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

II. Above-ground growth and control of Imperata cylindrica

KURNIATUN HAIRIAH[1], MEINE VAN NOORDWIJK[2] and SLAMET SETIJONO[1]
[1]*Soil Science Department, Faculty of Agriculture, Brawijaya University, Malang 65145, Indonesia*;
[2]*DLO-Institute for Soil Fertility Research, P.O. Box 30003, 9750 RA Haren (Gn), The Netherlands (address for correspondence)*

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Abstract

Fast growing, climbing leguminous cover crops such as the velvet beans can be used to reclaim weed-infested, degraded soils in the humid tropics, especially land covered by the grass *Imperata cylindrica*; they climb over the grass leaves and shade the grass out if their cover lasts long enough. Tolerance of two species of velvet bean to eroded soils was investigated by removing topsoil and directly sowing into the subsoil; plots where topsoil was not removed were used as a control. The response to small amounts of P fertilizer and lime was also tested. Removal of the topsoil resulted in retarded growth of both species, in increased dry matter content of the shoot, in decreased specific leaf area and in increased leaf weight ratio, due to shorter internodes. Six weeks after planting the leaf area index (LAI) was about 1.2 where topsoil was retained, sufficient for a shading effect on *Imperata*. Where topsoil had been removed, the LAI was only 0.6. *Mucuna pruriens* var. *utilis* showed a faster aboveground growth than *M. deeringiana*; the species did not differ in tolerance to eroded soil. Small amounts of P fertilizer had no significant effect on the growth of both *Mucuna* species. Shoot:root ratios, on a dry weight basis, were much lower when topsoil had been removed, about 3.7 and 2.4 for *M. p. utilis* and *M. deeringiana* respectively, compared to 6.2 and 3.3 where topsoil was retained. Removal of topsoil led to reduced Mg and to increased Al concentrations in roots, and to increased levels of Mn and Al in shoots. In the second year no effect of lime or residual effect of P application was found on growth of *Mucuna* or *Imperata*. Removal of the topsoil had little effect on the growth of weeds after the cover crop had been harvested. Due to the high Al tolerance of *Imperata*, reclamation by *Mucuna* will be less effective if the topsoil has been lost by erosion.

Introduction

About 10 out of 190 million ha of land in Indonesia have become unsuitable for traditional soil management practices (Anonymous, 1990), due to invasion by coarse grass species, mainly *Imperata cylindrica*, locally known as alang-alang. As an alternative to costly and environmentally undesirable reclamation of *Imperata*-infested land with herbicides, fast growing leguminous species may be used, which can shade out the grass (Brook, 1989). Akobundu and Poku (1985) found that *Mucuna pruriens* (L) DC var. *utilis* (Wall. ex Wright) Baker ex Burck could cover *Imperata*-infested fields in West Africa in a period of 19 weeks. Field observations on acid soils in Nigeria and Indonesia (Hairiah and Van Noordwijk, 1989), showed

that, of several leguminous species tested, *Mucuna pruriens* var. *utilis* produced the highest biomass and exhibited the fastest growth. *Mucuna* has creeping and twining stems and can climb into the grass leaves, pull them down and cover the grass. Van Eijk-Bos (1987) reported that *M. deeringiana* (Bort) Small is effective at controlling *Imperata* in Columbia. The two *Mucuna* species differ in longevity, *M. p. utilis* dies after about four months, whilst *M. deeringiana* has a growth cycle of about nine months.

In order to be a viable option for small farmers, a cover crop should perform well over a considerable range of soil conditions, where *Imperata* infestation is a problem. Field experiments on an acid soil in Lampung showed that *M. p. utilis* did not perform well in the dry season, probably because of its rather shallow root system. The observation that *M. p. utilis* roots hardly penetrated into the acid subsoil (Hairiah and Van Noordwijk, 1989) led us to a laboratory study of the Al tolerance of *M. p. utilis* and, for comparison, of *M. deeringiana* (Hairiah et al., 1990). In roots, total P increased and $H_2PO_4^-$ concentration decreased with increasing Al^{3+} levels, but in the shoot both total P and $H_2PO_4^-$ were reduced. $AlPO_4$ can account for 30–60% of the Al^{3+} in the roots. In the field we may expect a relation between P availability and Al tolerance.

The research reported here concentrated on a comparison of the aboveground growth of *M. p. utilis* and *M. deeringiana* on a field site in Lampung, Indonesia. Different P availabilities were obtained by using two P sources, triplesuperphosphate (TSP) and Florida rock P. Bako Baon and Van Diest (1989) showed in pot experiments that well-nodulated *M. p. utilis* is able to use rock P. In order to study whether or not both species are able to grow in badly eroded situations, a further experimental factor was removal of the topsoil (10 to 15 cm) and sowing *Mucuna* seeds directly into the subsoil.

