 10 months of the year, mainly during a long dry season, and where the mean annual rainfall is in the range of 400 - 1200mm. These semi-arid areas are amongst the least favoured from an agricultural point of view and the yield of crops and pastures is generally very low. This situation results not only from the harshness of the climate but also from the fragility and the poor quality of the soils, whether chemical or physical properties are concerned (Charreau, 1974). The arid areas are obviously in a still more critical position.

Different approaches have been proposed to improve this situation but, up to now, the microbiological approach has been largely neglected. In this paper, we would like firstly to try to answer to the question whether microbiological methods have the potentiality of increasing the productivity of arid and semi-arid ecosystems, and secondly to point out the types of investigation which should be developed in order to extrapolate the microbiological methods with the highest potential to the field.

Trees play a prominent role in the arid and semi-arid areas since they provide not only timber and fuel, but also fodder and shade for the cattle; moreover they protect soils against erosion and even contribute to the reclamation of waste and desert lands. Consequently a special attention is given to the microbiological methods which could contribute to the establishment and development of trees in arid and semi-arid ecosystems.

1. POTENTIALITIES OF MICROBIAL INOCULATION

There is now ample evidence that by properly manipulating some elements of the soil microflora, one can significantly improve plant growth especially in harsh edaphic or climatic conditions. The soil microflora can be manipulated not only directly by acting upon the microorganisms, but also by acting indirectly through the plant or the soil. The direct approach implies the use of sterilization, inoculation procedures, and the application of specific inhibitors, or stimulating substances. Here, we are mainly concerned by the inoculation techniques. Five categories of microorganisms are involved: (1) *Rhizobium* (2) *Frankia* (3) endomycorrhizae (4) ectomycorrhizae (5) free living N_2-fixing bacteria.

1.1. *Rhizobium*

The potentialities of increasing crop yields by inoculating legumes with appropriate efficient *Rhizobium* strains, when the native *Rhizobium* population is inadequate, is well known in the humid tropics (see for example : Ayanaba and Dart, 1977). In arid semi-arid areas, however, there are few examples of successful *Rhizobium* inoculation. We would like to indicate here that inoculating *Acacia* at the nursery level can be highly beneficial if a competent effective *Rhizobium* strain is used (Table 1).

In soils that can be irrigated *Sesbania rostrata*, recently reported to bear stem nodules, is thought to have a high N_2-fixing potential if it is inoculated with its specific *Rhizobium*. A most interesting characteristic of this legume is its ability to actively fix N_2 in presence of high concentration of inorganic nitrogen (Dreyfus and Dommergues 1980a).

1.2. Non-leguminous N_2-fixing plants

Trees belonging to the *Casuarina* genus occur naturally in Australia, tropical Asia islands and the Indian Ocean border. Some species, such as *Casuarina equisetifolia*, have been introduced in semi-arid countries where they thrive satisfactorily, especially along the coasts. When Casuarina trees are nodulated, they fix 50 - 200 kg N_2 per ha per year (Dommergues, 1963; Silvester, 1977) and thus can colonize low fertility soils where other trees cannot be established. When the endophyte is absent, which occurs in many locations, artificial inoculation of nursery seedlings with crushed nodules is a prerequisite for successful afforestation. Such a method is risky because crude inocula may introduce pathogens so that using pure cultures of Frankia for inoculation is preferable. The recent isolation of Frankia strains from Casuarina (Gauthier et al., 1981) increases the possibility of such a practice in the near future. In a recent report on a tour in China(Dr. I. Watanabe,personal communication) reports that Coriaria sinica a non-legume N_2-fixing plant - which is currently under study at the Hunan Soil and Fertilizer Institute - is utilized by the peasants in West Hunan as green manure.

1.3. Ectomycorrhizae

The role of ectomycorrhizae in temperate countries is well documented but under tropical conditions most of the work has been hitherto restricted to the introduction of Pinus spp., which were generally shown to require the simultaneous introduction of ectomycorrhizae (Redhead, 1979). Table 2 illustrates the beneficial effect of ectomycorrhizal infection on Pinus caribaea grown in two different soils from Senegal. This example draws attention to the fact that the magnitude of the plant reaction to inoculation varies according to the availability of soil phosphorus. If the soil content in available phosphorus as determined by Truog's method (Jackson, 1964) is low, the response to ectomycorrhizal infection is generally clearly marked.

