

Aluminium avoidance by *Mucuna pruriens*

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The hypothesis was tested that the avoidance of acid subsoil by the velvet bean *Mucuna pruriens* is based on a mechanism acting on the whole root system rather than on individual roots. In a split-root experiment with circulating nutrient solution the growth of plants with Al-containing (+/+) or Al-free (0/0) solution on both sides of the root system was compared with that of plants which had a choice (0/+). Two levels of Al (110 and 185 μM) were tested at two levels of Ca (50 and 1250 μM). In the 185 μM Al treatment the concentration of monomeric Al varied between 53 μM , directly after refreshing the solution, and 5 μM at harvest time.

An external Al concentration of 110 μM had no effect on shoot and root dry weight, while 185 μM Al applied to both sides of the root system (+/+) increased root dry weight and reduced shoot dry weight and shoot/root ratio, compared with the 0/0 control. Application of 185 μM Al to half of the roots, led to a significant shift in root growth in favour of the control side; this response is described here as Al avoidance. On the basis of total root length, root dry weight and root surface area, the ratio of 0/+ roots was 3.1, 2.8 and 2.4, respectively.

Al avoidance at 185 μM Al was confirmed in another experiment, in which root response was measured to a local P source, supplied in a third compartment containing only KH_2PO_4 . A significant increase in root length and dry weight in this compartment was observed, when other roots of the same plant were growing in the presence of Al. This result indicates that Al avoidance by *Mucuna* roots is related to P preference.

Key words – Aluminium, calcium, *Mucuna pruriens* var. *utilis*, phosphate, root growth, split-root experiment, tolerance mechanism, velvet bean.

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Introduction

In general the primary symptom of Al toxicity is stunted root growth, normally followed by reduced shoot growth. In a number of plants, however, Al reduces growth of the shoot without effects on the roots (Balsberg Pålsson 1990). The inhibiting effect of Al on root elongation and cell division can be overcome by a range of physiological tolerance mechanisms (Clarkson 1969, Foy et al. 1978, Wissemeier et al. 1987, Klotz and Horst 1988). Relatively low concentrations of Al may even stimulate root and/or shoot growth (Hackett 1962, Van Hai et al. 1989, Hairiah et al. 1990). Both stimulation and reduction of root growth are explained by a model

of Bennet and Breen (1991), who focus on the root cap as an Al sensor and on subsequent hormonal signal transduction to the meristem, without feedback from other parts of the plant.

There is a large discrepancy between results of experiments on Al tolerance in the laboratory and in the field (Horst et al. 1990). Several explanations have been given for this gap. The complex nature of Al chemistry makes it difficult to relate toxic Al concentration of solution culture studies to concentrations found toxic in soils. Even the relative ranking of tolerance between cultivars may differ between solution culture and field studies. Tolerance mechanisms based on a local modification of the environment of the root tip (e.g. by

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exudation of organic acids which bind Al and by an increase of the rhizosphere pH), will be much more effective in the soil than in well-stirred nutrient solutions (Horst et al. 1990). However, the difference in Al-tolerance between field tests and physiological studies may not be fully explained by local soil modifications.

Most physiological studies and screening tests for selection and breeding of Al tolerance have been performed in homogeneous root media. Little attention has been given to the difference in homogeneity between experimental situations and actual soil profiles. The heterogeneity of soils allows the plants to choose, because parts of the root system encounter different soil conditions. Nutrient-stressed plants show preferences for root development in locally favourable soil conditions (De Jager 1982). Much less is known about mechanisms for avoidance of unfavourable soil conditions which are not toxic in an absolute sense.