Results for plant growth and mineral composition of both *Mucuna* species, as influenced by P fertilizer and removal of topsoil, are discussed in this article. Soil factors possibly responsible for shallow rooting were previously discussed (Hairiah et al., 1991a). Shading is probably the main effect of *Mucuna* on *Imperata* and therefore special attention was paid to the leaf area index.

Material and methods

Field experiment 1 (January–February 1989)

A field experiment was carried out in Ketapang (Lampung, Sumatra, Indonesia). Main factors in the experiment were removal of topsoil, P fertilization (none, triplesuperphosphate (TSP) and rock phosphate (rP)) and two *Mucuna* species. Treatments were arranged in a randomized block design and 3 replications; plot size was $3 \times 4\,m^2$; further details and soil data were described by Hairiah et al. (1991a). In the second year of observation, no new P fertilizer was added and observations were only continued on the plots with *M. p utilis*. All plots were split into two and lime applied to one half, according to the Indonesian recommendation ($1\,Mg\,ha^{-1}$ of $CaCO_3$ per $cmol_c$ of exchangeable Al per kg of soil; for the plots with topsoil this meant $0.6\,Mg\,ha^{-1}$ and for the plots without topsoil $1.9\,Mg\,ha^{-1}$).

Biomass production was measured 4, 5 and 6 weeks after planting (WAP). Aboveground samples were collected from $1\,m^2$ of every plot and root samples were excavated from 5 plants per plot, washed carefully on a 1 mm mesh sieve with rain water, dried at 70 °C, and ground for analysis of N, P, K, Ca, Mg, Al and Mn.

The leaf area per plant was calculated as product of total aboveground dry weight (SDW) and leaf area ratio (LAR). LAR was calculated as the product of LWR and SLA, where LWR is the dry weight ratio of leaf lamina and total shoot dry weight and SLA, the specific leaf area, is the ratio of leaf surface area and leaf dry weight (Chariello et al., 1989). SLA was determined by drying and weighing 20 leaf punches of $1.4\,cm^2$ each. LWR was measured by separation of leaf laminae from the rest of the plants. For analysis of macronutrient concentrations (Hairiah et al., 1990), composite samples of the whole shoot were made.

Composite soil samples were collected from every plot at 6 WAP, from three layers of soil 0–10, 10–20 (excluding any topsoil) and 20–

40 cm depth. Dried soil samples were analyzed (Anderson and Ingram, 1989) for pH(H_2O) (soil to water volume ratio 1:1), pH(KCl) (1 *M* KCl), exchangeable acidity (H and Al), cation exchange capacity (CEC, in 1 *M* CH_3COONH_4 at pH 7) and available P according to Bray-P_2 (0.03 *M* NH_4F + 0.1 *M* HCl; Bray and Kurtz, 1945). ECEC, effective cation exchange capacity, was estimated by addition of CEC and exchangeable H and Al. Percentage Al saturation was calculated as Al exchangeable, divided by ECEC. Concentrations of monomeric Al in soil solution were measured (Hairiah et al., 1991b; Kerven et al., 1989) in samples centrifuged from topsoil and subsoil (rewetted to field capacity).

Field experiment 2 (December 1989–February 1990)

The harvest of experiment 1 had destroyed most of the cover crops; subsequently, weeds were allowed to grow, and by the next rainy season (December 1989) the plots were covered by *Imperata* and other weeds. Before experiment 2 was started, composite soil samples were taken from each treatment, from 0–20 cm depth; air-dried soil samples were analyzed for organic C (Walkley and Black), total N (Kjeldahl), and Bray-P_2. Biomass of *Imperata* and other weeds was measured from 1 m^2 of each plot and samples were collected for chemical analysis.

All weeds were slashed at ground level and removed from the plots before *Mucuna pruriens* var. *utilis* was sown in the same plots as in experiment 1. The first sowing failed, due to heavy rail and partial flooding of the plots. After 10 days *Mucuna* was resown, but *Imperata* shoots were already regenerating. Six weeks after the second planting of *Mucuna* the biomass of *Imperata* and *Mucuna* was measured as before.

Transpiration rates of *Mucuna* were measured by growing plants in 0.5 l pots with topsoil or subsoil. Pots were wrapped in aluminium foil to prevent evaporation from the soil, brought to field capacity and positioned on a *Mucuna* plot, having plants of similar size (4 WAP). By weighing the pots every hour transpiration rates could be calculated. Measurements were repeated after 4 days, and then fresh and dry weights of the shoot were determined.

Glasshouse experiment 1: Aluminium tolerance of Imperata cylindrica

To compare the Al response of *Imperata cylindrica* with that of *Mucuna* observed in previous experiments (Hairiah et al., 1990) an experiment with three levels of Al (0, 110 and 370 μM), with three replicates was carried out in a glasshouse in the Netherlands. *Imperata* rhizomes were collected from an acid soil in Gajrug, Bogor (a description of the soil of this site is given by Hairiah et al., 1991a). The rhizomes were propagated in soil in a glasshouse; rhizome cuttings of a single node were grown in a 1/8-strength Hoagland solution (without Al treatment) to get a uniform sprout. After two weeks the sprouts were transferred to a modified 1/4 strength Hoagland solution with various Al concentrations; they were harvested 6 weeks after planting. The solution pH was adjusted daily to a value of 4.2, by adding 1 m*M* HCl or 0.1 m*M* KOH, as in previous experiments with *Mucuna* (Hairiah et al., 1990).

