1. Tropical Stress Ecology of Rhizobia, Root Nodulation and Legume Fixation

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INTRODUCTION

To adequately feed the world's increasing population it is essential that food production be increased in the Third World where it will be most needed. This aim is the mandate of the International Institutes funded by the Consultative Group on International Agricultural Research and the many national agricultural institutes throughout the tropical world. Moreover, an increasing number of scientists in the developed countries are becoming involved in solving problems which relate directly to tropical agriculture.

The potentially important role of legumes in maintaining soil fertility is well established. Grain legumes provide valuable nutritious seed and, when effectively nodulated, can yield in nitrogen-deficient soils where cereals and other non-leguminous crops would barely survive. It is no coincidence that legumes are a component of many of the traditional farming systems throughout the tropics. If food production is to be increased with more productive farming systems, the package of improvement practices is likely to include an increased input of biologically fixed nitrogen to complement the use of fertilizer nitrogen if it is available. It is important to bear in mind, however, that contrary to popular opinion, the growing of a legume crop does not necessarily result in a nitrogen gain for a farming system, except where an effectively nodulated forage legume is ploughed under as a green manure. If more nitrogen is removed in the harvested grain than was fixed in the nodules, a net depletion results, even if all vegetative residues are ploughed under. The greater the amount of soil nitrogen that is available to inhibit nodulation and fixation, and the higher the harvest index for nitrogen, the more is the likelihood that a nitrogen depletion would occur [1]. The correct grain legume should be selected for a specific use, be it high grain yield at the possible expense of

Cambridge University Press
978-0-521-10575-0 - Current Developments in Biological Nitrogen Fixation
Edited by N. S. Subba Rao
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some soil nitrogen or less grain yield with the expectation of nitrogen accretion to the soil.

Those involved with rhizobia and legumes should not assume that "improving" nitrogen fixation is necessarily the main priority in increasing legume production [2]. With judicious use of fertilizers, water management, insect control, disease control, superior cultivars etc., the inputs of biologically-fixed nitrogen may increase concomitantly and spontaneously. On the other hand there is no room for complacency: the natural environment is constantly changing and field crops are subjected to stresses throughout the growth cycle. There exist too many gaps in the understanding, particularly in terms of the responses of biological nitrogen-fixing systems to these stresses. The objective of this review is to focus on the main environmental stresses commonplace in tropical agriculture and on how they may affect survival of rhizobia in soil, the root-nodulation process, and the functioning of the effectively nodulated legume.

For background reading and to gain access to related aspects of *Rhizobium* and legume research the reader is referred to the excellent reviews on *Rhizobium* ecology [3], nodule initiation and development [4, 5], functioning of legume nodules [6], environmental effects [7], legumes in acid soils [8, 9], legume nutrition [10–13], and tropical agricultural legumes [14].

ACIDITY

In wet equatorial zones rainfall exceeds evapotranspiration for much of the year and as a result soils become thoroughly leached of calcium and magnesium leaving them markedly acid. Acid soils are characterized by high concentrations of hydrogen ions and free aluminium, and low concentrations of calcium and available phosphate. Some acid soils contain manganese at phytotoxic levels and in some molybdenum is unavailable.