The velvet bean, *Mucuna pruriens* (L.) D.C. var. *utilis* (Wall. ex Wright) Baker ex Burck is used throughout the humid tropics as a leguminous fodder and cover crop. On acid soils, common in the humid tropics, it forms a shallow root system (Hairiah and Van Noordwijk 1989). Studies in nutrient solutions showed that this species and the related *M. deeringiana* (Bort) Small were moderately tolerant of Al (Hairiah et al. 1990). An Al concentration of 110 μM at pH 4.2 even increased root fresh weight, Al concentrations above 185 μM hampered root growth and the shoot:root ratio continuously decreased with increasing Al concentration, indicating that the shoot was more affected than the roots. These results appeared contradictory to the shallow root development of *Mucuna* in the presence of an acid subsoil. Field tests showed, however, that if *Mucuna* was sown directly into a subsoil [pH (H_2O) 4.8; pH (1 M KCl) 3.9; 59% Al saturation], after removal of the topsoil [pH (H_2O) 5.1; pH (1 M KCl) 4.2; 18% Al saturation], a large root system was formed in the subsoil layers which hardly contained any roots when the topsoil was present (Hairiah et al. 1991a). For a further analysis, subsoil and topsoil were placed in meshbags at various positions in the soil profile. Again roots of *Mucuna* avoided subsoil, regardless of position and bulk density, if another choice was available.

We set up a split-root experiment to test whether the avoidance of Al-containing subsoil by *Mucuna* roots could be based on 'Al-avoidance', despite our observations on moderate Al-tolerance in water culture.

For several species the Al/Ca concentration ratio, rather than the Al concentration as such, is important in Al injury (Horst 1987); in other species Mg is involved in Al toxicity (Keltjens and Dijkstra 1991). To test whether Ca modifies Al-toxicity for the velvet bean, we used two Ca levels (50 and 1250 μM), in combination with two Al levels (110 and 185 μM).

In addition, we attempted to discriminate between two explanations for stimulation of root growth by in-

termediate levels of Al (Hairiah et al. 1990): I. The nutrient solution contained elements, such as P and Ca, at a supra-optimal level and Al reduced their toxicity. If this hypothesis is true a stimulation of root growth in the Al-containing solution should be expected in a split-root experiment, where half of the roots are exposed to an Al containing solution and the other half to a control solution without Al. II. The presence of Al negatively affected nutrient or water uptake and the plant showed a compensative 'functional equilibrium' response by increase of its root growth (Brouwer 1983). If this hypothesis is true a stimulation of root growth should be expected in both split-root compartments or even preferentially in the control compartment.

P uptake and especially transport to the shoot may be affected by the presence of Al. We used a simple test of the P status of the plant. Preferential root development near local P sources disappears when plants have reached an adequate P status (De Jager 1982). In a further experiment with *Mucuna*, a third split-root compartment was added, containing only KH_2PO_4 . Root development in this compartment was interpreted as indicator of the P status of the plant.

Materials and methods

Seeds of *Mucuna pruriens* var. *utilis* [obtained from Usaha Dagang (UD) Sri Bharata, Nglegok, Blitar, East Java, Indonesia] were germinated as previously described (Hairiah et al. 1990). After about 2 weeks, uniform plants were chosen and transferred to a split root system, in which the two halves of the root system in pots of 5 l volume could be exposed to circulating nutrient solution with (+) or without (0) Al, for 4 weeks.

A modified 1/4 strength Hoagland solution (Tab. 1) was circulated in the system. The pH of the nutrient solution was daily adjusted to 4.2 by adding 1 M HCl or 1 M-KOH. The nutrient solutions were initially renewed once a week and twice a week in the last two weeks. Solution samples were taken for determination of the

Tab. 1. Composition of nutrient solutions (mM). Micronutrients were applied in all solutions as H_3BO_3 11.5 μM , MnCl_2 2.30 μM , ZnSO_4 0.20 μM , CuSO_4 0.08 μM , Na_2MoO_4 0.13 μM , Fe as Ferro rexenol 22.5 μM .

Component	Nutrient concentration (μM)			
	50 μM Ca		1250 μM Ca	
	0 Al	+ Al	0 Al	+ Al
KNO_3	3.75	3.75	2.45	2.45
KH_2PO_4	0.15	0.15	0.15	0.15
MgSO_4	0.50	0.50	0.50	0.50
$\text{Ca}(\text{NO}_3)_2$	0	0	0.625	0.625
CaCl_2	0.05	0.05	0.625	0.625
AlCl_3 Exp. 1	0	0.110	0	0.110
Exp. 2	0	0.185	0	0.185
Exp. 3	-	-	0	0.185