Glasshouse experiment 2: Air-filled porosity of Mucuna *and* Imperata *roots*

In the field experiments, *Mucuna* seedlings failed after heavy rain in waterlogged soil, while *Imperata* did not suffer. Therefore, the air-filled root porosity for the two species was measured in a nutrient solution experiment. Plants were grown in a split root system with circulating aerated nutrient solution. Ten days before measurement, half of the roots were exposed to a solution with low partial O_2 pressure (about 0.003 MPa). Air-filled root porosity as a percentage of root volume was measured by pycnometer (Van Noordwijk and Brouwer, 1988).

Statistical analysis

Results in all experiments were analyzed with ANOVA (analysis of variance) by using the GENSTAT 5 computer program (Payne et al., 1987). 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 Test when more comparisons were involved ($p < 0.05$). In the case of uneven variances, data were logarithmically transformed. If no significant interactions between experimental factors were found, only main effects are discussed in the results.

Results

Soil parameters in the field experiments

Concentrations of monomeric Al in the soil solution in the topsoil and subsoil before planting were 1.89 and 2.3 μM, respectively. Other soil characteristics, as determined at 6 weeks after planting experiment 1, are shown in Table 1. Topsoil had a slightly higher pH(H_2O) and pH(KCl) than the two subsoil layers. ECEC was lowest at 10–20 cm depth and tended to increase below that depth. The percentage Al saturation was about twice as high in the subsoil as in the topsoil. Available P (Bray-P_2) was more than twice as high in the topsoil as in the two subsoil layers in non-fertilized plots with undisturbed profile. Soil data in equivalent layers for the plots where topsoil had been removed were similar to the control plots. P fertilization only had a statistically significant effect on Bray-P_2 in the 0–10 cm layer in plots where topsoil had been removed and rock-P was added.

At the start of experiment 2 (December 1989) the Bray-P_2 value after rock-P application was 37 and 40 mg kg^{-1} on plots where topsoil was retained and removed, respectively, more than twice as high as in year 1; for the control and TSP treatment Bray-P_2 was approximately the same as in year 1. The C_{org} and N_{tot} contents in the 0–20 cm layer, averaged over the P treatments, were 20 and 1.9 g kg^{-1} respectively where topsoil was retained and 13 and 1.3 g kg^{-1} where topsoil had been removed.

Growth analysis in field experiment 1

Statistical analysis of the data for the first year showed no significant interaction between plant species and soil treatments (removal of topsoil and P fertilizer addition). Table 2 therefore shows data for the main effects only. *M. p. utilis* produced significantly more biomass ($p < 0.01$) than *M. deeringiana* but no effect was found on LAR.

Removal of the topsoil caused a pronounced (and highly significant, $p < 0.001$) retardation of shoot development in both species and a slight, but statistically significant, decrease in LAR. A low LAR indicates a plant morphology that is less effective in providing cover (shade) per unit dry weight. LAR is the product of LWR and SLA, which were affected in opposite directions

Table 1. Soil properties in the first year at 6 weeks after planting, averaged over the three P treatments which gave no significant effect, except on Bray-P_2 in the 0–10 cm layer (see footnote). Values followed by different letters are significantly different ($p < 0.05$)

Depth (cm)	pH		Exch. H	Exch. Al	ECEC	Al-saturation (%)	Bray-P_2 (mg kg^{-1})
	(H_2O)	(KCl)	($cmol_c\ kg^{-1}$)				
+ top soil							
0–10	5.5^{a}	4.8^{a}	0.5^{NS}	0.9^{b}	9.8^{a}	9.7^{b}	18.8^{a}
10–20	5.3^{ab}	4.4^{b}	0.6	1.4^{a}	7.9^{b}	18.3^{a}	11.5^{c}
20–40	5.2^{bc}	4.3^{b}	0.7	1.5^{a}	8.5^{ab}	17.2^{a}	5.5^{e}
− top soil							
0–10	5.2^{abc}	4.4^{b}	0.6	1.4^{a}	7.5^{b}	18.6^{a}	$13^{b,1}$
10–20	5.2^{bc}	4.3^{b}	0.6	1.5^{a}	7.7^{b}	20.2^{a}	7.0^{d}
20–40	5.0^{c}	4.3^{b}	0.6	1.6^{a}	8.7^{ab}	18.9^{a}	5.0^{e}

1. P fertilizer effect on Bray-P_2 in layer 0–10 cm: 8.5^{b}, 11^{b} and 21^{a} for control, TSP and rock P, respectively.

