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Tolerance to acid soil conditions of the velvet beans *Mucuna pruriens* var. *utilis* and *M. deeringiana*

I. Root development

KURNIATUN HAIRIAH[1,3], MEINE VAN NOORDWIJK[2] and SLAMET SETIJONO[1]
[1]*Soil Science Department, Faculty of Agriculture, Brawijaya University, Malang 65145, Indonesia and* [2]*Institute for Soil Fertility Research, P.O. Box 30003, 9750 RA Haren, The Netherlands.* [3]*Present address: Department of Plant Biology, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands*

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Abstract

Velvet beans, fast growing leguminous cover crops used in the humid tropics, are shallow rooted on acid soils. This might be due to an inherent branching pattern, to an intrinsic toxicity of the acid subsoil or to a relative preference for root development in the topsoil. Such preference could be based on soil chemical factors in the subsoil or on physical factors such as penetration resistance or aeration.

In a field experiment with two species of velvet bean (*Mucuna pruriens* var. *utilis* and *M. deeringiana*) all topsoil was removed and plants were sown directly into the acid subsoil. Root development was neither affected by this treatment nor by P fertilization or liming. In the absence of topsoil good root development in the exposed upper layer of subsoil was possible, so the hypothesis of a toxicity per se of the subsoil could be rejected.

To test whether poor root development in the subsoil in the presence of topsoil is due to an inherent branching pattern of the plant or to a relative preference for topsoil, a modified in-growth core technique was used. Local topsoil and subsoil and an acid soil with a higher exchangeable Al content were placed in mesh bags at different depths and at different bulk densities, with and without lime and/or P fertilizer. A comparison of root development in mesh bags placed in the topsoil or subsoil showed that position and thus inherent branching pattern is not important. Root development in the subsoil was poor when this soil was placed in a mesh bag in the topsoil, but in an acid soil of much higher exchangeable Al content and higher percentage Al saturation more roots developed. In a second experiment in mesh bags, bulk density of the repacked soil in the range 1.0–1.5 g cm^{-3} had no significant effect on root development. P fertilization and a high rate of liming of the soil placed in the mesh bag had a positive effect on root length density. It is concluded that poor root development in the acid subsoil under field conditions is due to a relative preference for topsoil. Al saturation and bulk density of the soil are not directly involved in this preference, but differences in availability of P and Mg or in Ca/Al ratios might play a role.

Introduction

Crop growth in the acid soils typical of the humid tropics is often limited by a number of factors including low pH, toxicities of Al and Mn, and deficiencies of P, Ca, Mg (Blamey and Edwards, 1989). Diagnosis of limiting factors for specific sites is essential for selecting suitable crops and cultivars (Scott and Fisher, 1989) and/or selecting suitable sites for agriculture. Preliminary studies on root distribution of the leguminous cover crop *Mucuna pruriens* var. *utilis* (vel-

vet bean) in acid soils in Nigeria and S. Sumatera showed that Mucuna roots hardly penetrate into the subsoil (Hairiah and Van Noordwijk, 1989). In dry periods crop establishment is poor, probably due to poor root penetration into the subsoil. As root damage usually is the first sign of Al toxicity, the Al saturation level of the subsoil might be the cause of the poor root growth, but other soil chemical or soil physical factors, such as mechanical impedance or poor aeration might be involved as well. Laboratory studies using solution cultures at pH 4.2 showed that two species of velvet bean, *Mucuna pruriens* (L) DC var. *utilis* (Wall. ex. Wright) Baker ex Burck and *M. deeringiana* (Bort) Small, have a moderate tolerance to Al; an Al^{3+} concentration of 0.3 meq L^{-1} was even found to stimulate root development (Hairiah *et al.*, 1990). Poor root development in the subsoil under field conditions can be due to:

1. an inherent branching pattern,
2. toxic soil conditions in this zone, or to
3. a relative preference for more favourable conditions in the topsoil.

It is possible to distinguish between these three hypotheses by experiments in which the number of choices for the root system are either decreased or increased. By removing all topsoil as one of the treatments in a field experiment, plants are forced to grow into the subsoil. If subsoil conditions are unsuitable for root development (hypothesis 2), a small root system would be expected under these conditions. If an inherent branching pattern is involved (hypothesis 1) or if only a relative preference for topsoil exists (hypothesis 3), a much stronger root development in the subsoil would be expected when the topsoil would be removed. Tests of the relative preference of root systems for expansion under different soil conditions can be made by placing various types of soil in various positions, packed to various bulk densities and with various soil amendments (*e.g.* lime or P fertilizer). Such 'split-root' experiments in the field can be done using a modified 'in-growth core' technique (Cuevas and Medina, 1988). If an inherent branching pattern restricts subsoil rooting (hypothesis 1), the position of the mesh bag should determine root development in each bag in an experiment in which topsoil and subsoil are placed in mesh bags in two positions (top and sub). If a soil quality factor, *e.g.* Al toxicity, is primarily responsible, the nature of the soil and not its position would determine root growth. If penetration resistance would be a major factor, root growth in the repacked topsoil and subsoil would differ from that in the same soil and position, undisturbed. By filling mesh bags with soil of different bulk density, lower and higher than that of the natural profile, critical levels for bulk density can be determined. A further test of the possible role of Al toxicity can be made by placing a soil with a higher Al level than the local subsoil in mesh bags in the topsoil. By including the same soil treated with P fertilizer or lime, alleviation of Al stress by improved P or Ca supply can be tested.