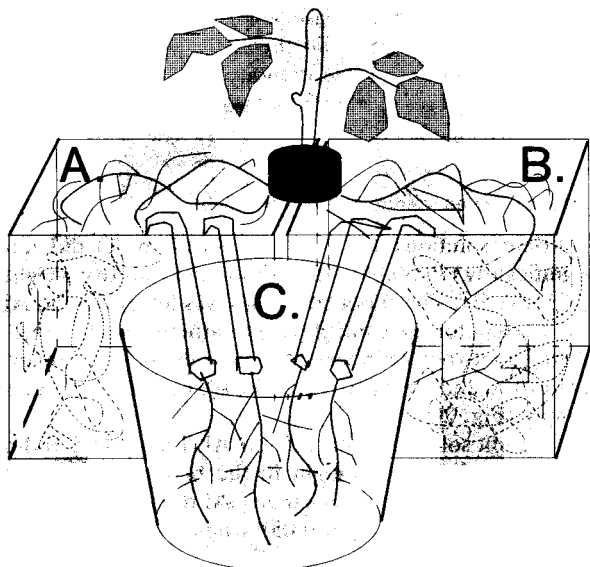


Fig. 1. Schematic design of split root Experiment 3. Containers A and B are connected to circulating nutrient solutions. Some roots from A and B were led into a third pot (C) containing 1 mM KH_2PO_4 . Nutrient solutions were aerated separately (not shown).

concentration of inorganic monomeric Al, using a method modified from Kerven et al. (1989). To a sample volume of 3 ml, 0.5 ml of a solution of phenantroline (0.2%, w/w) and ascorbic acid (0.5%, w/w) was added, and 0.2 ml of 0.0375% (w/w) pyrocatechol violet. Subsequently 1 ml of a hexamine buffer was added, with the following composition: 75 g hexamethylentetramine plus 2 ml of 32% (w/w) ammonia (pH adjusted to 6.2 with 5 M HCl) and diluted to 500 ml. The whole sample was thoroughly mixed and absorption was measured photometrically at 580 nm after 1 min. Standard solutions were prepared from AlCl_3 in the range 2–25 μM Al, in 1 mM HNO_3 to avoid polymerization (Hairiah et al. 1991b).

Three experiments were carried out in a glasshouse with control of temperature and humidity at the DLO-Institute For Soil Fertility in Haren, The Netherlands, under natural light conditions (April–August). Day temperature was kept at 27–30°C and night temperature at 20°C, with a relative humidity of the air of about 95%, close to that under natural growth conditions.

Treatments

Plants with two halves of the root system exposed to the same solution, either with (+/+) or without (0/0) Al, were compared with plants where the two halves were in different solutions (0/+), in a randomized block design with 6 replicates. Experiment 1 was conducted in April–June 1990; the effect of 0 and 110 μM of Al was tested in combination with two Ca levels, 50 and 1250 μM (Tab. 1). Experiment 2 was conducted in July–August 1990 with a higher Al level (185 μM). Experi-

ment 3 was conducted in May–June 1991, with a Ca level of 1250 μM and 185 μM Al. To test whether Al avoidance was related to preferential root growth at a local P supply, roots were carefully led, through drinking straws, into a third pot containing only 1 mM KH_2PO_4 at pH 4.0 (Fig. 1).

Harvesting and analysis

Plants were harvested after 4 weeks on solution (6 weeks after sowing). Excised roots were rinsed 3 times in deionized water, blotted between two layers of tissue paper, centrifuged for 30 s, weighed and then dried in an oven at 100°C for 48 h and weighed again. Root diameter and root length were measured (Hairiah et al. 1990) from subsamples stored in a freezer at –20°C. Microscopic sections were prepared from roots grown with and without Al. Shoot and root samples were analyzed for total P, K, Ca, Mg and Al (Hairiah et al. 1990), in triplicate. Due to an accident, shoot material of experiment 2 was lost. Cation contents are expressed on a tissue water basis (Leigh and Johnston 1983), P on a dry weight basis.

Statistical analysis

Results were analyzed with ANOVA (analysis of variance) by using the GENSTAT 5 computer program (Payne et al. 1987), and Duncan's multiple range test when significant ($P < 0.05$) treatment effects were found. In case of uneven variances, a logarithmic transformation of data was used. For the statistical analysis of root data, the following contrasts were tested: (a) all roots grown in Al-containing solution (from +/+ and 0/+ treatments) versus all roots grown in Al-free solution; (b) the two sides of the 0/+ treatment; (c) +Al roots of 0/+ plants versus roots of +/+ plants. For the test of Al avoidance the difference in root weight between the two sides of the split-root system of plants with the same solution in the two compartments (0/0 and +/+) was used as background variation.