It appears that acidity is less of a constraint to cowpea rhizobial survival in soil than is desiccation or high temperature [15]. Thus, in an acid soil at Onne in Nigeria (pH 4.6, annual rainfall 2,500 mm) the cowpea rhizobial count was 4.3×10^4/g soil, whereas at Maradi in the sahel-savannah zone in Niger Republic (pH 6.1, annual rainfall 600 mm) the count was 4.9×10^2/g soil. Laboratory studies of the effects of acidity on rhizobia from soils such as these have been based on growth in synthetic media. However, because rhizobia vary in the ability to withstand conditions associated with acid soils, the acid tolerance of rhizobia cannot be predicted from the growth rate or acid production characteristics in liquid media at higher pH [16]. Moreover, because slow-growing rhizobia produce an alkaline reaction in most growth media [9] caution is needed when testing their ability to tolerate low pH-using conventional techniques. Growth media may be modified by changing the carbon source to arabinose from mannitol which is customarily recommended [17], so that pH is stabilized and remains at the initial low value throughout much of the growth cycle [18]. Alternatively, studies may be made during the early phase of growth up to visible turbidity before significant pH changes occur [19]. Although slow-growing rhizobia are in general more tolerant of low pH than the fast-growers, strain to strain differences exist [20]. *Rhizobium meliloti* is particularly sensitive to acid conditions [21]. Some slow-growing rhizobia native to acid soils are acid-requiring and grow only at approximately pH 4.5 [18]. On the other hand in a survey of 65 strains of slow-growing rhizobia of mixed origin, in liquid media acidity (pH 4.5 or 4.8) prevented the growth of 29 per cent of the strains and slowed the growth of most of the rest. Low phosphate levels limited the growth of some strains but with less severity than did acid. Aluminium (50 μM) was the most severe stress factor, stopping growth of 40 per cent of the strains. Tolerance of acidity was not necessarily correlated with tolerance of aluminium, since aluminium increased the lag time or slowed the growth rate of almost all of the strains which were tolerant of low pH [22]. A complementary study showed that while high manganese (200 μM) and low calcium (50 μM) had adverse effects on slow-growing rhizobia which varied from strain to strain in severity, neither was as severe a stress as aluminium, and strains which were tolerant of aluminium were also tolerant of manganese and low calcium [23]. The adverse effects of acid and aluminium on rhizobial growth appear to be bacteriostatic rather than bacteriocidal [24]. Unfortunately because of the lack of information in these surveys of rhizobial responses to acid-associated stresses, no correlation can be drawn between patterns of resistance or susceptibility and the type of soil from which the rhizobia originated.

The ability to grow in liquid media which mimic acid soil conditions may indicate an ability to survive in such soils with the potential to later colonize the host rhizosphere. An agar plate method for the rapid screening of rhizobia for tolerance to acidity and aluminium has recently been developed and is amenable for screening large numbers of rhizobial isolates [25]. This rapid screening technique may be used to reduce numbers for subsequent more critical examination in liquid media. Rhizobia which had been identified as tolerant of acid (pH 4.5) and aluminium (50 μM) in liquid media nodulated better and were more effective on cowpeas in an acid (pH 4.6) cum high aluminium soil than strains which had been identified as sensitive [26]. However, the pre-screening of rhizobia in acid liquid media was less useful when mung bean was used as the host in a soil of pH 5.0. The main cause of symbiotic failure in mung bean was sparsity of nodules which occurred even with some of the strains which grew in acid-defined media containing aluminium. These strains nodulated cowpea reasonably well in the same soil adjusted to pH 4.6, indicating a greater acid sensitivity in the nodulation process of mung bean [16]. Clearly, when testing the nodulating ability of rhizobia in acid conditions, an acid tolerant host is required.

When growing on mineral nitrogen, most legume species are only slightly adversely affected by acidity down to pH 4.0. Indeed some species actually grow better at pH 4.0 than in less acidic conditions, e.g. *Stylosanthes humilis* [27]. Legumes dependent on the root nodule symbiosis for nitrogen showed a range of responses to low pH, but in general nodulation was reduced or eliminated at pH values below 5 [27, 28]. In a survey of the effects of liming on eight soils of pH 3.4–4.25 the critical pH for nodule initiation and development in soybean was in the range 4.5–4.8 [29]. The inhibition of nodulation appears to result from a combination of low calcium and low pH since it was alleviated by increasing either calcium or pH [9]. Nodule initiation was more restricted when pea plants were exposed to pH 4.5 at two or three days after inoculation than at one or four days [30]. The lesion in the infection process which is induced by calcium deficiency and acidity has not been identified [9]. The nitrogen fixing activity of nodules is also adversely affected by acidity in many species [27, 28].

The presence of available aluminium in acid soils inhibits nodulation directly [31] and indirectly by stunting root growth, and also tends to compound the effects of low levels of calcium by inhibiting its uptake [8]. The mean nodule number of twelve soybean cultivars was highly correlated with primary root calcium content and inversely correlated with level of available aluminium in the soil. Exposure of nodulated roots of *Phaseolus vulgaris* to aluminium, however, had no effect on nodule development or function [31]. The inhibitory effect of the aluminium-calcium interaction on soybean nodulation varied with soil type. In two soils of higher Ca : Al ratio, mean growth of thirteen soybean cultivars at pH 4.5, although reduced in comparison with plants at pH 6, was the same whether they were relying on mineral nitrogen or nodule-fixed nitrogen. With 2×10^6 rhizobia/seed as inoculum nodule number and weight were the same at pH 4.5 as at pH 6 [33]. These findings indicate that at least for soils of this type, improvement of aluminium tolerance is more likely to be achieved by manipulating the plant rather than the *Rhizobium*. However, taking pains to use rhizobia that are stress tolerant has proven to be a wise precaution with soybean. In the acid, high aluminium soil at Onne in Nigeria mentioned earlier, soybean supplied with 150 kg N/ha gave a 74 per cent increase in grain yield in response to a lime application of 1 t/ha. A prior screening of effectiveness of rhizobia in the same soil led to the identification of two superior strains of *R. japonicum*. Plants inoculated with either of these strains did not respond to liming and yielded 1.9–2.1 t/ha of seed, approximately 43 per cent higher than the N + lime treatment [34].