In arid/semi-arid areas, some trees, especially Eucalyptus spp., are among the most adaptable and most interesting plants for providing wood and fuel. These trees bear characteristic ectomycorrhizae which have been studied for many years in Australia by Chilvers and co-workers (Chilvers, 1968; Seviour and Chilvers, 1972; Chilvers, 1973; Seviour et al. 1978). Laboratory experiments indicated that artificial inoculation of one Eucalyptus species (E. gummifera) by Pisolithus tinctorius, a well-known ectomycorrhizal fungus often used for inoculating *Pinus* spp., was successful (Mullette, 1976) but, to the best of our knowledge, results of nursery experiments on the effect of ectomycorrhization of *Eucalyptus* spp. have not yet been reported. In our laboratory in Dakar, we are currently initiating this type of investigation in collaboration with ISRA (Institut Sénégalais de Recherche Agricole).

1.4. Endomycorrhizae (VAM)

Endomycorrhizae of the vesicular-arbuscular type (VAM) occur in almost all soils including arid or semi-arid soils (Diem *et al.*, 1981). Up to now, we do not have any field data about the effect of VAM inoculation on plant yields. However, recent pot experiments carried out by our group in Senegal indicate that beneficial effects can be expected when the populations of VAM fungi in the soil are low and when one of the following conditions is fulfilled: the soil content in available P is low or the plant is infected by nematodes. Thus VAM would improve crop yields not only in P deficient soils, but also in soils infested with nematodes.

Enhancement of plant phosphorus uptake is a well known function of VAM infections in plants and "legumes appear to be very responsive to this infection probably because they are relatively poor foragers for phosphate" (Munns and Mosse, 1980). Table 3 indicates that *Vigna unguiculata* inoculated with a VAM fungus had more nodules and a larger nitrogen content in shoots than uninoculated plants, confirming experimental studies of the last decade carried out by B. Mosse and co-workers (Munns & Mosse, 1980) and by Gianinazzi-Pearson *et al.* (1979).

In arid/semi-arid countries, especially in Western Africa, nematode attacks are often responsible for poor crop yields. This harmful effect may partly be attributed to the fact that pathogenic nematode populations decrease VAM infection (Fox and Spasoff, 1972; Schenk and Kinloch, 1974; Germani *et al.*, 1980). Conversely, there are some indications that VAM infection may tend to restore the yields of plants infested with nematodes to levels measured in the absence of nematodes. Table 4 illustrates this favourable effect of VAM infection on N_2 fixation and yield of soybean. Another experiment, not reported here, indicates that VAM and added phosphate have similar effects on growth and nodulation of cowpea infested with nematodes; it has thus been concluded that VAM assisted the plant more by enhancing P uptake than by reducing nematode infestation.

Besides these effects, VAM probably help plants to thrive in water stressed conditions. Thus, Moawad (1978) found that the amount of water used to produce 1 g of dry matter was much lower in mycorrhizal than in non-mycorrhizal plants growing in a comparatively dry soil fertilized with $Ca_5(PO_4)_3OH$ (Table 5). According to a recent review (Diem et al., 1981), soil type affects VAM more in arid or semi-arid conditions than in humid regions. Thus in dry conditions which prevail in Pakistan, VAM spores are much more abundant in loamy soils than in sandy ones (Khan, 1971 and 1974; Saif et al., 1975). In cultivated Senegalese soils, such a relation between soil texture and VAM abundance was less marked, but it was clear that VAM fungi did not proliferate in sandy soils during the dry season.

1.5. Free-living N_2-fixing bacteria

1.5.1. Rhizospheric N_2 fixation

Various bacteria other Rhizobium are known to develop in association with roots of higher plants. This association, termed "associative symbiosis" by Burns and Hardy (1975), has been assumed for many years to be a significant source of nitrogen for the agro-systems, especially in tropical conditions. The term associative symbiosis is somewhat misleading since it implies a similarity between this association and true symbiotic systems, whereas in fact this relationship presents many differences which are summarized in Table 6. A recent international symposium on N_2 fixation has therefore aptly recommended to replace the term "associative symbiosis" by "biocoenosis". At a practical level, two questions arise:

1.5.1.1. What is the actual amount of N_2 fixed by the process ?

Most estimations on rhizospheric N_2 fixation have been carried out using the acetylene reduction method. This method, however, often leads to overestimations for different reasons, but more especially because incubations are too long thus introducing indesirable modifications of the system under study.