Results

Monomeric Al concentration of the solutions

In Experiment 1 (110 μM Al) the concentration of monomeric Al was about 61 μM , directly after Al addition. Prior to refreshing the solution 3, 4, 5 and 6 weeks after planting, 11, 9, 3 and 2 μM monomeric Al were measured, respectively, independent of Ca supply. In Experiment 2 (185 μM Al) the concentration of monomeric Al decreased from 53 μM , directly after Al addition, to 27, 19, 3 and 5 μM , respectively, prior to refreshing the solution at 3, 4, 5 and 6 weeks after planting. In Experiment 3 (185 μM Al) the decrease was from 61 μM , directly after Al addition, to 36, 24, 4 and 12 μM , respectively. In an experiment without plants it

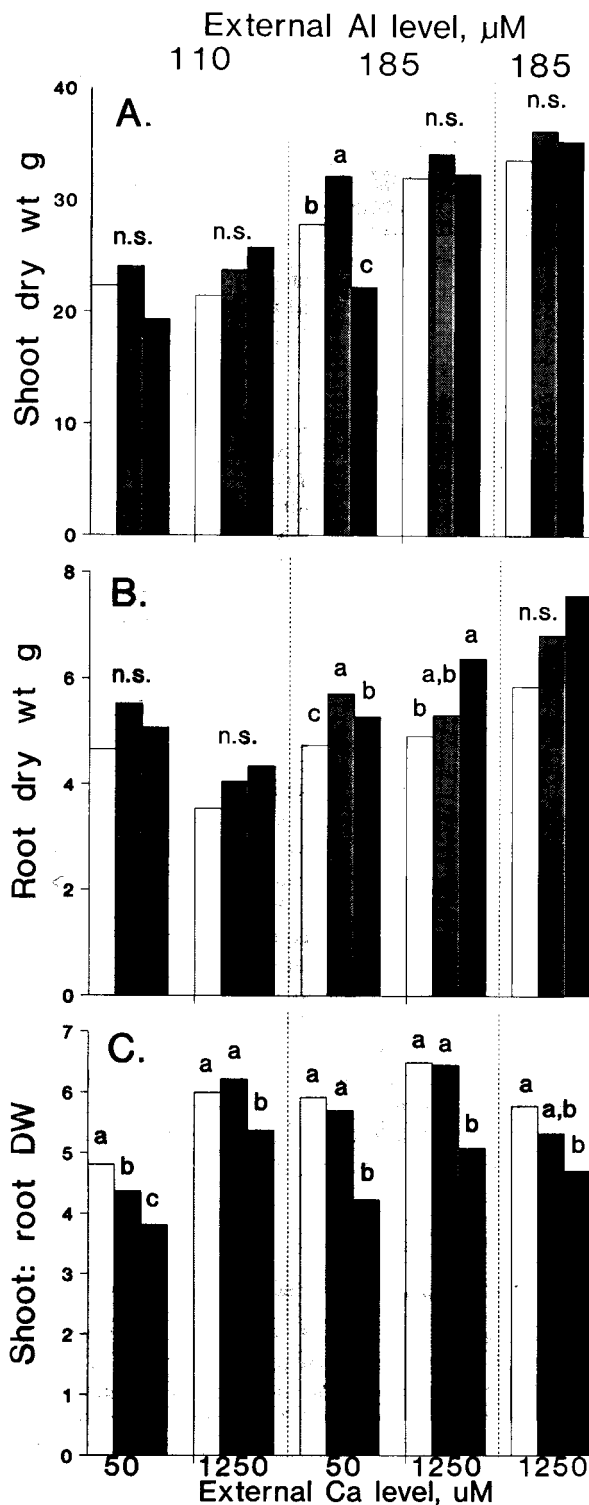


Fig. 2. Shoot dry weight (A), root dry weight (B) and shoot: root ratio (C) of *Mucuna* at two levels of Al and Ca. Split root experiment with three combinations of Al-free (0) and Al containing solution (+): 0/0, white; 0/+, gray; +/+, black. Within each Ca treatment, columns with different letters differ significantly ($P < 0.05$; $n = 24$).

was found that an increase in pH of the solution, as actually occurred between the daily pH adjustments, caused a similar decrease in monomeric Al; no specific Al-binding affect of exuded organic acids was evident (Hairiah et al. 1991b).