Root response to removal of the top layer of an acid soil is described here in combination with P fertilization and liming for the two species of velvet bean mentioned. Mesh bag experiments to test the relative preference for various soil conditions were performed as well. Aboveground plant development will be discussed in a subsequent paper. Here we will focus on the three hypotheses mentioned for poor root development in the subsoil under normal field conditions.

Materials and methods

Field experiments

The research was carried out at the field site of the N management project in Ketapang (Lampung, Sumatera, Indonesia). Climatic conditions (annual rainfall about 2.3 m) and the soil on this site, a hapludult, are described by Van der Heide *et al.* (1991). The plot where the present experiments were done had been cleared of secondary forest one and a half year before. The land was cleared by cutting and burning the aboveground vegetation, leaving the larger tree stumps in place. Before Mucuna was planted the area was cleared of *Imperata cylindrica* and some other weeds.

Experiment 1 was carried out in the middle of the rainy season, in January–February 1989. Two species of *Mucuna* were tested: *M. pruriens*

(L) DC var. *utilis* (Wall. ex. Wright) Baker ex Burck and *M. deeringiana* (Bort.) Small. Seeds were obtained from UD Sri Bharata Blitar (E. Java) and Uraba, Columbia, respectively. The treatments included zero-P and P applied as TSP (100 kg ha^{-1}, containing 20 kg P per ha), and as Florida rock phosphate (500 kg ha^{-1}, containing 100 kg P per ha). From half of the plots the dark-colored topsoil (10 to 15 cm) was removed. In the first four weeks after planting weeds were removed from the plot.

Experiment 2 was carried out in January–February 1990. After experiment 1, weeds were allowed to grow and by the start of experiment 2 the plots were covered by Imperata and other weeds. Plots were again cleared by slashing and removing the biomass from the plot. As in experiment 1 no significant differences were found between the two species, only *M. p. utilis* was used in the second experiment. The treatments of experiment 1 were tested for residual effects. As a split-plot factor, lime was applied as $CaCO_3$ to half of each plot. The application rate was 1 t $CaCO_3$ per ha (containing 40% Ca) for each milli equivalent of exchangeable Al per 100 g of soil: to plots where the topsoil was kept this amounted to 0.6 t ha^{-1}, for plots were topsoil was removed to 1.9 t ha^{-1}. In the second eperiment weeds were not removed after planting Mucuna.

In both experiments three seeds were planted per hill at a spacing of 25 × 50 cm; the seedlings were thinned to one after 1 week. Treatments were arranged in a randomized block design with 3 replications. The blocks were selected on the basis of their NH_4-acetate-extractable P content.

Root observations

Root samples were taken 4, 5 and 6 weeks after planting (WAP) for experiment 1, and at 6 weeks after planting for the experiment 2, in one block only. Samples were taken with a pinboard (Schuurman and Goedewaagen, 1971) of 90 × 50 × 10 cm, each sample containing 1 plant. After washing away the soil, the root sample was cut into layers of 10 cm depth and subdivided according to distance to the plant, *i.e.* 0–5 cm, 5–15 cm, 15–25 cm, respectively. For each sample root length was determined using the line intercept method of Tennant (1975). Root pattern as observed from soil pits was copied on a fine-grid paper (Fig. 1). In the same soil pits, penetration resistance was measured per 10 cm layer horizontally by using a pocket penetrometer. The average of 3 replicate measurements in 9 soil pits is presented.

Mesh bag experiments

In the first year an in-growth core (mesh bag) experiment was carried out within the main plot of the field experiment. Holes of 10 cm diameter and 10 or 20 cm deep were made with an auger at 12.5 cm from the nearest plant, in the plant row. Nylon sacks with a mesh size of about 5 mm were placed in the auger hole and filled with soil, at approximately the original bulk density (about 1.3 g cm^{-3}) using a technique described by Cuevas and Medina (1988). Any remaining gaps were filled with loose soil.