The following calculation made by K. Martin at the IRRI meeting held at Los Banos in 1979 (International Rice Research Institute 1979, p. 259) suggests that N_2 fixation should be much lower than formerly claimed by some authors. "Data obtained from the Waite Institute in Adelaide show a transfer of photosynthate to the root system of field-grown wheat between early tillering and flowering that is equivalent to about 1,800 kg C/ha. This is in contrast to a carbon content at the root system, which can be recovered at flowering by washing away the soil, of some 400 kg C/ha. Thus, there has been a wastage of root tissue during the active growth period equal to more than 70% of the root mass produced.

Allowing for 30% of the root carbon occuring in liquid and other compounds, which is not readily available for microbial decomposition, there would be some 1,000 kg C/ha available to the microflora and microfauna.

There is some doubt about the amount of carbon required for the heterotrophic fixation of N_2 but a common estimate is 30-40 kg C/ha N_2 fixed. If the amount of carbon and N_2 located in the root system of flooded rice is of the same order of magnitude as for wheat, one can obtain an upper limit of heterotrophic N_2 fixation equivalent to 25-30 kg N/ha. The actual amount of N_2 fixed per 1,000 kg of available C/ha would be much less because no allowance has been made for root respiration and this would induce competition for the carbon among the different microbial populations, many of which may not be capable of N_2 fixation.

One should add that <u>in situ</u> different factors (especially soil water content, combined nitrogen, root pathogens etc...) tend to markedly reduce rhizospheric N_2 fixation. Therefore we assume that the amount of N_2 fixed through this process should probably be in the range of 0-15 kg/ha".

1.5.1.2. What is the effect of rhizospheric N_2 fixers on plant yield ?

Surprisingly, the results obtained in our laboratory (G. Rinaudo, unpublished data) indicate that there is no relation between the rhizospheric N_2 fixation (measured by its acetylene reduction activity or ARA) and plant growth. However we found that some N_2-fixing Azospirillum strains, even those which induced a low rhizospheric ARA, could significantly enhance plant growth when inoculated in the rhizosphere of rice seedlings placed in large plastic pouches (Table 7). This favourable effect of inoculation can be attributed to the production of growth-stimulating substances by the bacteria introduced in the rhizosphere, as already suggested by Brown (1975). This conclusion is supported by the finding that highest yields were obtained by inoculating rice with Azospirillum strains which synthesized AIA the most actively (Diem, Gauthier and Rinaudo, unpublished data). However these results, which were obtained in glass-house conditions, could not be replicated in the field, probably because the colonization of the root system was not as satisfactory as it was in the glass-house trials. In the field the response to inoculation with N_2-fixers is generally not marked and it varies largely from one trial to another. Subba Rao (1979) reported that, whilst inoculation with Azospirillum could increase yields, such responses were variable depending on the initial N status of the soil and the variety of crop planted. The variability in response to inoculation can be also explained by an inadequate rhizosphere root colonization which is due to different factors, including competition by native rhizosphere root microorganisms. Summarizing, we agree with the recent conclusion that "to date, firm data have not been published to establish that Azospirillum and free-living N_2 fixers contribute substantial amounts of nitrogen and increase crop yields under field conditions" (National Academy of Sciences, 1979).

1.5.2. N_2 fixation in relation to organic manures and crop residues

High N_2 fixation rates obtained in the laboratory by incorporation of such organic energy sources have seldom been reported in the field because the amount of organic matter incorporated under such conditions is usually much lower (0.1% instead of 1%) in order to avoid the depletion of inorganic nitrogen which would be detrimental to the plant. One should add that it is difficult to evaluate nitrogen balances in the field because of the magnitude of sampling errors and the occurrence of uncontrollable factors. Despite these limitations, Abd-el Malek (1971) obtained substantial nitrogen gains by incorporating additional plant residues into different Egyptian soils characterized by their low organic content and their richness in calcium carbonate. Unfortunately, no data was given regarding the plant yields.

It should be stressed here again that since heterotrophic N_2 fixation is very sensitive to oxygen, this process is only significant in saturated or near saturated soils. Thus in arid/semi-arid conditions, it should only be taken into consideration for irrigated soils.