Table 2. Effect of treatment on shoot growth parameters of *M. utilis* and *M. deeringiana* 6 weeks after planting: specific leaf area, SLA; leaf weight ratio, LWR; leaf area ratio, LAR = SLA × LWR; dry matter content, DMC, of leaves and stem plus petioles; leaf area index, LAI = LAR × shoot dry weight. Interactions between main effects were not significant. NS = no significant difference ($p > 0.05$); values followed by different letters are significantly different

Treatment	SLA ($m^2 g^{-1}$)	LWR ($g g^{-1}$)	LAR ($m^2 g^{-1}$)	DMC leaves (%)	DMC stem (%)	Shoot weight ($g m^{-2}$)	LAI ($m^2 m^{-2}$)
Species							
M. p. utilis	0.032^a	0.63^{NS}	0.019^{NS}	23^{NS}	18^{NS}	53^a	0.97^a
M. deeringiana	0.030^b	0.67	0.020	22	17	36^b	0.74^b
Soil							
+ top	0.034^a	0.60^b	0.021^a	20^b	15^b	56^a	1.15^a
− top	0.027^b	0.70^a	0.018^b	25^a	19^a	33^b	0.55^b
Fertilizer							
0 P	0.029^b	0.66^{NS}	0.019^{NS}	25^a	20^a	44^{NS}	0.83^{NS}
+ TSP	0.032^a	0.64	0.019	20^b	15^b	52	0.97
+ rock P	0.031^a	0.64	0.020	22^b	17^b	38	0.75

by removal of the topsoil: SLA decreased (probably due to a higher dry matter percentage in the leaves) and LWR increased, probably due to shorter stem internodes.

The addition of TSP and rock-P significantly increased SLA and decreased the dry matter percentage, but had no effect on LAR. Effects of P fertilization on aboveground biomass of both species 4, 5 or 6 WAP were not significant; only when data for the three harvests were combined did a significant increase of biomass due to TSP become apparent.

LAR was constant over time (4, 5 and 6 weeks after planting) and treatments only had a small effect, so that the LAI was approximately proportional to aboveground biomass. The development of LAI with time is shown in Figure 1. The highest LAI obtained was 1.3 for *M. p. utilis* when topsoil was retained. When topsoil was removed, LAI at 6 WAP was only 0.7 for *M. p*

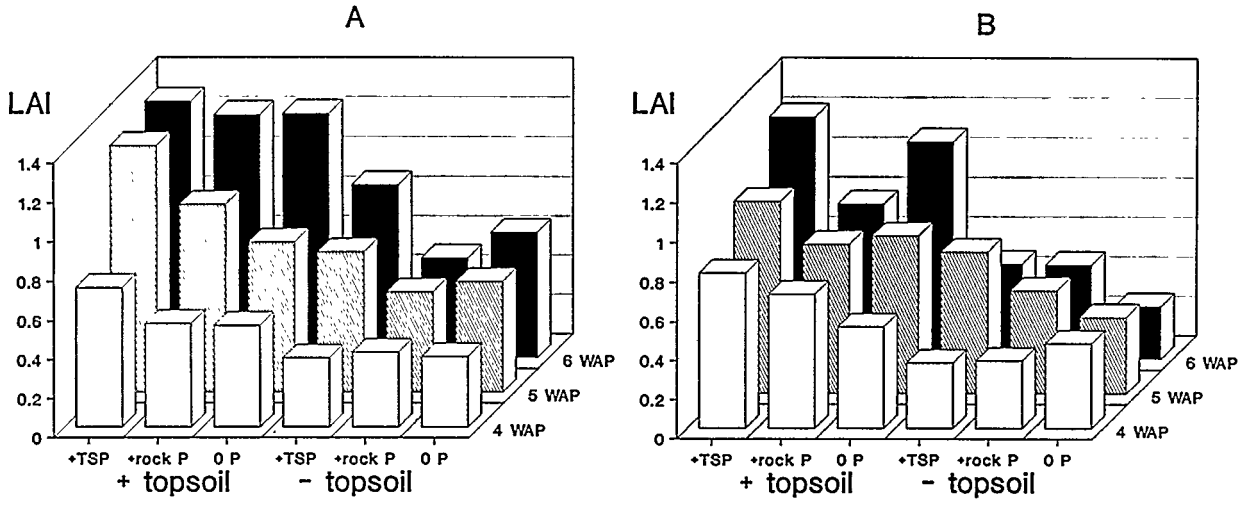

Fig. 1. Leaf area index (LAI) development over time (in the first year) for plots where topsoil was retained (+) or removed (−); A. *M. p. utilis*, B. *M. deeringiana*.

utilis and 0.4 for *M. deeringiana*. Fertilization with TSP gave a partial, but not statistically significant compensation for the removal of topsoil. In the period from 4 to 6 WAP, the rate of increase of shoot dry weight was approximately constant: about 20 and 10 kg ha^{-1} day^{-1} when topsoil was retained or removed, respectively.