Subsoil was placed in a mesh bag both in the topsoil and in the subsoil, and topsoil likewise in both positions (Fig. 1). A very acid soil with a high Al saturation from Gajrug, W. Java, was also placed in a mesh bag in the topsoil position. To the Gajrug soil, phosphate was applied as TSP (equivalent to 500 kg ha^{-1}) as additional factor. Composite samples of the soil used for filling the mesh bags were analyzed (Table 1).

In the second year the root response of *M. p. utilis* to different soil types (local topsoil, local subsoil, Gajrug topsoil, Gajrug subsoil) was tested at different bulk densities (1.0, 1.15, 1.3, 1.5 mg cm^{-3}). Lime was applied at three rates, *i.e.* 0, 1 t $CaCO_3$ per ha for all types of soil and 1 t $CaCO_3$ per ha for each milliequivalent of exchangeable Al per 100 g of soil. To the local soil, phosphate was applied as TSP (equivalent to 0 or 500 kg TSP per ha). Root development in the various mesh bags was observed at 6 weeks after planting. Root weight, root length density, and nodulation were determined in 5 replicate samples.

Results were analyzed with ANOVA (analysis of variance) by using the GENSTAT 5 computer program; when significant treatment effects were found a t-test was used if less than 5 treatments were to be compared, and Duncan's Multiple Range Rest when more comparisons were in-

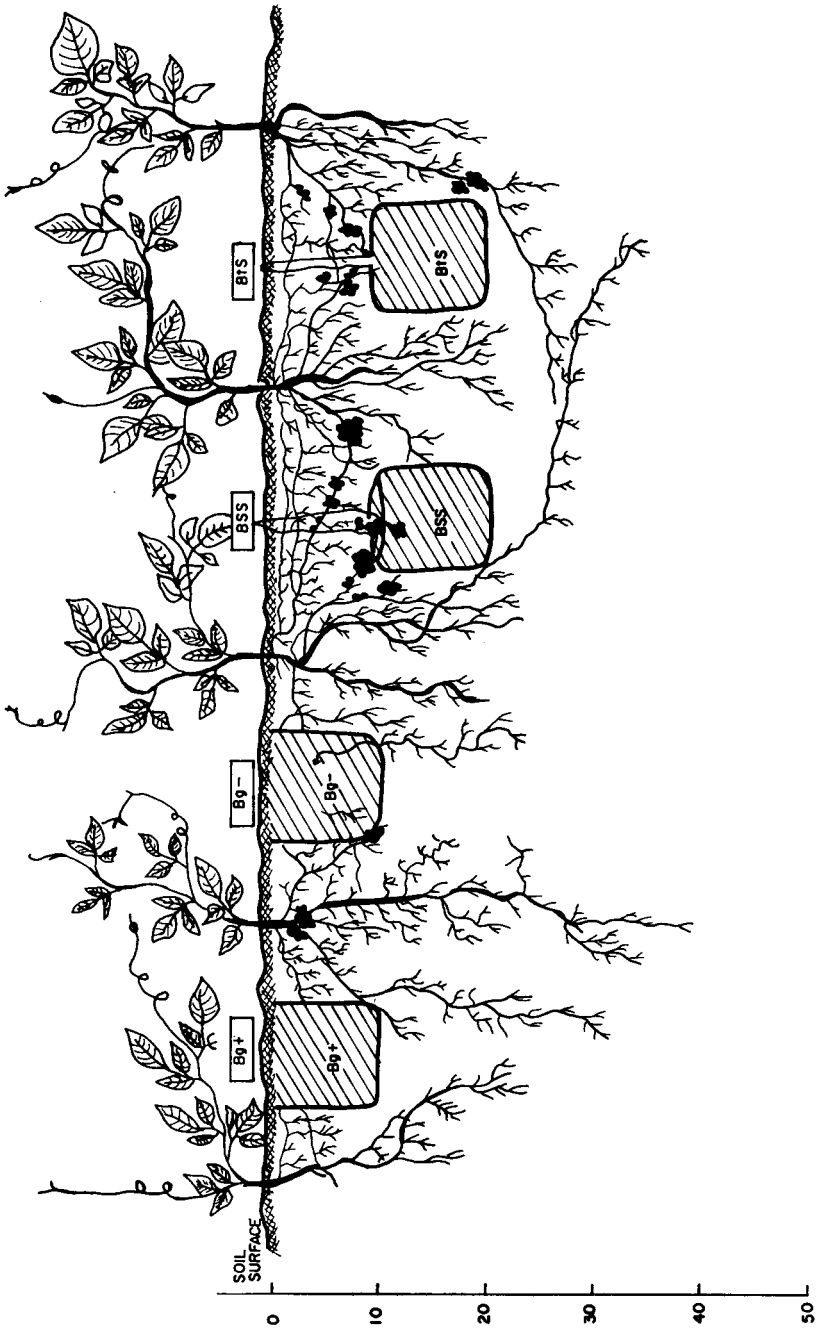

Fig. 1. Root system of Mucuna and the position of mesh bags used as in-growth core.