Phosphorus deficiency is common in the acid soils of the tropics and in clay soils of high iron and aluminium content, phosphorus may be strongly adsorbed making the use of fertilizers uneconomic [12]. In some soils liming alleviates phosphorus deficiency but in others it may exacerbate it [35]. Although species and cultivars differ in their nutritional needs, legumes have a relatively high phosphorus requirement for optimum growth [36]. Some require significantly more phosphate to reach optimum yields when relying on symbiotically fixed nitrogen in comparison to when supplied with fertilizer nitrogen [37].

Little work has been done on root nodulation at low phosphorus levels. Indications are that phosphorus deficiency limits nodulation indirectly by limiting legume growth rather than the infection process *per se* [8, 38], although there is evidence to imply that some rhizobia are more able to nodulate at lower phosphate levels than others [11]. Nodule development requires adequate phosphorus [39, 40] and nodules accumulate a higher phosphorus content than roots [41]. A number of experiments in which sterile soils were inoculated with vesicular-arbuscular mycorrhizal fungi have established their important role in the phosphorus nutrition of plants, particularly in phosphorus-deficient soils [41, 42–46]. In comparison to the gramineae the legume root system is typically restricted in its geometry, making it particularly dependent on mycorrhizal infection [11]. For example, with a phosphate-deficient Brazilian soil (sterilized, pH 5.3) applications of rock phosphate or mycorrhiza increased the vegetative yield of *Stylosanthes guyanensis* by factors of 2.2 and 8 respectively and increased whole-plant per cent phosphorus by factors of 1.6 and 3 respectively; increased nodulation and nitrogen fixation were concomitant with improved phosphorus nutrition [41]. Very little mycorrhizal work has been done in very acid soils and although their efficiency is known to be influenced by pH [47] at least some mycorrhizas do function below pH 5. Inoculation of a sterile soil (pH 4.5) with mycorrhiza increased the growth of *Pueraria phaseoloides* by 12-fold. Addition of rock phosphate further improved yield by only 10–25 per cent, showing that without amendments phosphate was unavailable rather than grossly deficient [46].

The scant evidence available indicates that high manganese levels are unlikely to inhibit the growth or survival of rhizobia in acid soils [9]. Manganese toxicity mainly affects legume growth *per se* rather than nodulation in particular [8, 9, 48], and tolerance of manganese varies considerably between and within legume species [9]. However, variations among strains of *R. phaseoli* were found in their ability to nodulate and fix nitrogen in conditions where manganese was marginally phytotoxic [49]. The adverse effects of manganese were alleviated by liming [49].

Legume species also vary in the capacity to tolerate molybdenum deficiency in acid soils. In a Brazilian acid soil *Stylosanthes* grew well without molybdenum fertilization, whereas siratro and *Centrosema* responded positively to molybdenum fertilization. In the same soil six cultivars of *Phaseolus vulgaris* responded to molybdenum fertilization only in conjunction with liming to a pH greater than 5.4. Further liming in excess of pH 5.8 caused a sufficient desorption of molybdenum in the soil that a response to

Cambridge University Press
978-0-521-10575-0 - Current Developments in Biological Nitrogen Fixation
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molybdenum fertilization was no longer obtained [13, 50]. The lack of response to added molybdenum was later shown to be the result of the presence in the soil of an inhibitory factor for nodulation which was removed by liming to pH 5.9, rather than an inability of *P. vulgaris* to take up molybdenum or translocate it at the lower pH [51].