Effects of Al on shoot and root dry weight

Nutrient solutions with 110 μM Al (Exp. 1) did not significantly ($P < 0.05$) affect shoot and root dry weight (Fig. 2A,B). The shoot:root ratio was lower for the Al (+/+) than for the control (0/0) treatment. An intermediate shoot:root ratio was found for the 0/+ treatment at low Ca, and a value close to the 0/0 control at high Ca supply (Fig. 2C).

Nutrient solutions with 185 μM Al (Exp. 2 and 3) did not affect shoot dry weight in the high Ca treatment (Fig. 2A). At the low Ca supply, Al reduced shoot dry weight significantly ($P < 0.05$) when applied to both sides of the root system; in the 0/+ treatment shoot dry weight was significantly higher than in the 0/0 control. In Experiment 2, root dry weight in the +/+ Al treatment was significantly higher ($P < 0.05$) than that in the 0/0 control, at both Ca levels. In Experiment 3 a similar, but not significant, increase was found. In Experiment 2 at the low Ca concentration, the 0/+ treatment resulted in the highest total root dry weight; at the high Ca level root dry weight for 0/+ was intermediate between the 0/0 and the +/+ controls. The shoot:root ratio on a dry weight basis was approximately the same for the 0/+ and the 0/0 treatment and it was clearly lower for the +/+ treatment, at both Ca levels.

Effects of Al on root morphology

As observed before (Hairiah et al. 1990), roots of *Mucuna* growing in a solution with Al were thicker and whiter than in a solution without Al. The white color was due to cortical air spaces as evident by microscopy (results not shown). Large cortical air spaces, which were absent in control roots, were positioned opposite the phloem sections.

Table 2 shows root parameters from Experiment 2. Average root diameter was increased and specific root length (m g^{-1}) was decreased in the presence of Al, at both Ca levels. The increase in average root diameter by Al was due to less branching and to thicker roots in each order of branch root development. In the presence of Al the fraction of roots with a diameter less than 0.45 mm decreased from 74 to 51%; the average diameter for these roots increased from 0.31 to 0.35 mm and that for thicker roots from 0.73 to 0.81 mm. Root diameter distributions for the 0 and + roots of 0/+ plants were equal to those of 0/0 and +/+ plants, respectively. Main axes of roots grown in the +Al solution were at least as long as those in control solution, but they carried less branches. If all other parameters remain the same, the specific root surface area ($\text{m}^2 \text{g}^{-1}$) decreases with in-

Tab. 2. Root parameters in Experiment 2; average root diameter, specific root length (per unit dry weight), L_{rw} , and specific root surface area (per unit dry weight), A_{rw} . Ca concentrations 50 or 1250 μM .

Al treatment	Diameter, mm		L_{rw} , m g ⁻¹		A_{rw} , m ² g ⁻¹		
	50	1250	50	1250	50	1250	
0/0	0	0.43 c	0.44 c	183 ab	240 b	0.25	0.33
	0	0.44 c	0.43 c	192 a	284 a	0.27	0.38
0/+	0	0.41 c	0.42 c	201 a	263 ab	0.26	0.35
	+	0.50 b	0.57 ab	205 a	210 c	0.32	0.38
+/+	+	0.67 a	0.54 b	153 bc	206 c	0.32	0.35
	+	0.67 a	0.60 a	144 c	180 c	0.30	0.34

creasing average root diameter (Van Noordwijk 1987). Table 2 shows, however, a small increase in specific root surface area with an increasing average root diameter due to the presence of Al at low Ca supply, and no effect at high Ca supply. The increased air spaces in the cortex (due to the presence of Al) led to an increase in root diameter without reduction of the specific root surface area.