Table 1. Selected soil properties of the four soils used for filling mesh bags: local topsoil (0–15 cm), local subsoil (15–45 cm), and topsoil (0–30 cm) and subsoil (30–60 cm depth) collected from Gajrug, W. Java; K, Na, Ca and Mg were extracted with 1 *N* NH_4-acetate at pH 7.0, Al with 1 *N* KCl (Anderson and Ingram, 1989)

Soil type	pH H_2O	pH KCl	P-Bray	K	Na	Ca	Mg	Al	ECEC	% Al saturation
				(meq/100 g)						
Local top	5.1	4.2	20	0.12	0.71	2.1	0.38	0.71	4.02	18
Local sub	4.8	3.9	5	0.11	0.66	0.24	0.10	1.60	2.71	59
Gajrug top	5.1	3.6	5	0.39	0.95	4.74	1.78	16.06	31.6	67
Gajrug sub	4.9	3.6	*	0.27	0.90	1.40	0.65	17.73	27.6	85

volved ($P < 0.05$). When variances were uneven, a logarithmic transformation of data was used.

Results

Effects of removal of topsoil. P fertilization and liming

Figure 2A and B shows root length density, L_{rv} (cm cm^{-3}), per depth interval for the two species in experiment 1, at 6 WAP. For all treatments an approximately linear decrease of log L_{rv} with depth was found. As the pinboard observations were not replicated, no statistical analysis of the results was possible. The data suggest, however, that in *M. P. utilis* (Fig. 2A) the decrease in L_{rv} with depth was more rapid when the topsoil was removed than when it was retained. Root length density in the 0–10 cm layer did not appear to be affected by treatments; L_{rv} in the 0–10 cm layer in the plots where topsoil was removed was

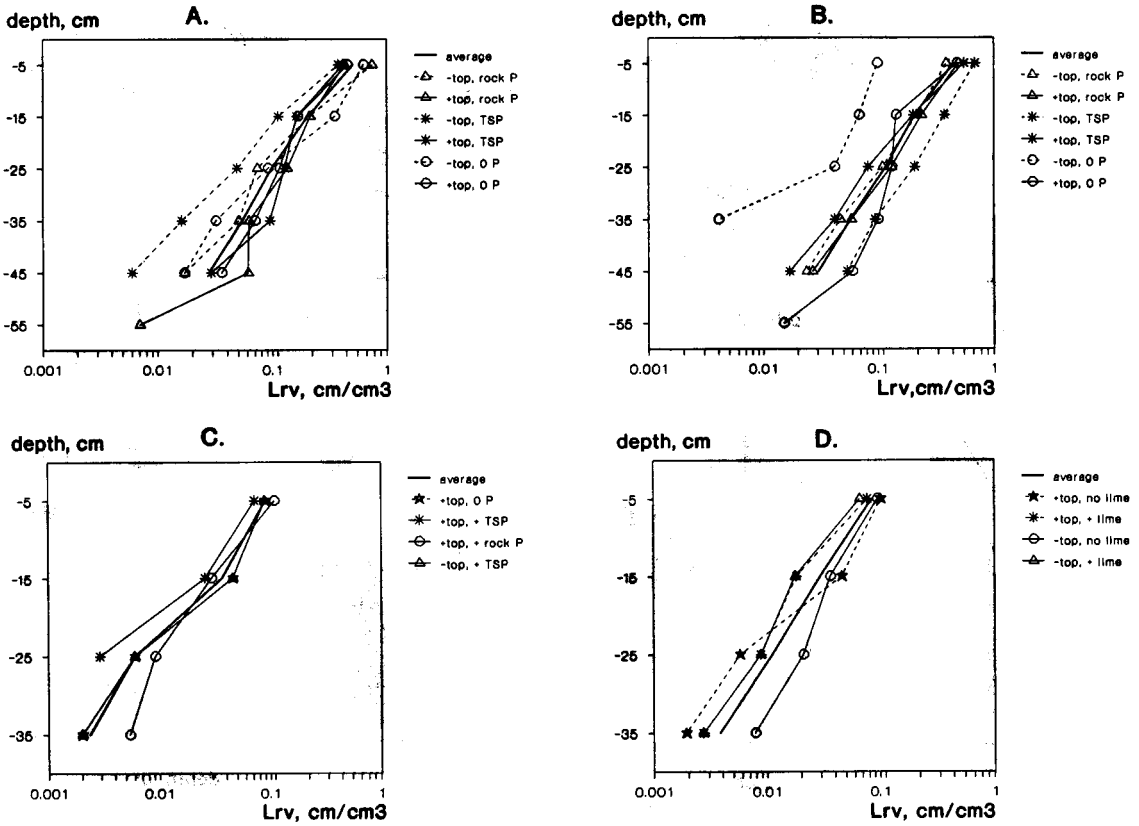

Fig. 2. Root length density, L_{rv}, as a function of depth; Experiment 1: **A.** *M. p. utilis*; **B.** *M. deeringiana*; Experiment 2 (*M. p. utilis* only): **C.** residual effect of P fertilization, **D.** effect of liming.

much higher than that in the equivalent 10–20 cm layer where topsoil was retained.