Depending on the degree of tolerance to acid conditions, some species respond more strongly than others to lime application [52]. Legumes in acid soils dependent on nodule fixed nitrogen generally derive greater benefit from liming than when there is sufficient mineral nitrogen available [27]. Two notable exceptions to this rule have recently been reported with soybean, as already outlined [16, 34] although available phosphorus level may be critical in this regard since basal applications of phosphorus were made in both of these cases. High levels of lime application, where pH is raised to 6–7, can have deleterious effects on plant growth [35]. The reasons for this are not well understood, particularly since the adverse effects may be transient [53], and in fact the explanation may vary with different soils and different species. Phosphate deficiency has been implicated [35, 54], and so also have magnesium and zinc deficiencies [54]. Neither plant symptoms nor leaf analyses for eight elements gave an indication of the reason for growth depression by liming in eight legumes growing in an oxisol. In the same trial seven other species showed no adverse effect of liming [53]. It appears unlikely that yield depression of legumes at high lime rates results from an adverse effect on the root nodule symbiosis since non-legumes may be similarly limited in growth [35]. Clearly, if economic considerations alone do not dictate judicious use of lime to mitigate the effects of acid soil conditions, the possibility of compounding the nutritional problems should do so.

SALINITY AND ALKALINITY

In reviewing the literature on salinity a basic problem emerges. The many different notations used to quantify salinity often make it difficult to readily compare data from different studies. For convenience here, salinity levels in soils will be quoted with the S.I. unit mS/cm, and *in vitro* as per cent concentration on a w/v basis so that comparison may be made between soil and *in vitro* data and some of the latter will also be quoted as mS/cm (for general reference, 1 mS/cm = 1 mmho/cm, 1 per cent NaCl has an electrical conductivity of 16 mS/cm).

Saline soils are common in regions of arid or semi-arid climate where transport of soluble salts to the ocean does not occur because of low rainfall [55, 56]. They are characterized by the presence of high levels of neutral salts in the surface layers resulting from the capillary rise of water when evaporation exceeds precipitation. In the flood plains of rivers, low-lying lake margins and coastal plains, saline groundwater within a few metres of the soil surface can be a major contributory factor. The predominant salts are usually sulphates and chlorides of sodium, calcium and sometimes magnesium, and small quantities of carbonates and bicarbonates are often present. These soils are only moderately alkaline, with pH about 8, and their agricultural use usually demands irrigation. However, this may actually exacerbate the problem since river water may contain significant levels of dissolved salts [55]. Artificial saline soils have resulted from irrigation [56].

Rhizobia exhibit a large range of sensitivities to salinity. Three of eleven diverse rhizobial types failed to grow at 0.6 per cent sodium chloride (an electrical conductivity of 10 mS/cm) and the others showed a 3.7-fold range in sensitivity in terms of fractional reduction in growth [57]. *R. trifolii* appears to be a saline sensitive species; eight strains isolated from *Trifolium alexandrinum* were completely growth-inhibited at 0.7 per cent sodium chloride [58] and another six *T. alexandrinum* isolates had their growth severely reduced or eliminated at 1 per cent levels of chlorides and sulphates of sodium, potassium and magnesium [59]. In contrast five rhizobial strains from *Sesbania cannabina, Crotolaria juncea* and soybean were uninhibited by 1 per cent levels of these same salts and four of them grew at 3 per cent levels [60]. The growth of six strains isolated from *Dolichos lablab* was unaffected or actually stimulated at sodium chloride levels up to 1.6 per cent (25 mS/cm) but was severely inhibited although not eliminated at 3.2 per cent [61]. Four strains of *R. meliloti* grew well at 3 per cent levels of chloride and sulphate salts of sodium, potassium and magnesium. A fifth strain of *R. meliloti* showed differential tolerance to these salts. It was 17, 49 and 80 per cent inhibited in growth at 3 per cent levels of sodium chloride, magnesium chloride and magnesium sulphate respectively, but failed to grow at only 0.4 per cent potassium chloride and 0.6 per cent potassium or sodium sulphate [59].

No correlation was found between the ability of a *Rhizobium* strain to grow at 0.6 per cent sodium chloride and whether it originated from a saline or non-saline soil [57]. Considering this in conjunction with the fact that rhizobia are differentially tolerant to high levels of different salts leads to the conclusion that rhizobial growth studies in saline media should be interpreted with caution. Moreover, rhizobia may survive in soils at salinity levels much higher than those at which growth is restricted or eliminated in media [57].