Al avoidance by roots

In Experiment 1 (110 μM Al) no significant differences were found in root dry weight between the two sides of the root system for the 0/+ treatment. Figure 3 shows the root dry weight for both sides of the root system for Experiments 2 and 3 (185 μM Al). At both Ca levels, a highly significant difference ($P < 0.01$) between the + and the 0 side of the 0/+ treatment was observed. Root weight on the 0 side of 0/+ plants was significantly higher than for 0/0 plants and that for the + side was significantly lower than for +/+ plants. The ratio of 0 roots to + roots of 0/+ plants was 2.7, 3.1 and 2.4 on a basis of root dry weight, root length and root surface area, respectively. In Experiment 3 a ratio of root weights (0/+) of 2.0 was found.

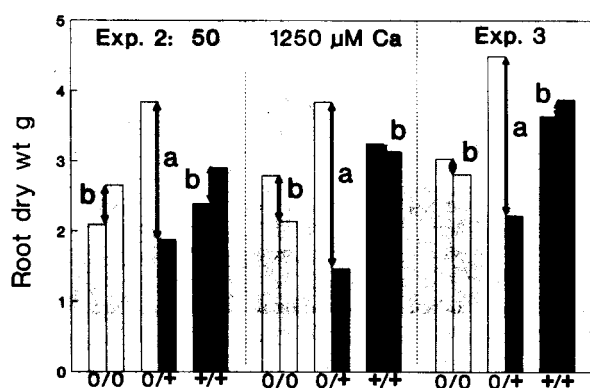


Fig. 3. Root dry weight for the two sides of the split root plants in Experiment 2. Letters indicate significantly different ($P < 0.05$; $n = 24$) contrasts between the two sides of a single plant.

Root growth in KH_2PO_4 solution (Experiment 3)

In Experiment 3 the hypothesis was tested that the presence of Al in solution induced P shortage in the plants. Root development in a third pot, containing only KH_2PO_4 , was used as indicator of P status of the plant. Table 3 shows that control plants (0/0) had a significantly lower root dry weight and root length in this medium than 0/+ plants, with intermediate values for +/+ plants. Specific root length (L_{rw}) did not show significant treatment effects; in the third pot it was lower than in the other root compartments (Tab. 2).

Chemical composition of roots and shoots

Table 4 shows the chemical composition of roots and shoots. In the statistical analysis each Ca level was treated as a separate experiment. When Experiments 1 and 2 were treated as Al \times Ca experiments (which is not strictly correct due to incomplete randomization) significant interactions between Al and Ca were found only for the Ca^{2+} and Mg^{2+} concentration of the roots. The reduction in Ca^{2+} and Mg^{2+} concentration by Al was more pronounced in the high Ca treatment than in the low Ca treatment. Otherwise, effects of Al and Ca treatments were additive.

Al exposure resulted in increased root concentrations of P and Al^{3+} and reduced concentrations of Ca^{2+} and Mg^{2+} (Tab. 4). In Experiment 2, +Al roots from 0/+ plants had a higher concentration of P, Al^{3+} and sum of cations than roots of +/+ plants. Otherwise, the chemical composition of roots was completely determined by the surrounding solution and it was not influenced by the treatment given to the other half of the root system.

In Experiments 1 and 2, a low Ca level of the solution reduced root concentrations of Ca^{2+} and Mg^{2+} , espe-

Tab. 3. Root development in a third compartment, containing 1 mM KH_2PO_4 , in Experiment 3. NS = non significant, * and ** = significant, ($P < 0.05$) and ($P < 0.01$), respectively.

Al-treatment	0/0	0/+	+/+
Dry weight, mg **	35 b	231 a	125 ab
Root length, m *	3.2 b	29.2 a	13.7 ab
L_{rw} , m g ⁻¹ NS	87	122	105

Tab. 4. Chemical composition of roots. Cations are expressed on a 'tissue water' basis (fresh - dry weight). RWW = relative water weight (tissue water per unit dry weight). SC = sum of cations times valency. Values followed by the same letter are not statistically different; each Ca level is considered as a separate experiment.

