Original article

Effect of aluminium on bananas (*Musa* spp.) cultivated in acid solutions. II. Water and nutrient uptake

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Effect of aluminium on bananas (*Musa* spp.) cultivated in acid solutions. II. Water and nutrient uptake.

Abstract — **Introduction**. A previous paper showed that Al in the nutrient solution affected the growth, biomass production and chemical composition of bananas (*Musa* spp.). This paper aims at providing complementary results on the effect of Al on water and nutrient uptake by young banana plants. **Materials and methods**. Vitroplants of five cultivars (Grande Naine, Agbagba, Obino l'Ewaï, Igitsiri and Kayinja) were grown for 40 d in a phytotron with a temperature close to that of their cropping areas. Dilute nutrient solutions without Al and with 78.5 µM Al were supplied continuously with peristaltic pumps. Measurements of daily water and nutrient uptake were carried out twice a week. Rhizosphere acidification or alcalinisation were also monitored. **Results and discussion**. Aluminium reduced plant water uptake and cumulative detrimental effects were observed. After 40 d, water uptake was only 30–40% of the control. Without Al, nutrient uptake (Ca, Mg, K, P, NO_3–N, NH_4–N) increased with time, whereas Al inhibited the uptake of all elements, particularly Mg. As for water absorption, cumulative effects were observed: after 40 d, most nutrient uptake rates were reduced by more than 50% relatively to the control. The plantain bananas, Agbagba and Obino l'Ewaï, were more resistant to Al than the others. Changes of temperature are likely to modify Al sensitivity as one cultivar, Kayinja, showed greater Al sensitivity at 28/25 °C than at 24/20 °C.

***Musa* / aluminium / water uptake / nutrient uptake / soil pH**

Effet de l'aluminium sur les bananiers (*Musa* spp.) cultivés en solutions acides. II. Absorption d'eau et d'éléments nutritifs.

Résumé — **Introduction**. Dans un article précédent, il a été montré que l'aluminium (Al) introduit dans la solution nutritive affectait la croissance, la production de biomasse et la composition chimique des bananiers (*Musa* spp.). Le travail présenté vise à fournir des résultats complémentaires concernant l'effet de Al sur l'absorption d'eau et d'éléments nutritifs. **Matériel et méthodes**. Les vitroplants de cinq cultivars de bananiers (Grande Naine, Agbagba, Obino l'Ewaï, Igitsiri et Kayinja) ont été cultivés pendant 40 jours en phytotron, à des températures proches de celles trouvées dans leurs aires de culture. Des solutions nutritives sans et avec 78,5 µM Al ont été continuellement apportées aux plants à l'aide de pompes péristaltiques. Des mesures de l'absorption quotidienne d'eau et d'éléments nutritifs ont été effectuées deux fois par semaine. L'acidification ou l'alcalinisation de la rhizosphère ont été également contrôlées. **Résultats et discussion**. L'aluminium a réduit l'absorption d'eau par les plants et des effets nocifs cumulatifs ont été observés. Après 40 jours, l'absorption d'eau a été seulement de 30 à 40 % par rapport à celle des plants témoins. Sans Al, l'absorption d'éléments nutritifs (Ca, Mg, K, P, NO_3–N, NH_4–N) a augmenté avec le temps, alors que la présence de Al a empêché l'absorption de tous ces éléments, en particulier du magnésium. Comme dans le cas de l'eau, des effets cumulatifs ont été observés : après 40 jours, la plupart des taux d'absorption d'éléments nutritifs ont été réduits de plus que 50 % par rapport aux plants témoins. Les bananiers plantains (Agbagba et Obino l'Ewaï) ont été plus résistants à Al que les autres cultivars. Les variations de température sont susceptibles de modifier la sensibilité à Al ; en effet, le cultivar Kayinja a montré une plus grande sensibilité à Al à 28/25 °C qu'à 24/20 °C.