M. deeringiana (Fig. 2B) in the plots where topsoil was removed and P was added had a root distribution-in-depth that was similar to that in plots where the topsoil was retained. On plots where topsoil was removed and no P was added, root development clearly lagged behind.

Figure 3 shows the results for the specific root length, L_{rw}. In *M. P. utilis* (Fig. 3A) L_{rw} increased with depth, except in the deepest layer, where non-branched root tips dominated. Treatment effects on L_{rw} were not apparent. In *M. deeringiana* (Fig. 3B) more variation in L_{rw} existed, but no clear treatment effects appeared.

In all pinboard samples good nodulation was observed; no quantitative data are available due to problems with sample storage. Where topsoil was removed good nodulation was found, even in the absence of P fertilization.

In the second year (Fig. 2C) no residual effects of P fertilization on root length density of *M. p. utilis* were observed. Liming did not improve root development in the presence or absence of topsoil (Fig. 2D).

Root development in in-growth cores

Statistical analysis showed that *M. p. utilis* produced a significantly higher root dry weight than *M. deeringiana* in the mesh bags, but there was no significant difference in specific root length and root length density between the two species (Table 2). Root growth in the subsoil, whether in the 'top' or 'sub' position, was poorer than that in the topsoil. Table 2 shows that root dry

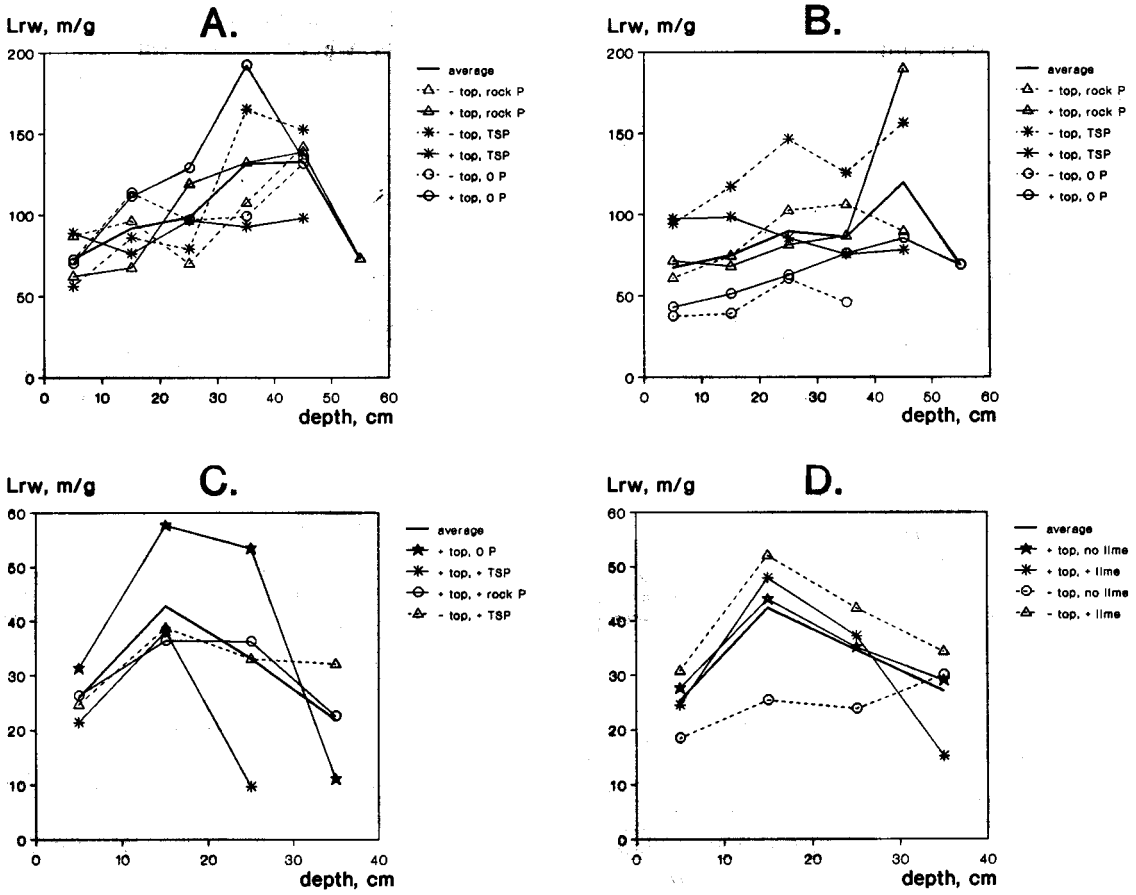

Fig. 3. Specific root length, L_{rw}, as a function of depth; Experiment 1: **A.** *M. p. utilis*; **B.** *M. deeringiana*; Experiment 2 (*M. p. utilis* only): **C.** residual effect of P fertilization, **D.** effect of liming.

Table 2. Effect of treatment on root dry weight density, D_{rv}, specific root length, L_{rw}, and root length density, L_{rv}, of Mucuna at 6 weeks after planting (mesh bag technique); numbers followed by different letters indicate significant ($P < 0.05$) differences, NS = not significantly different ($P < 0.05$), * = on local subsoil only

Main treatment	D_{rv} (mg cm^{-3})	L_{rw} (mg^{-1})	L_{rv} (cm cm^{-3})
Experiment 1:			
Species:		NS	NS
M. utilis	1.571 a	103	0.164
M. deeringiana	1.018 b	82	0.131
Soil position:		NS	
Topsoil in 'top'	0.218 b	98	2.080 a
Topsoil in 'sub'	0.170 b	126	2.026 a
Subsoil in 'top'	0.060 c	72	0.416 b
Subsoil in 'sub'	0.043 c	103	0.376 b
Gajrug soil, 0 P	0.118 bc	86	0.868 b
Gajrug soil, + P	0.276 a	71	2.001 a
Experiment 2:			
Soil:		NS	
local subsoil	0.033 p	41	0.139 q
Gajrug topsoil	0.072 q	58	0.422 p
Gajrug subsoil	0.044 q	57	0.242 p
Liming:		NS	NS
0	0.038 q	53	0.218
1 t ha^{-1} $CaCO_3$	0.040 q	52	0.206
1 t ha^{-1} $CaCO_3$ per meq Al	0.071 p	51	0.379