Experiment Treatment	RWW, g g ⁻¹	P, μmol g ⁻¹	K ⁺ , mM	Ca ²⁺ , mM	Mg ²⁺ , mM	Al ³⁺ , mM	SC, mM _e
Al 110 μM, Ca 50 μM (Exp. 1)							
0/0 0	19.8 NS	89 b	102 NS	1.09 NS	13 NS	0.2 b	133 b
0/+ 0	19.3	80 b	105	1.09	12	0.2 b	132 b
+ 0	18.6	132 a	104	1.02	13	12 a	169 a
+/+ +	20.3	141 a	94	0.91	13	12 a	159 a
Al 110 μM, Ca 1250 μM (Exp. 1)							
0/0 0	20.8 NS	90 NS	85 NS	7.1 a	23 ab	0.3 b	146 NS
0/+ 0	20.3	82	89	7.0 a	25 a	0.2 b	154
+ 0	22.0	126	77	5.2 b	17 b	13 a	159
+/+ +	21.6	124	80	5.3 b	16 b	12 a	159
Al 185 μM, Ca 50 μM (Exp. 2)							
0/0 0	19.9 NS	78 b	101 NS	0.63 NS	12 a	0.3 c	128 NS
0/+ 0	19.7	71 b	101	0.69	11 a	0.2 c	126
+ 0	21.2	140 a	88	0.53	5.5 b	22 a	167
+/+ +	21.9	125 a	86	0.52	4.7 b	16 b	144
Al 185 μM, Ca 1250 μM (Exp. 2)							
0/0 0	21.1 NS	79 c	88 NS	5.2 a	24 a	0.2 c	148 bc
0/+ 0	22.5	78 c	89	4.2 b	19 b	0.1 c	136 c
+ 0	19.0	161 a	79	4.2 b	13 c	28 a	198 a
+/+ +	21.3	121 b	82	2.9 c	9.0 d	16. b	154 bc
Al 185 μM, Ca 1250 μM (Exp. 3)							
0/0 0	17.4 NS	101 b	100 NS	5.8 a	21 a	0.4 c	154 b
0/+ 0	18.1	97 b	105	5.4 a	18 ab	0.3 c	153 b
+ 0	16.5	138 a	95	4.0 b	18 ab	45 a	274 a
+/+ +	17.3	111 b	99	3.4 b	14 b	34 b	238 a

cially in the absence of Al. In both experiments K⁺ concentration was increased at low Ca level, but no significant effect of the Ca level on the Al concentration in the roots was observed. In Experiment 2, the sum of cation concentrations was reduced at low Ca level. In Experiment 1, a low Ca level of the solution increased the P concentration of roots, especially in the presence of Al. Data for Experiment 3 agree with those for Experiment 2, at similar Al and Ca levels.

Data on chemical composition of the shoot (Tab. 5) were only available for Experiment 1 and 3. No signif-

icant ($P < 0.05$) Al×Ca interactions or Al treatment effects were found in Experiment 1. In Experiment 3 Al treatment induced a significant ($P < 0.05$) decrease of shoot Mg and P concentration. Decrease in the Ca level of the solution from 1250 to 50 μM in Experiment 1 led to a highly significant decrease ($P < 0.01$) of shoot Ca²⁺ concentration and, contrary to the effect on the roots, increase of Mg²⁺ concentration; the sum of the cation contents decreased. P concentration of the shoot was reduced at low Ca level of the nutrient solution. The presence of a third pot with KH₂PO₄ (Exp. 3) signif-

Tab. 5. Chemical content of shoot; see further explanation in Tab. 4. ¹Plants with a third KH₂PO₄ compartment had a significantly higher K content: 194 versus 165 mM.

	RWW, g g ⁻¹	P, μmol g ⁻¹	K ⁺ , mM	Ca ²⁺ , mM	Mg ²⁺ , mM	Al ³⁺ , mM	SC, mM
Al 110 μM, Ca 50 μM (Exp. 1)							
0/0	5.37 NS	72 NS	236 NS	15 NS	31 NS	0.55 NS	329 NS
0/+	5.69	74	206	15	31	1.70	300
+/+	5.49	74	223	13	35	2.36	321
Al 110 μM, Ca 1250 μM (Exp. 1)							
0/0	4.74 NS	94 NS	210 NS	112 NS	16 NS	0.05 b	464 NS
0/+	5.12	70	147	108	11	0.68 a	388
+/+	4.65	68	182	111	14	0.14 b	433
Al 185 μM, Ca 1250 μM (Exp. 3)							
0/0	6.04 NS	76 a	178 NS ¹	77 NS	13 a	0.84 b	359 NS
0/+	6.04	78 a	187	78	12 a	0.25 c	366
+/+	5.89	65 b	174	78	8.2 b	1.41 a	348

icantly increased the K^+ , but not the P content of the shoot.