Shoot:root ratio in experiment 1

Figure 2 compares above- and belowground biomass production for all treatments. Root data were discussed more fully by Hairiah et al. (1991a). Removing topsoil reduced S/R ratio. S/R ratios were higher in *M. p. utilis* than in *M. deeringiana*; average values for the two species at 6 WAP were 6.2 and 3.3, respectively, when topsoil was retained, and 3.7 and 2.4 when topsoil was removed. S/R ratios generally decreased with time. P fertilization had no clear effects on the S/R ratios.

Growth of Imperata *and other weeds in the period between field experiments 1 and 2*

Imperata and weed biomass at the start of experiment 2, 10 months after experiment 1, are shown in Table 3. A significant interaction between removal of the topsoil and P fertilization was found, but no difference between the two previously grown *Mucuna* species. Rock P fertilization increased *Imperata* regrowth significantly where topsoil had been removed; with TSP the increase was not significant.

Table 3. Biomass ($g\,m^{-2}$) of *Imperata* and other weeds (Other) at the start of the second field experiment; differences between values in the same column followed by the same letter are not statistically significant

	Topsoil maintained		Topsoil removed	
	Imperata	Other	*Imperata*	Other
No P	367^{ab}	330^{ab}	208^{b}	160^{b}
TSP	508^{a}	446^{a}	324^{ab}	276^{ab}
Rock P	343^{ab}	451^{a}	407^{a}	342^{ab}

Aboveground biomass and transpiration in field experiment 2

Table 4 shows aboveground biomass of *Imperata* and *Mucuna* in the second year. For *Mucuna*, but not for *Imperata*, a significant effect of removal of topsoil was found. Soil amendments (residual effect of P fertilization and recent liming) had no effect on either species. *Imperata* had a significantly higher shoot dry weight. LWR and LAI than *Mucuna*, and a lower SLA and LAR. In the second year the LAR of *Mucuna* was higher than in the first year, especially where topsoil was retained, due to both a high SLA and LWR value.

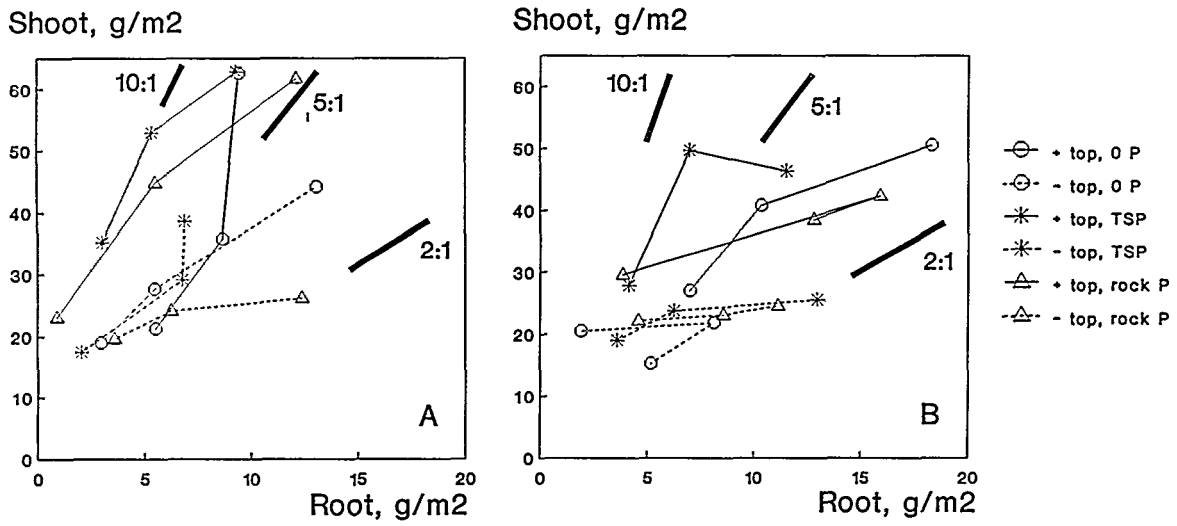

Fig. 2. Shoot:root ratio on a dry weight basis at 4, 5 and 6 weeks after planting (in the first year) for the six treatments; A. *M. p. utilis*, B. *M. deeringiana*.

