Aluminium tolerance of Mucuna
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SUMMARY

In the humid tropics leaching of N and other nutrients to the subsoil may occur throughout the growing season. Typically, soils in this zone have a low soil pH, a high Al saturation of the cation exchange complex and low levels of Ca and P in the subsoil. Efficiency of N-use under such conditions generally is very low, due to a combination of high leaching rates and shallow root development. The ability to develop a deep root system is important in this situation for recovery of nutrients leached early on.

From a number of leguminous cover crops tested, the velvet bean *Mucuna pruriens* var *utilis* gave the highest biomass production on acid soils in Nigeria and Indonesia, and it was the most suitable in control of the weed *Imperata cylindrica*. However, it had a very superficial root system. Inhibition of root growth on acid soil is usually caused by Al toxicity, but other soil factors, such as mechanical impedance or poor aeration might be involved as well.

Laboratory experiments showed that the response of roots of *Mucuna pruriens* var. *utilis* to Al depended on the duration of exposure and the type of experiment. In a short-term (24-48 hours) study, the usual reduction of root elongation rate by Al was found. In contrast, solution culture studies (pH 4.2; NO₃⁻ as N source) over a longer period of time (4 weeks) showed that *M. p. utilis* and the related species *M. deeringiana*, had an increased root dry weight at 110 µM or 185 µM Al³⁺, compared to controls without Al. The moderate Al-tolerance found in solution culture contradicted with the shallow root development of *Mucuna* in acid subsoil.

Field tests in Lampung (Indonesia), showed that if both *Mucuna* species was sown directly into the subsoil, after removal of the topsoil, a large root system was formed in the subsoil layers which hardly contained any roots when topsoil was present in the soil profile. Topsoil and subsoil were placed in mesh bags at various positions in the soil profile and various bulk density; *Mucuna* roots avoided the subsoil regardless of position and bulk density. P fertilization and higher liming rates applied in the mesh bag had a positive effect on root length density. Such field evidence suggested a combination of acid-subsoil tolerance (when roots had no choice) and acid-subsoil avoidance (when roots could choose between sub- and topsoil).

The hypothesis that subsoil avoidance was based on an Al avoidance acting at the level of the intact root system rather than individual roots, was tested in split-root experiments on a nutrient source, at pH 4.2. Al, 50 µM applied to both sides, was compared with 1000 µM applied to one side. Reduced shoot/root growth caused by Al in nutrient containing solution was restored to increased growth to the control plant. Al avoidance reaction to increased branching of the plant indeed occurred.

In conclusion, a very strong avoidance preference after root development in heterogeneous model of intact root system was observed.

In a split-root experiment, preference after root development in heterogeneous model of intact root system was observed.

Total P concentration increased, while the H₂PO₄⁻ concentration decreased on NO₃⁻ grown plants compared to H₂PO₄⁻ grown plants. Ionic strength of the plant was less pH-dependent. Al tolerance of *M. deeringiana* was about 19 % of Al tolerance of *M. p. utilis* as Al-PO₄³⁻, this was reduced however, no evidence for a higher concentration (relative to control plants). The composition of a nutrient solution can be enriched between NO₃⁻ and P to maximize major Al tolerance.
experiments on a circulated nutrient solution. In such an experiment with NO$_3^-$ as N source, at pH 4.2, the growth of *M. p. utilis* with Al (+/+) or without Al (0/0) in both sides, was compared with that of plants with a choice (0/+). An Al concentration 185 μM applied to both sides of the root system (+/+), increased root dry weight and reduced shoot/root ratio compared to the control (0/0). Application of such an Al-containing solution to half of the root system (0/+), led to a significant shift in root growth to the control side. In further experiments the hypothesis was tested that the Al avoidance reaction was related to the local response of plants under P stress leading to increased branch root development close to a P source. Increasing the P supply to the plant indeed resulted in the disappearance of the Al avoidance.

In conclusion, Al tolerance in a homogeneous medium can be accompanied by a strong avoidance of Al in a heterogeneous root environment. To obtain cultivars with a deep root development in acid subsoils, it is necessary to test for Al-avoidance in a heterogeneous medium as a natural soil. Screening for Al tolerance of single roots or intact root systems in a homogeneous seems inadequate.

In a split-root experiment with NH$_4$NO$_3$ (1 : 1) as N source, *Mucuna* roots had no preference after 2 weeks, but after 4 weeks a preferential root development in Al-containing solution was found, in contrast to Al avoidance found with NO$_3^-$ nutrition.

Total P concentration in the roots was increased in the presence of Al (185 μM), while the H$_2$PO$_4^-$ concentration in the root tissue was reduced, when *Mucuna* was grown on NO$_3^-$ nutrient solution with 150 μM P, daily pH adjustment to pH 4.2 and an ionic strength of 8 - 10 mM. It was estimated that at maximum 40 - 60 % of the root Al content could be present as Al-PO$_4$ precipitates. In subsequent experiments with continuous pH control, the increase in total P content of the roots in solutions containing Al was less pronounced. N form (NO$_3^-$ and NH$_4^+$) had little effect on the Al tolerance of *Mucuna* in nutrient solution. It was estimated that with NO$_3^-$ nutrition about 19 % of Al in the root might be bound as Al-PO$_4$. If all non-ionic P was bound as Al-PO$_4$, this would represent 32 % of the Al in the roots. With NH$_4^+$-nutrition, however, no evidence of Al-PO$_4$ precipitation was obtained, as the non-ionic P concentration (with or without Al in the solutions) was similar to that of the NO$_3^-$-fed control plants. Therefore, Al-PO$_4$ precipitation in the root of plants grown in NH$_4^+$ solution can be excluded; as the Al tolerance of *Mucuna* did not differ drastically between NO$_3^-$ and NH$_4^+$ nutrition, it was concluded that Al-PO$_4$ precipitation is not a major Al tolerance mechanism for *Mucuna*. 

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Primary root damage due to Al toxicity occurred in the cell elongation zone, 2-3 mm behind the root tip. Measurements of the external pH on the root surface showed a slight alkalinization in the subsoil (from 4.7 to 5.2) and an acidification in the topsoil (from 5.8 to 5.5). The pH around the root tip was independent of the overall external pH, which depended on the NO$_3^{-}$/NH$_4^+$ uptake ratio. In the (partial) NH$_4^+$ nutrition, the Al toxicity was low eventhough the external pH was not increased. Al detoxification by increasing the pH of the external medium was not important for Mucuna. Precipitation of polymeric Al forms in the apoplast with a pH of 5.5 or higher may be important.

Suppression of the grass Imperata by Mucuna mainly depends on intensity and duration of shading. Leaf area index (LAI) of Mucuna at 6 weeks after planting was estimated at about 0.8 which corresponds with 50 % light interception. The highest LAI of M. p. utilis obtained in 6 weeks was 1.3, and provided an almost complete cover of the soil. It probably reduced light intensity at ground level by less than 80 %. A LAI of 2.6 is required for 90 % light interception. Even for the best growing Mucuna it would require more than 6 weeks before sufficient shading effects on Imperata would start. As M. p. utilis normally dies off after about 4 months, the shading would affect vigor of Imperata but certainly not eliminating it. M. deerigiana, may be more useful in Imperata control because of its long growth cycle. Growth of Mucuna in the presence of topsoil was only just enough to affect Imperata and any reduction in growth rate due to erosion of the topsoil indicates that Mucuna will not be sufficiently effective in Imperata control.