Phosphate application*		NS	
no P	0.052 p	50	0.278 p
+ P	0.029 q	49	0.131 q

weight in the topsoil was not significantly different ($p < 0.05$) in the 'top' and the 'sub' position. As position had no significant effect in either soil, we may conclude that a soil quality factor is involved, not an inherent branching pattern or position-related factor such as aeration.

Root dry weight and root length in the Gajrug soil without P were higher than those in local subsoil, but the differences were not statistically significant. Application of P to the Gajrug soil increased root dry weight significantly, and led to a dry weight higher than, and a root length equal to, that in the local topsoil.

In the second year's experiment root dry weight and root length density in the Gajrug topsoil and subsoil were significantly ($p < 0.05$) higher than those in local subsoil. The high rate of liming (1 t $CaCO_3$ per ha for each milliequivalent of Al exchangeable per 100 g soil) significantly ($p < 0.05$) increased root dry weight, but not root length density. P application to local subsoil significantly increased root dry weight and root length density.

The root length densities, L_{rv}, in the mesh bags are compared with those for the equivalent pinboard samples (same depth and distance to the plants) in Table 3. In four out of the five comparisons made, the root length density in the mesh bag was higher than that in an equivalent volume of undisturbed soil. The specific root length was similar for the two methods, except for *M. deeringiana* in the topsoil comparison. However, further tests of the effect of various soil bulk densities on root growth showed no significant difference.

Data on nodulation in the mesh bags are given in Table 4. Of the mesh bags containing topsoil a larger fraction was nodulated and nodule dry weight was higher than for the subsoil. Position effects were smaller than the differences among soils. In Gajrug soil without P fertilizer nodulation was similar to that in the subsoil; P fertilization slightly improved nodulation. *M. deering-*

Table 3. Comparison of root length density (L_{rv}), specific root length (L_{rw}) determined by two techniques of root sampling at the same position. A = in-growth core, B = pinboard; for experiment 2: BD = bulk density (g cm^{-3})

Position:	*M. p. utilis*		*M. deeringiana*	
	L_{rv} (cm cm^{-3})	L_{rw} (mg^{-1})	L_{rv} (cm cm^{-3})	L_{rw} (mg^{-1})
Experiment 1:				
A. topsoil – 'top'	2.46	88	1.76	112
B. 0–10 cm	0.61	86	0.72	51
A. subsoil – 'sub'	0.62	97	0.12	56
B. 10–20 cm	0.34	116	0.24	49
Experiment 2:				
A. topsoil, BD 1.3	0.68	78		
A. topsoil, BD 1.15	0.50	59		
B. 0–10 cm, BD 1.3	0.10	46		

iana seemed to be better nodulated than *M. p. utilis*.