***Musa* / aluminium / absorption d'eau / absorption d'éléments nutritifs / pH du sol**

1. Introduction

Aluminium (Al) excess is a major stress limiting plant growth and crop yield in acid soils of tropical and subtropical regions [1–3]. Many authors have reported that plant roots and shoots were drastically affected when soluble monomeric Al ion increases in soils or nutrient solutions [4–9]. Other effects of Al resulted in a reduced water [10–12] and nutrient uptake [13–15].

Surprisingly no systematic studies were reported so far on banana despite of its crucial importance as a local staple food and export product in nearly 120 tropical countries [16]. In a previous paper [17], we showed the detrimental Al effect on root and shoot growth, biomass production and chemical composition of banana plants. It was also noted that the sensitivity of banana plants to Al stress was depending on cultivar and temperature. This paper reports on complementary results on water and nutrient uptake.

2. Materials and methods

2.1. Plant materials and culture conditions

Details on plant material and experimental conditions were given in a previous paper [17]. This study deals with five banana cultivars; Grande Naine (AAA dessert banana), Agbagba (AAB medium false horn plantain) and Obino l'Ewaï (AAB french plantain) are common in the low altitude areas of West Africa; Igitsiri (AAA-EA, 'beer variety') and Kayinja (ABB, a 'cooking variety' but known in Eastern Africa as a 'beer variety') are cultivated in the East African highlands. The experiments were conducted in growth chambers at 448 $\mu E \cdot m^{-2} \cdot s^{-1}$ photon flux density 12 h per day, 90% relative humidity, 28/25 °C day/night temperature for the three low altitude cultivars, and 24/20 °C day/night temperature for the two 'beer varieties' cultivated in the highlands. These temperatures are close to those encountered in the respective cropping areas. One experiment at 28/25 °C was also performed with Kayinja to assess possible effects of temperature on Al sensitivity.

Vitroplants, supplied by Vitropic (Montpellier, France) for Grande Naine and produced by ourselves in the *Musa* Germplasm Transit Centre (Heverlee, Belgium) of the International Network for Improvement of Banana and Plantain (INIBAP) for the four other cultivars, were weaned for 3 weeks in aerated nutrient solution tanks. The six tallest homogeneous individuals from a batch of 50 vitroplants for each cultivar were chosen. Their average height was 7.5 cm for Grande Naine, 15 cm for Kayinja, 17.1 cm for Agbagba, 17.1 cm for Obino l'Ewaï and 8.0 cm for Igitsiri. They were transferred to 2.5-L pots (one plant per pot).

Nutrient solutions were supplied continuously by peristaltic pumps at a rate of 104 $mL \cdot h^{-1} \cdot pot^{-1}$ so that the mean residence time of solution in pots was 1 d [18]. This device allowed to use input solutions with known chemical composition and to sample output solutions at a given time. Half of the plants (*i.e.*, three pots per cultivar) were supplied with a solution having the following composition, in macroelements (mM): 0.9 $Ca(NO_3)_2$, 0.05 $CaSO_4$, 0.05 $CaCl_2$, 0.5 KCl, 0.25 K_2SO_4, 0.05 $MgCl_2$, 0.05 $MgSO_4$, 0.1 NH_4Cl, 0.05 $(NH_4)_2SO_4$, 0.05 NaH_2PO_4, and in microelements (µM): 80 H_3BO_3, 80 FeEDTANa, 8 $MnCl_2$, 0.8 $ZnSO_4$, 0.8 $CuSO_4$, 5.6 $(NH_4)_6Mo_7O_{24}$. The other banana plants were supplied with the same solution to which 78.5 µM Al were added as $Al_2(SO_4)_3$ $18H_2O$. The two treatments were noted '–Al' and '+Al', respectively. The pH of the nutrient solutions was not adjusted but was the one which naturally resulted from the preparation of the solutions: 5.2 for the –Al treatment and 4.2 for the +Al treatment [17].