2. LIMITATIONS AND RESEARCH NEEDS

The more important research and development needs related to the use of microbiological technologies in arid/semi-arid countries include the following :

2.1. Symbiotic N_2 fixation by legumes

2.2. Limitations

Some woody legumes such as *Acacia albida* or *Acacia senegal* (Jung, 1969; Bernhard - Reversat, 1977) are nodulated when they are at the seedling stage in the laboratory or in nurseries, but they seldom bear nodules as adult plants. This lack of nodules in the field was attributed by Bernhard-Reversat and Poupon (1979) to an active nitrate production in the soil. Drought may also be an important limiting factor of symbiotic fixation in forest ecosystems as it is in agrosystems.

2.1.2. Research needs

- Encourage introduction of actively fixing legumes (annual or perennial), resistant to major stresses in arid/semi-arid conditions

- Improve technology for production, and use of Rhizobium inocula specific to introduced legumes, when this procedure appears to be necessary.

- Develop the study of the interactions between endomycorrhizae and Rhizobium.

2.2. Non-leguminous N_2 fixing plants

2.2.1. Limitations

To date, trees belonging to one genus of N_2-fixing non-legumes, Casuarina, are widely introduced in semi-arid countries, but the culture of these trees is restricted to the coastal zone where air humidity compensates the soil water deficiency.

2.2.2. Research needs

- Surveys should be conducted to discover new woody and non-woody N_2-fixing non-legumes adapted to arid/semi-arid environments.

- Explore the possibility of using recently discovered non-legumunous N_2 fixing plants, such as Colletia spinosissima (Miguel et al. 1978), Datisca cannabina (Chaudhary, 1979), Coriaria sinensis, either in dry or in irrigated sites.

- Improve our knowledge on the growth requirements and culture of already isolated endophytes in order to develop methods of mass production of inocula.

2.3. Ectomycorrhizae

2.3.1. Limitations

The use of ectomycorrhizae should theoretically be limited to soils deficient in phosphorus and characterized by low populations of ectomycorrhizal fungi.

2.3.2. Research needs

- Survey should be conducted to determine the best ectomycorrhizal fungal strains adapted to arid/semi-arid environments.
- Different tree species should be evaluated for their ability to benefit from their association with the best ectomycorrhizal fungal strains (e.g. Eucalyptus sp.).
- Dependable laboratory cultures of ectomycorrhizal fungi would be very useful for obtaining massive inocula.

2.4. Endomycorrhizae (VAM)

2.4.1. Limitations

D.S. Hayman (1980) recently stressed that "undue faith in mycorrhiza as an agriculture elixir should be tempered by a realistic appraisal of which aspects might best be exploited on a practical scale".

To date, VAM fungi have not been grown in pure culture, thus we do not have any practical method for obtaining massive inocula which would be necessary for inoculating annual crops such as Vigna or peanut. Consequently endomycorrhizal inoculation is practically restricted to the nursery level, which obviously is of interest for perennial plants such as Citrus (in irrigated conditions) or trees used for reafforestation (e.g. Acacia spp. Azadirachta indica).

On the other hand one should stress again that the most dramatic effect of VAM infection is to be expected only in soils characterized by a low content in available phosphorus and by limited native populations of VAM.

2.4.2. Research needs

- Strains should be selected for environmental adaptation as well as "effectiveness" of the plant cultivar - strain combination.
- More information is needed on how endomycorrhizae improve the drought resistance and the resistance to diseases of the host plants (biological control).

- Investigations should be initiated on the possibility of culturing endomycorrhizae on synthetic media; if these attempts were successful, optimum conditions for growth should be determined in order to propose dependable methods for producing inocula.

2.5. Free living N_2-fixing bacteria

2.5.1. Rhizospheric N_2 fixation

Since the impact of this process on plant yield in arid/semi-arid conditions is probably negligeable, the development of further investigations on this particular process is not recommanded.

2.5.2. N_2 fixation in relation to organic manures and crop residues

In arid and semi-arid conditions, free living N_2-fixing bacteria can be active only in some specific environments, namely in irrigated soils. An area that needs attention is the search of feasible field techniques that could induce optimum N_2 fixation through amendments in the presence of nitrogen fertilizer (Matsuguchi , 1979).