Discussion

The small effect of removal of the topsoil on root development and the improved rooting in the upper zone of the subsoil under these conditions shows that no toxicity *per se* of the subsoil (hypothesis 1) is involved.

The poor root development in mesh bags filled with subsoil placed in a topsoil position and the good root development in topsoil placed in the subsoil shows that shallow root development of Mucuna in the field is not due to an inherent branching pattern (hypothesis 2). We thus conclude that a relative preference for root development in the topsoil (hypothesis 3) is the most likely explanation. The determining factor could be of a chemical or of a physical nature.

Root growth in the mesh bags was much better than in equivalent volumes of soil sampled with the pinboard method (Table 3). Although soil bulk density in the mesh bag was adjusted approximately to the natural condition of the soil in experiment 1, the increased root development in the repacked soil in the mesh bag suggested that penetration resistance might play a role in the normal soil profile. Mechanical impedance of the soil, as measured with a pocket penetrometer, was slightly higher in the upper layer of the subsoil than in the topsoil (Fig. 5). The second year's experiment showed, however, that bulk density had no effect on root length density in the range tested, which is wider than that found in the field. Although some doubts exist as regards the homogeneity of the bulk density within the mesh bags, we may conclude that bulk density is not a major factor in the preference of roots for the topsoil. A second soil physical factor, poor aeriation in the normal subsoil, might hinder Mucuna root development. A split-root experiment in a nutrient solution with *M. p. utilis* with and without aeration showed that

Table 4. Dry weight of nodules per unit soil (mg cm^{-3}), and dry weight of nodules per unit root dry weight (mg mg^{-1} roots) in the mesh bags at 6 WAP

Treatment	Fraction of nodulation		Nodule dw. (mg cm^{-3} soil)		Nodule dw (mg mg^{-1} root dw)	
	M. ut.	*M. dee.*	*M. ut.*	*M. dee.*	*M. ut.*	*M. dee.*
Topsoil in 'top'	0.6	1.0	0.051	0.237	0.183	1.513
Topsoil in 'sub'	0.8	1.0	0.024	0.066	0.146	0.491
Subsoil in 'top'	0	0.4	none	0.083	none	1.338
Subsoil in 'sub'	0.4	0	0.020	none	0.312	none
Gajrug topsoil, 0 P	0.4	0.0	0.012	0.001	0.117	0.007
Gajrug topsoil, + P	0.4	0.6	0.029	0.094	0.103	0.346

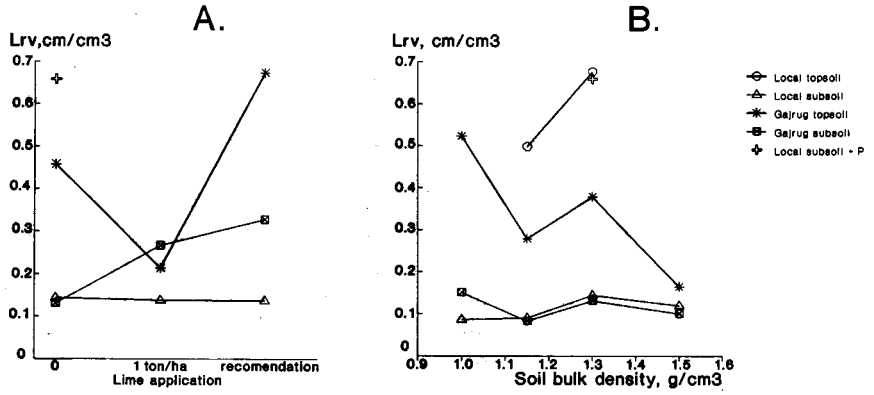

Fig. 4. Results of in-growth core experiment in the second year: **A.** effect of liming, **B.** effect of soil bulk density.

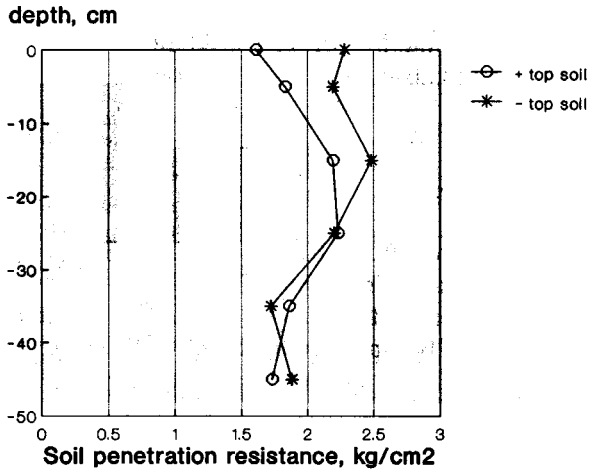

Fig. 5. Mechanical impedance of the soil as measured horizontally in a soil pit with a pocket penetrometer with a blunt tip.