The addition of salt to three soils of different textures greatly reduced the ability of four strains of *R. japonicum* to withstand air-drying. Survival was best in the more organic, higher clay soil and there were significant differences in the numbers of the four strains after four weeks [62].

The mechanism of salt tolerance of a *Rhizobium* strain isolated from mesquite in the Sonoran Desert has been explained in terms of its ability to accumulate L-glutamate intracellularly at high concentrations, i.e. at a 34-fold higher level than normal at 2.9 per cent sodium chloride, constituting 88 per cent of the amino acid pool [63]. *R. japonicum* strains forming non-slimy small colonies were found to be more salt labile (at 0.26 per cent sodium chloride) than those forming slimy large colonies [64]. A similar correlation between slimy colony type and tolerance of 0.5 per cent sodium chloride was observed in a survey of 139 rhizobial isolates from cowpeas grown at three West African locations (Table 1). However, it is noteworthy that the mesquite *Rhizobium* described above has a non-slimy colony type [65].

Table 1. Correlation of cowpea rhizobial colony type (on yeast extract mannitol agar) with salt tolerance

Colony type	No. of isolates tested	Fraction (%) growing at NaCl levels of			
		0%	0.5%	1.0%	2.0%
Slimy	73	100	100	12.3	0
Non-slimy	66	100	4.6	0	0

Source: Stowers, Kormendy and Eaglesham [66].

The degree of salinity tolerance of a *Rhizobium* strain appears to be of only limited use in predicting the effects of salinity on its ability to form root nodules. The nodulation potential of eleven strains of *R. meliloti* was significantly reduced at 0.4 per cent sodium chloride (6.6 mS/cm) and eliminated at 0.7 per cent sodium chloride (11 mS/cm), although none of the strains was significantly growth-inhibited by these salt levels in liquid media [67]. Extracts of a saline soil which eliminated infection thread formation in alfalfa did not affect survival of *R. meliloti* [68].

Very large differences in salt tolerance were found among twelve pasture and forage legumes [69]. A survey of the salt tolerance of 31 plant species included temperate legumes, tropical legumes and tropical grasses [70]. The legumes were inoculated with rhizobia, but the excellent growth of the grasses indicated that the soil was abundant in nitrogen. The mean salinity values (mS/cm) which reduced plant yields by 50 per cent were estimated by a mathematical model to be 7.6±0.8, 6.4±1.9 and 14.2±5.6 (in sodium chloride equivalents: 0.5, 0.4 and 0.9%) for the temperate and tropical legumes and grasses respectively; mean values of soil salinity which reduced plant yields to zero were 11.9±4.1, 12.6±3.0 and 21.6±8.3 (0.75, 0.8 and 1.4%). The most salt-tolerant legume was alfalfa (10.2 mS/cm for half yield and 18.8 mS/cm for zero yield), but *Macroptilium lathyroides* and siratro were almost equally tolerant. These levels of salinity which had serious effects on legume growth would not be excessive for many rhizobial strains, as detailed above.

Few studies have been reported on the effects of salt stress on legumes grown with nitrogen supplied in comparison with those dependent on nodule-fixed nitrogen. It is usually difficult, therefore, to appraise to what extent the adverse effects of salinity are on nodulation and fixation rather than on plant growth *per se*. The indications are that root-nodule dependent legumes are more saline-labile than when nitrogen-fed. This has been clearly shown in the case of *Cicer arietinum*, although significant variation in effectiveness among rhizobial strains existed at 0.46 per cent sodium chloride [71]. The growth of nodulated *Glycine wightii* was more adversely affected by a two-week salinity treatment of 8 mS/cm than was that of nitrogen fertilized plants [72]. The nodulation process, nodule development and the amount of nitrogen fixed were all inhibited, but were quickly regained after removal of the stress. Tissue injury resulting in leaf abscission occurred only in the nodulated plants, probably the result of nitrogen stress coupled with saline stress, but no nodule loss was noted indicating adaptability of nodules to increases in substrate salinity [72]. A comparison of salinity effects was made with alfalfa and soybean, using both nodulated and nitrogen-fertilized plants [73]. The two species responded differently to sodium chloride applications up to 8 mS/cm. At the highest salinity, alfalfa nodule weight was reduced by only 18 per cent whereas the whole plant weight was reduced by 55 per cent in both the nodulated and non-nodulated plants. At the same salt level soybean nodule weight and nodulated plant weight were both reduced by about 80 per cent whereas nitrogen-fed soybean weight was reduced by only 60 per cent. Clearly the root nodule symbiosis in alfalfa was relatively resistant to saline conditions, while adverse effects on the symbiosis *per se* contributed to poor growth in soybean. However alfalfa's salinity tolerance varied with the salt. Potassium chloride had a more strongly adverse effect on alfalfa nodulation than did magnesium chloride. At 0.3 per cent, both salts significantly reduced nodulation but had no effect on seed germination or early seedling growth [74].