Table 4. Aboveground biomass of *Imperata* and *Mucuna* in the second year at 6 WAP. No significant effects of soil treatments (liming and P fertilization) were found; for *Imperata* no difference was found between plots with and without topsoil

	SLA ($m^2 g^{-1}$)	LWR ($g g^{-1}$)	LAR ($m^2 g^{-1}$)	Shoot DW ($Mg ha^{-1}$)	LAI ($m^2 m^{-2}$)	N ($g kg^{-1}$)
Imperata	0.0145^c	1.0^a	0.0145^c	0.980^a	1.41^a	10.6^c
Mucuna						
+ topsoil	0.0476^a	0.875^b	0.0426^a	0.191^b	0.79^b	34.0^a
− topsoil	0.0415^b	0.656^c	0.0263^b	0.173^b	0.40^c	31.4^b

Removal of the topsoil had no significant effect on the transpiration rate of *Mucuna* per plant. The plants growing in topsoil had a significantly higher fresh weight, and transpiration rate per unit fresh weight was significantly higher for plants growing in subsoil (0.147 ml g^{-1} h^{-1} versus 0.117 for plants growing in topsoil). The plants growing in subsoil had a significantly higher dry matter percentage (21.3 versus 17.6%) and the transpiration rate per unit dry weight was the same. Based on the LAR values of Table 4, determined for slightly older plants, the transpiration per unit leaf surface area was 26 and 16 ml m^{-2} h^{-1} for subsoil and topsoil, respectively. No evidence was obtained therefore to support the hypothesis that water uptake was restricted where roots were directly exposed to the subsoil.

Chemical composition of plants in field experiments

The chemical composition of the plants in experiment 1 is shown in Table 5. Cation concentrations were expressed on a tissue water basis (fresh weight − dry weight) (Leigh and Johnston,

Table 5. Chemical composition of shoots and roots in year 1 at 6 WAP; N and P are expressed per unit dry weight, cation concentrations are expressed per unit tissue water. Only main effects are given. The factor P fertilizer had no significant effects on chemical composition of the shoot. NS = no significant difference; values followed by different letters are significantly ($p < 0.05$) different

	N	P	K^+	Ca^{2+}	Mg^{2+}	Mn^{2+}	Al^{3+}	Ca/Al ($mol\ mol^{-1}$)
	($g kg^{-1}$)		($meq L^{-1}$)					
Shoot								
Species								
M. p. utilis	34.9^{NS}	2.2^{NS}	123^{NS}	73^b	44^b	1.2^b	68^a	2.23^b
M. deeringiana	36.6	2.2	113	107^a	49^a	1.7^a	48^b	3.91^a
Soil								
+ topsoil	35.0^{NS}	2.3^{NS}	109^a	84^{NS}	39^{NS}	1.1^b	46^b	3.53^{NS}
− topsoil	36.5	2.1	127^b	97	54	1.7^a	70^a	2.60
Roots								
Species								
M. p. utilis	223.1^b	1.6^{NS}	23^{NS}	0.95^{NS}	7.9^b	0.11^{NS}	42^{NS}	0.10^{NS}
M. deeringiana	27.5^a	1.9	24	0.52	10.9^a	0.12	38	0.02
Soil								
+ topsoil	25.3^{NS}	1.9^{NS}	26^{NS}	1.27^{NS}	10.6^a	0.11^{NS}	30^b	0.12^a
− topsoil	27.5	1.6	21	0.17	8.2^b	0.12	0.01^a	0.01^b
Fertilizer								
no P	24.2^{NS}	1.4^b	23^{NS}	0.35^{NS}	8.2^{NS}	0.14^{NS}	41^{NS}	0.02^{NS}
TSP	25.4	2.0^a	22	0.32	11	0.11	45	0.01
rock P	26.3	1.9^a	26	1.5	9.1	0.10	33	0.15

1983). Removal of topsoil significantly increased Mg, Mn and Al concentrations in the shoot. The two species differed in all cation concentrations except K and Mg. *M. deeringiana* contained more Ca and Mn, and less Al than *M. p utilis*. P fertilization had no significant effect on any nutrient concentrations in the shoot. The removal of topsoil led to a higher dry matter content of shoots; an analysis of variance showed no significant effects in cation concentrations per unit dry weight.

The two *Mucuna* species differed significantly in N and Mg concentrations of the roots. Removal of the topsoil decreased Mg concentrations and Ca/Al ratio, and increased Al concentrations significantly. Both P sources led to a significant increase in root P concentration. Fertilization with rock-P tended ($p < 0.10$) to increase the Ca concentration and Ca/Al ratio of roots.

The chemical composition of *Imperata* and other weeds at the start of experiment 2 is shown in Table 6. TSP fertilization significantly increased N and P concentrations when the topsoil was removed. No significant effects of treatments on other cation and concentrations were found.

In experiment 2, *Mucuna* had a slightly, but significant, lower N concentration where topsoil had been removed. The N concentration of *Mucuna* was three times higher than that of *Imperata* (Table 4).

Aluminium response of Imperata *in solution culture*

Dry weight of *Imperata* in the nutrient solutions is shown in Figure 3; Al up to 370 μM significantly increased root dry weight but had no significant effect on rhizome dry weight and shoot production.