M.p. utilis can increase its air-filled root porosity from 3.4% to 5.0% in response to poor oxygen supply (Hairiah and Van Noordwijk, unpubl.); because of this response we may expect that Mucuna roots are able to penetrate about a decimeter into a non-aerated medium (De Willigen and Van Noordwijk, 1989) and that they are not extremely sensitive to reduced aeration. Aeration of the subsoil in the mesh bags should be better in the top- than in the sub-position and little difference in root development was found between these positions. Physical explanations are thus not likely and we may focus on chemical differences between subsoil and topsoil as primary causes of shallow root development.

Topsoil and subsoil differ in pH, P content and Al saturation (Table 1):

a) pH. The difference in pH between topsoil and subsoil as such cannot be responsible for the poor root development in subsoil. In solution culture experiments (Hairiah *et al.*, 1990), maximum root development was found at a solution pH of 4.2, considerably below the pH(H_2O) of the subsoil.

b) Deficiency of P. The difference in P availability between topsoil and subsoil may be partly responsible for the root development observed. Addition of P to local subsoil and to Gajrug soil significantly increased root growth (Table 2). When no choice is available, as for the plants grown after removal of all topsoil, the low P level as such does not restrict root development. If a choice is available, however, as in the mesh bag split-root experiment, preferential root development in the soil with increased P supply (equivalent to 500 kg TSP ha^{-1}) was found. Many plants, when deficient in P, show a strong increase in root branching in local zones of high P supply (De Jager, 1985). In the field experiment, little response to P fertilization was found when the topsoil was removed, except for *M. deeringiana*. However, the amount of P added (100 kg TSP ha^{-1}) may have been too low to produce a significant response and the fertilizer may not have penetrated far enough into the

subsoil. Bolan *et al.* (1985) found that P availability in acid soils is very low, due to sorption of phosphate by Al and Fe hydroxides. Conversely, adding P may also have reduced monomeric Al content.

c) *Al saturation.* Local subsoil has a much higher Al saturation than the topsoil. The respective Al concentrations in roots in this experiment, about 6.3 and 8.5 g kg^{-1} for roots grown in topsoil and roots grown in subsoil (Hairiah *et al.*, 1990), are comparable with those for roots grown in a nutrient solution containing Al at a concentration of 0.19 and 0.29 mmol L^{-1}, respectively. In solution experiments an Al concentration of 0.11 mmol L^{-1} increased root fresh weight of both Mucuna species but not shoot fresh weight. Al concentrations higher than 0.19 mmol L^{-1} hampered both root and shoot growth. Al toxicity might thus play a role in poor root development in the subsoil and poor growth of the plants when forced to grow into the subsoil. However, the relatively good root development in the Gajrug soil, with an even higher Al saturation shows that Al saturation of the soil complex is not directly related to Mucuna root growth. Bruce *et al.* (1988) showed that the activity of monomeric Al in soil solution gives a better prediction of Al effects on soybean root elongation than the Al saturation of the complex. Further soil chemical analysis of the soils used is necessary to check this parameter and to determine Ca/Al activity ratios in soil solution.

Horst *et al.* (1990) found that the Al tolerance of soybean in a sand culture was higher than in a nutrient culture; they formulated a hypothesis that mechanical impedance in the sand culture may increase exudation of organic acids by the root and thus reduce Al toxicity. Our results do not confirm this hypothesis; root development in the subsoils used did not increase with increasing soil bulk density.

d) *Mn availability.* Shoot Mn concentration of plants forced to grow into the subsoil was higher than that for plants grown in the presence of topsoil (Hairiah *et al.*, 1990). Usually, however, Mn-toxicity primarily leads to shoot damage and not to reduced root growth (Scott and Fisher, 1989).

e) *Deficiency of Ca and Mg.* Roots forced to grow into the subsoil had an extremely low Ca content, although Ca and Mg contents of the shoot were normal (Hairiah *et al.*, part II, in preparation). In the mesh bag experiment the high rate of liming increased root growth in the subsoils used. On the plots where topsoil was removed, however, no clear response to lime addition was found. The difference might be due to poor penetration of lime into the soil in the field experiment. Ca and/or Mg may play a role in the relative preference of roots for the topsoil.

It may be concluded that poor root development of velvet beans in the subsoil is due to a relative preference for the topsoil. Al saturation and bulk density of the soil are not directly involved in this preference; differences in availability of P and Mg or in Ca/Al ratio between topsoil and subsoil might play a role.

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