In a comparison of salt tolerance of nodule-dependent cowpeas and mung beans, nodule initiation was severely reduced at 0.3 per cent sodium chloride [75]. Although nodule development was not affected in either species at this level of salinity, nitrogen fixing efficiency (nitrogen accumulated per unit of nodule tissue) was 43 per cent reduced in mung bean and unaffected in cowpea. This reduction in symbiotic efficiency may constitute the degree to which mung bean growth potential was limited by the saline conditions. The most saline-susceptible aspect of cowpea growth was nodule initiation.

Nodulation of the soybean cultivar Amsoy was inhibited at sodium chloride concentrations above 0.6 per cent (9.8 mS/cm) and eliminated at 1.2 per cent. Microscopic examination of the roots showed that at 1 per cent sodium chloride very few rhizobia were attached to root hairs and very few root hairs were deformed, indicating a salinity-induced lesion in the very early stages of the infection process [76]. Detached soybean nodules were sensitive to relatively low levels of salinity, their acetylene reducing activity being reduced by approximately 20 per cent by contact with a sodium chloride solution of 0.25 per cent [77].

Large variations in sensitivity to salt stress may exist between cultivars of a single species. When salt was applied in irrigation water from three weeks after planting to soybean, two cultivars, Lee and N53-509 were unaffected in their seed yields at a soil salinity of 9.6 mS/cm, whereas four other cultivars including Jackson and Improved Pelican failed to yield. Nitrogen was supplied at 112 kgN/ha so no conclusion may be drawn regarding relative tolerances of the symbioses. There was no correlation between the effects of salinity on seed germination and its effects on later vegetative and reproductive growth, e.g. at 10.1 mS/cm the germination rates of Lee, Jackson and Improved Pelican were equally reduced, by 15-20 per cent [78].

Alkaline soils can develop from saline soils with low calcium reserves. After a drop in the water table, soluble salts are washed down the profile and exchangeable calcium is replaced by sodium. Soil carbon dioxide forms carbonate and bicarbonate ions and these react with sodium to raise the pH [56]. Soil conductivity is usually less than 4 mS/cm with the pH in the range 8.5-10 [55]. Less intensive leaching of saline soils with higher calcium content can produce saline-alkaline soils with a conductivity of more than 4 mS/cm and a pH usually less than 8.5 [55, 56].

Clearly, the constraints to rhizobial survival, nodulation and legume growth pertaining to saline soils also apply to saline-alkaline soils. Very few data have been reported on the effects of high pH on rhizobial growth, nodulation or legume growth. Six legume species, *Melilotus parviflora, Sesbania aculeata, Trifolium alexandrinum, Cyamopsis tetragonoloba,* cowpea, lentil and pea, were planted in a highly saline-alkaline soil (36.5 mS/cm, pH 10.3) which had been uncultivated for 65 years and were examined for nodules after 60 days [79]. They were found on all species (although not on every plant examined) except pea, demonstrating that at least some rhizobial types can survive extreme saline-alkaline conditions for long periods. Soil dilution and plant infection tests indicated that rhizobia capable of nodulating *M. parviflora* and *S. aculeata* were in preponderance at $2.8-3.0\times 10^3$/g soil. In view of the saline lability of the infection process noted earlier, the observation of nodulation in this soil is surprising. However it may be significant that nodule scoring was delayed until 60 days; rhizosphere effects may have gradually ameliorated conditions sufficiently for the sparse nodulation observed. Beneficial effects of legume roots on both high and low extremes of soil pH have been reported [68].

None of 17 strains of *R. japonicum* showed significant growth in liquid media at pH 8.5 [80]. By contrast, in two surveys of 23 rhizobial isolates from eight diverse legume species (not including soybean) all were found to grow well in non-saline conditions at pH values up to 10 [81]. An examina-