CONCLUSION

We would like to conclude by calling the attention on the following two points :

1. A special effort should be made in order to promote the introduction of trees in arid/semi-arid ecosystems, which has been already strongly advocated for the humid tropics by a recent panel meeting of experts in Nairobi (Mongi and Huxley 1979). In arid/semi-arid conditions trees contribute to the welfare of a population in several ways :
   - They provide shade and fodder for cattle (during the July 1980 dry spell in northern Senegal part of the cattle was saved by grazing two legume trees : *Acacia albida* and *Tamarindus indica*).
   - They protect the soil against wind, water erosion and leaching, produce organic matter that improve the soil structure and chemical status, bring up nutrients from deeper horizons to the surface where they can be absorbed by annual crops.
   - They provide fuel and timber in locations were these commodities are specially meager.

2. Harnessing microbial processes for the benefit of agriculture and agroforestry is mostly a task that should be tackled by microbiologists. But the help of other experts (agronomists, nematologists, plant pathologists, plant breeders etc...) is necessary. In other words, a multidisciplinary effort is desirable in order to get successful results in the future.

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Table 1. Effect of inoculation of three West African *Acacia* species by fast- and slow-growing strains of *Rhizobium* in a non sterile nursery soil (Bel Air)[a].

(Dreyfus and Guèye, 1980, unpublished data)

	Rhizobium strains	Height (cm)	Shoot total N	Nodules (no per plant)	Nodule fresh weight (g per plant)
senegal	901 (F)[b]	22	2.2	14	0.2
	903 (F)	20	2.1	16	0.2
	801 (S)[c]	6	0.4	4	0.05
	756 (S)	7	0.4	3	0.03
	uninoculated	7	0.4	2	0.1
albida	901 (F)	20	1.4	4[d]	0.1
	903 (F)	24	1.3	3[d]	0.1
	801 (S)	27	2.2	10	0.2
	756 (S)	30	2.3	12	0.3
	uninoculated	24	1.6	5	0.1
seyal	901 (F)	31	2.0	15	0.6
	903 (F)	20	1.6	10	0.3
	801 (S)	28	2.0	13	0.5
	756 (S)	19	1.5	10	0.4
	uninoculated	19	1.5	12	0.3

a plants were harvested when 2 months old

b (F) fast-growing strains of *Rhizobium*

c (S) slow-growing strains of *Rhizobium*

d nodules formed by native slow-growing "cowpea" strains of *Rhizobium*

Table 2. Effect of ectomycorrhizal infection (*Pisolithus tinctorius*) on growth of *Pinus caribaea*[1] grown on two different sterile soils.

(Kabrê and Diem, 1980; unpublished data).

	Control	*Pisolithus tinctorius*	LSD (P = 0.01)
"Dior" Soil[2]			
Height (cm)	17.2	22.9	5.9
Shoot weight[3] (g/plant)	3.45	6.59	2.3
"Deck" Soil[2]			
Height (cm)	9.4	23.0	5.9
Shoot weight[3] (g/plant)	0.83	7.85	2.3

(1) 7 month-old plants

(2) characteristics of the soils (ultisols) used in the experiment :

	"Dior" soil	"Deck" soil
Total P (ppm)	268	190
Available P, Olsen (ppm)	40	20
Available P, Truog (ppm)	40	2
pH (KCl)	7.0	6.2

(3) weight expressed on a dry matter basis

Table 3. Effect of endomycorrhizal infection (*Glomus mosseae*) on growth and nodulation of *Vigna unguiculata*(4) cv. N-58-185 grown in a non sterile soil

(Ollivier and Diem, 1980; unpublished data)

	Control	*G. mosseae*	Phosphorus(3)
Shoots (g/plant)(1)	3.4	4.5	5.5
Roots (g/plant)	1.0	2.4	1.3
Nodules (g/plant)	0.099	0.141	0.168
VAM infection frequency (%)	94	99	92
VAM infection intensity (%)	84	92	84
Total N (mg/plant)(2)	77	108	118
Total N (%)(2)	2.24	2.37	2.16
Total P (mg/plant)(2)	3.40	6.21	8.74
Total P (%)(2)	0.10	0.14	0.16

(1) All weights expressed on a dry matter basis

(2) Shoots only

(3) Phosphorus added as K_2HPO_4, 0.5 g/kg soil (Dior). Characteristics of "Dior" soil given in Table 2.