Discussion

The data presented here confirm that root dry weight of *Mucuna pruriens* var. *utilis* was increased (compared to an Al-free solution) by solutions containing 185 μM of Al in a homogeneous test condition (Hairiah et al. 1990). The increased root dry weight was accompanied by an increase in total root surface area, because specific root surface area, A_{rw} , remained constant. No difference in total root length was found, because specific root length, L_{rw} , decreased.

The experiments with 185 μM Al indicated that the increase in root weight was not a local effect of Al. The stimulation may be interpreted as a 'functional equilibrium' response at the whole-plant level to an inhibited root function (nutrient or water uptake). Al induced effects on P uptake are likely. The presence of Al led to a decrease in shoot P content (significant in Experiment 3). The stronger root development in the third pot in Experiment 3, with only KH_2PO_4 , also indicates that Al treated plants were short in P.

At a reduced Ca supply, Al toxicity was more pronounced. The 'low' Ca level used in the current experiments led to shoot Ca levels lower than those observed in the field on an acid soil (K. Hairiah, unpublished). *Mucuna* apparently tolerates soils with a low Ca supply and Al/Ca interactions appear to be relatively unimportant for this species in the range tested.

In Experiment 2 and 3, at 185 μM Al, *Mucuna* roots in the 0/+ treatment clearly had a preference for the solution without Al; they avoided Al, in agreement with the subsoil avoidance in the field (Hairiah et al. 1991). Al avoidance occurred at an Al concentration which in a standard water culture experiment (without choice) led to increased root dry weight. Consequently, mechanisms for Al avoidance should involve communication between the various parts of the root system; the response to Al of a single root depends on the conditions encountered by other roots, in addition to the mechanisms considered by Bennet and Breen (1991).

The simplest explanation for the Al-avoidance is based on a competition between various parts of a root system for common internal resources, e.g. carbohydrates. Al induced retardation of growth of a single root might lead to a competitive advantage for other roots, which are not in contact with Al and thus will continue to grow. Such a situation may become consolidated and prevent subsequent recovery of root growth in the presence of Al, as observed in a homogeneous medium.

The symptoms of Al avoidance by *Mucuna*, appear to be the complement of P preference as described by De Jager (1982). In the present split-root experiments the external P concentration was the same in the solutions with and without Al, but internal shortage of P in +Al roots could be due to adsorption of phosphate to poly-

nuclear Al-complexes formed in or on the root system (McCormick and Borden 1974). In *Mucuna*, Al accumulates in the root rather than in the shoot and total P content in the root was increased by Al (Tab. 4). Earlier we found that although total P concentration increased, the concentration of free phosphate ions in the root tissue was reduced to virtually zero by an Al concentration of 185 μM (Hairiah et al. 1990). Exposing beech roots to a solution with Al for 21 days caused a 5-fold decrease in the vacuolar inorganic phosphate concentration, measured by ^{31}P NMR (Jensen et al. 1989), probably due to Al-P complex formation in substrate and root cell walls.

In conclusion, Al-containing solutions may lead to Al- PO_4 precipitation in the root and, above a certain threshold, to P deficiency in the whole plant. P-deficiency may induce stimulated root growth in plants grown in a homogeneous medium, and preferential (branch) root development in a heterogeneous medium in areas with a favourable P supply. We suggest that Al avoidance of *Mucuna* is actually based on Al-induced P deficiency and preferential root growth near localized P sources. A logical consequence is that Al avoidance should be more pronounced at reduced P supply and that it may be absent with improved P supply. The hypothesis will be tested in subsequent experiments, with control of the monomeric Al concentration.

The Al avoidance described here has an important bearing on selection of crop cultivars for a better root development in acid subsoils. Usually the topsoil is less acid and the presence of organic matter reduces Al toxicity in this layer. To obtain cultivars with a deep root system it is not sufficient to screen for Al tolerance of single roots (in a homogeneous medium) but it is also necessary to test against Al avoidance in heterogeneous media.

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