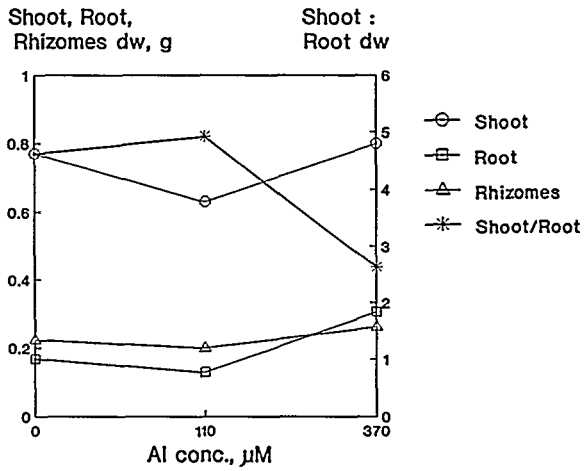

Fig. 3. Shoot and root dry weight of Imperata at 6 weeks after planting in nutrient solutions with various Al concentrations.

Air-filled root porosity in response to low oxygen supply

Mucuna roots showed a significant increase in air-filled root porosity on exposure to low oxygen supply, from 3.4 to 4.8% (v/v). *Imperata* had a much higher air-filled porosity in aerated solution, 8.2%; the increase to 9.8% in response to low oxygen supply was not statistically significant.

Discussion

Cause of subsoil toxicity to Mucuna

Removal of the topsoil led to a major reduction in shoot:root ratio of *Mucuna*, to increased dry

Table 6. Chemical composition per unit tissue water of aboveground *Imperata* biomass at the start of the second year experiment

	N	P	K^+	Ca^{2+}	Mg^{2+}	Al^{3+}	ΣC
	($g\,kg^{-1}$)		($meq\,L^{-1}$)				
+ top 0 P	12^{a}	0.4^{abc}	230^{NS}	182^{NS}	182^{NS}	153^{NS}	747^{NS}
+ top TSP	11^{a}	0.5^{ab}	291	274	174	137	873
+ top rock P	11^{a}	0.4^{ab}	235	215	176	220	846
− top 0 P	5.0^{b}	0.3^{c}	210	90	154	175	630
− top TSP	14^{a}	0.5^{a}	455	162	149	154	921
− top rock P	7.0^{b}	0.3^{bc}	194	149	187	117	647

matter content and higher Mn and Al concentrations in the shoot. Root development was not strongly affected when plants were directly sown into the subsoil with its high exchangeable Al level (Hairiah et al., 1991a).

From the retarded shoot growth we may speculate that either a substance was present at toxic levels in the shoot or that an essential root function was affected. Given the climatic conditions during the experiment, differences in water availability are not likely to be responsible for the retarded growth after removal of the topsoil. Water uptake might be a factor, however, as the high Al concentrations in combination with low Ca concentrations of roots growing in the subsoil might affect membrane integrity (Horst, 1987) and thus increase the resistance of entry of water into the root. In wet soil, as in nutrient solutions, the hydraulic conductivity of roots (rate of water uptake per unit root surface area per unit difference in water pressure) largely determines the root surface area required for water uptake and, in the absence of nutrient limitations, for plant growth (De Willigen and Van Noordwijk, 1987). The measurements of transpiration rate, however, indicated that transpiration rates per unit shoot fresh weight and per unit leaf surface area were higher for plants growing in subsoil. The increased dry matter percentage of the shoot may indicate a stimulated transpiration rate, not a restriction of water uptake due to poor functioning of roots.

Shoot:root ratios and shoot dry matter content in the field were similar to those in solution culture experiments (Hairiah et al., 1990). A comparison of shoot nutrient concentrations for this field experiment with those obtained for non-nodulated plants in solution culture shows that N concentrations in the field were rather high. The P concentration was in the range obtained in nutrient solutions with non-toxic Al concentrations up to 0.56 meq L^{-1}. The relatively small, and insignificant effects of the small P doses used in the experiment might be due to strong adsorption of P to the soil (Blamey and Edwards, 1989), but it also indicates that P stress even after removal of the topsoil was not severe. The K and Mg concentrations in tissue water in this experiment were similar to those obtained in a nutrient solution and the effect of removal of topsoil was not significant. For Ca, the concentration in tissue water in the shoot was only half of that found in the solution culture experiments, and removal of topsoil had no significant effect.

Al concentration in the shoot was much higher (about 40 versus 2.4 meq L^{-1}) than found in solution culture experiments at the highest Al level tested (1.12 meq L^{-1}). The low Ca levels in roots and shoot and the high Al levels show that the Ca/Al ratio in tissue water in the field differed from that in the solution culture experiments. Horst (1987) reported Al injury in cowpea when the molar concentration ratio Ca/Al in solution culture was less than 0.27. Subsequent solution culture experiments by Hairiah et al. (1992), however, showed that a 25-fold reduction in the Ca concentration of a nutrient solution (50 instead of 1250 μM Ca) had only a small effect on the toxicity of 185 μM Al to *Mucuna* (Ca/Al ratio 0.27 and 6.8, respectively). The Ca concentration of the shoot was only 30 meq L^{-1} in the low Ca treatment.