(4) 60 day old plants.

Table 4. Effect of VAM infection (*Glomus mosseae*) on nodulation and N_2 fixation of *Glycine max* (cv. 44.A73) non infested or infested with nematodes (*Scutellonnema cavenessi*) [1]

(Germani, Ollivier and Diem, unpublished data).

	Plant dry weight		N total (mg/ plant)	P total (mg/ plant)	N_2 fixation		VAM frequency %	Nematodes [3]
	Shoots	Roots			Nodules	ARAP [2]		
	1	2	3	4	5	6	7	8
Non infested with nematodes								
Control	2.7 a	1.2 a	45 a	2.2 a	0.109 a	3.9 a	0	0
VAM inoculation	4.2 c	1.5 a	116 b	5.9 b	0.320 c	6.0 a	69 a	0
Infested with nematodes								
Control	1.0 b	0.7 b	21 a	0.8 c	0.029 b	0.6 b	0	6800 a
VAM inoculation	3.6 ac	1.7 a	106 b	4.9 b	0.313 c	7.4 a	48 b	12840 b

(1) 46-day old plants. All weights expressed as g (d.w.) per plant . Soil ("Bel Air" 30 - 50 cm horizon) was autoclaved before inoculation with *Rhizobium* (USDA 118) or VAM.

(2) ARAP : acetylene reduction activity expressed as micromoles C_2H_4 per plant per h.

(3) Number of nematodes per pot.

Numbers in a column not having the same letter differ pP = .01 (columns 1, 3, 4, 5, 6, 7, 8) or .05 (columns 2) Mann-Whitney tests).

Table 5. Water consumption (expressed in ml/g dry weight) by <u>Eupatorium</u> <u>odoratum</u> and <u>Tagetes</u> <u>erecta</u> at two levels of soil water content (80 and 20% available water) and with two forms of P (Moawad, 1978).

Plant species	Mycorrhizal treatment	$Ca(H_2PO_4)_2.H_2O$		$Ca_5(PO_4)_3OH$	
		80%	20%	80%	20%
<u>odoratum</u>	NM	1208	1207	2860	4112
	M	1237	1177	1574	1436
<u>erecta</u>	NM	1073	1005	2563	3397
	M	923	1060	1180	1421

M : Not inoculated with VAM

: Inoculated with VAM

Table 6. Comparaison of legume and rhizosphere N_2-fixing systems.

Nitrogen-fixing system	Bacterial strains	Specificity	Bacterial infection	Amount of energy (expressed in moles of glucose) required to fix 1 mole of nitrogen	Protection against oxygen	Fate of fixed N_2
Legume-*Rhizobium* symbiosis	*Rhizobium*	Certain	Intracellular	1	By plant cell and pigments such as lehaemoglobin	Directly used by the legume as NH_4^+-N
Rhizosphere N_2-fixing system	Many belonging to various genera; often associated with other microorganisms	Probably no specificity	Apparently limited to rhizoplane, moribund or dead root cortical cells, and to root residues	3-4 (aerobic fixers) 8-10 (anaerobic fixers). Some environmental factors could presumably increase efficiency two-or threefold	No protection by host-plant. Bacterial protection often inadequate. Partial protection by waterlogging	Probably not directly used by the plant

Table 7. Influence of soil inoculation on rice yields. Results expressed as g (dw) per plant[1] (Rinaudo, unpublished).

Treatment	Grain yield	Shoots	Roots	Total
Uninoculated	5.6 ± 0.9	14.3 ± 2.4	5.2 ± 1.1	25.1 ± 2.8
7001[2]	7.0 ± 0.1	18.8 ± 1.0	7.8 ± 0.7	33.6 ± 1.0
R07[2]	6.7 ± 0.5	18.1 ± 1.6	10.3 ± 1.3	35.1 ± 3.0
7029R2[2]	7.3 ± 0.2	21.0 ± 0.5	13.9 ± 0.4	42.2 ± 0.5
DK93[2]	6.6 ± 0.6	16.0 ± 1.9	8.0 ± 0.5	30.6 ± 3.1
BK85[2]	5.2 ± 0.4	12.8 ± 1.6	6.7 ± 1.2	24.2 ± 2.7

(1) Mean of five replicates ± S.E of this mean

(2) Reference of the strain of *Azospirillum* used for inoculating the soil