On highly acid soils, Mn toxicity may limit plant growth. Blamey and Edwards (1989) found that 0.7 mg g^{-1} Mn is the critical concentration in plant tissue of cowpea. Horst (1988) described the effects of Mn toxicity in a large number of cowpea varieties; a considerable reduction in shoot dry weight occurred when leaves contained more than 1 mg g^{-1} on a dry weight basis. For *Mucuna* we found about 0.175 mg g^{-1}, much less than the critical level for cowpea. Critical leaves can differ between species, however, and the possibility of Mn toxicity after removal of the topsoil cannot be excluded.

In conclusion, we suggest that high Al and (possibly) Mn shoot concentrations in plants directly grown in the subsoil may partly explain the retarded growth. No indications were obtained for growth limitations by reduced water, N, P, K or Mg uptake after removal of the topsoil. Al levels in the shoot, even for plants grown in the presence of topsoil, were much higher than those found in plants grown at toxic Al concentrations in nutrient solution.

The use of Mucuna *for* Imperata *control*

Imperata has a great regeneration capacity due to its rhizomes. Therefore, for effective control it is essential to minimize the number of viable buds and at least prevent them from forming

new aerial shoots. Suppression of *Imperata* by *Mucuna* probably depends on intensity and duration of shading. Eussen (1978) found that the relative growth rate (RGR) of *Imperata* shoots and rhizomes over a period of 2–6 months was reduced only by 50% for an 80% reduction in light intensity. The amount of shade provided by a crop is related to the LAI, but it also depends on leaf geometry. For an ideal distribution of leaves, the ground would be completely covered when the LAI is 1.0, but because of overlapping leaves, higher LAI's are required to obtain complete cover in practice. Measurements of light interception by cover crops on an acid soil in S.E. Nigeria (Hairiah and Van Noordwijk, 1986) showed 50 and 90% light interception by *M. p. utilis* at 0.25×0.25 m plant distance at 4 and 6 weeks after planting, respectively, when the aboveground biomass was 40 and 130 g m^{-2}, respectively.

Slower development of plant cover in the present experiment compared to that in Nigeria was partly due to the lower plant density (a factor 2). The LAI was not determined in the experiment in Nigeria, but assuming the LAR to be the same as in the present experiment, we can estimate that a LAI of 0.8 for *Mucuna* corresponds with 50% light interception and that a LAI of 2.6 was required for 90% light interception. The highest LAI of *M. p. utilis* obtained in this experiment, 1.3, seemed to provide an almost complete cover of the soil, but it probably reduced light intensity at ground level by less than 80%. We can conclude that, even for the best growing *Mucuna* in this experiment, it would take more than 6 weeks before effects on *Imperata* similar to those described by Eussen (1978) could be expected. For *M. p. utilis*, which dies after about 4 months, the shading would probably be effective for a little over 2 months at most. This period will affect the vigor of *Imperata* but it will not eliminate the grass, as shown in other field experiments in Lampung (Guritno et al., 1992). Despite the slower establishment, *M. deeringiana* may be more useful in *Imperata* control because of its longer growth cycle. *Imperata* control by use of short-lived *Mucuna* varieties is not possible without other weeding techniques. If more time is available, the long-lived *M. deeringiana* may be successful (unpublished observations).

Growth of *Mucuna* in the presence of topsoil was only just sufficient to affect *Imperata*. Any reduction in growth rate due to the removal of the topsoil (by erosion) would render *Mucuna* even less effective. Eussen (1978) showed that the harmful effect of *Imperata* on other plant species is partly due to allelopathic activity. However, no difference in development of *Mucuna* seedlings was observed, with and without *Imperata*. Re-growth of *Imperata* was not affected by removal of the topsoil, which agrees with the high Al tolerance shown by *Imperata* in nutrient solution. At 370 μM Al, *Mucuna* virtually failed in a previous experiment (Hairiah et al., 1990), while *Imperata* was not affected. The two *Mucuna* species did not differ much in tolerance under such conditions. *M. deeringiana* was possibly slightly more tolerant of Al (lower Al, higher Ca and Mg concentration), but it had a higher Mn concentration than *M. p. utilis*. The P requirement of both species probably did not differ.

The reduced shoot/root ratio and absolute stimulation of root development of *Imperata* by 370 μM Al in solution culture is similar to effects found for *Mucuna* at 100 μM Al (Hairiah et al., 1990). Hairiah et al. (1992) concluded that stimulation of *Mucuna* root growth by Al may be due to Al-induced P deficiency.

In the second year, *Mucuna* failed to control *Imperata*, as shown by the high shoot dry weights (Table 4). In this second year, the first sowing of *Mucuna* failed due to very wet conditions and *Imperata* had started to re-grow when *Mucuna* was re-sown. The better tolerance to waterlogging of *Imperata* can be partly explained by its higher air-filled root porosity. Temporary waterlogging after heavy rainfall is typical for the humid tropics, especially where the infiltration capacity of the soil has been affected by physical soil degradation. Any retardation of *Mucuna* growth, by Al toxicity or waterlogging, means that it cannot cover *Imperata* in the time available.

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