2.2. Measurements

Water and nutrient absorption measurements were carried out twice a week during 40 d. Water uptake was assessed by weighing input and output solutions of each pot over 1 d. Nutrient uptake was calculated as the difference between daily input and output quantities for each pot, *i.e.*, the difference between the product of concentration and solution volume at input and output. The cumulative water and nutrient uptake was calculated using the General Linear Models (GLM) procedure of the statistical software SAS (SAS institute, 1985). Calcium (Ca), magnesium (Mg) and Al were measured by Direct Current Plasma (DCP) emission spectroscopy, potassium (K) by atomic absorption spectrophotometry, NO_3–N and NH_4–N by Kjeldahl distillation, phosphorus (P) by colorimetry, and pH by specific electrodes.

The net release of H^+/OH^- ions by roots was assessed from the pH values observed in output solutions [17]. To that purpose, pH buffering curves (*i.e.*, pH vs. H^+/OH^- added) were established for solutions similar to those supplied to plants. Regression polynomial equations fitting these curves were then used to recalculate the net H^+/OH^- release by plant roots.

2.3. Statistical analyses

The General Linear Models (GLM) procedure of the statistical software SAS [19] was used for statistical analysis of the data. Significant differences were considered at $p = 0.05$ and mean values were ranked by the Scheffé's multiple range test when more than two groups of data were compared by analysis of variance (ANOVA) or by *T*-test paired method when only two groups of data were compared.

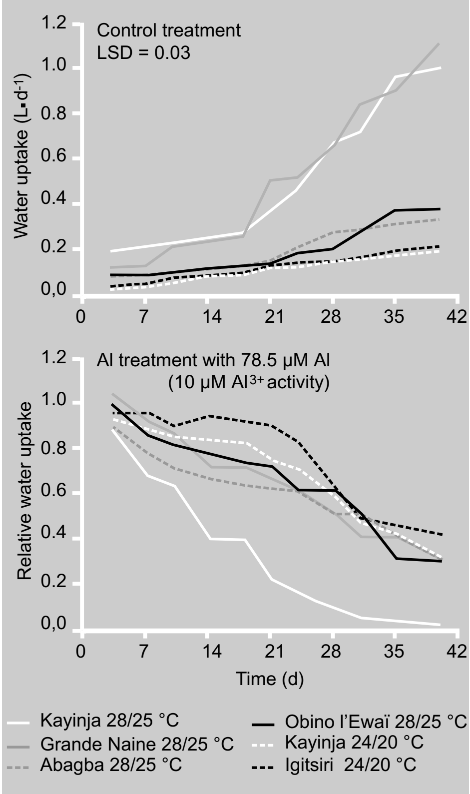


Figure 1.
Evolution of water uptake by five cultivars of *Musa* during their culture at two temperatures. Absolute values with LSD are given for the control treatment without Al. Relative values, *i.e.*, ratio of values with and without Al, are given for treatments with Al to easily compare the depressive Al effects for different banana cultivars (average values of three replicates).

3. Results

3.1. Water uptake

Without Al, the daily water consumption regularly increased with time in response to increasing plant needs (*figure 1*). Three water uptake responses can be discriminated statistically (*table I*): high for Grande Naine and Kayinja at 28/25 °C, intermediate for Agbagba and Obino l'Ewaï at 28/25 °C, and low for Igitsiri and Kayinja at 24/20 °C.

With Al, water uptake was significantly reduced (*tables I, II*) and the Al detrimental effect increased with time relatively to the control. After 40 d, the relative water uptake was in the range 30–40%, except for the Kayinja cultivar at 28/25 °C which was almost dying at the end of the culture. It is worth noticeing that Kayinja behaved like the other cultivars when temperature was lower (24/20 °C).

3.2. Nutrient uptake

The curves obtained with the nutrient uptake measurement have similar shapes to those shown for water uptake (*figures 2, 3*): without Al, nutrient uptake increased with time; the Grande Naine and Kayinja cultivars at 28/25 °C had the highest average uptakes (*table I*), but the differences with the other cultivars tend to vanish for K, P and NH_4–N uptake after about 30 d.

With Al, nutrient uptake was significantly reduced (*tables I, II*) and, as for water uptake, the difference with the control treatment increased with time. Magnesium

Table I.
Cumulative water (L) and nutrient (mg) uptake by banana plants grown during 40 d in nutrient solutions without Al (–Al) or with 78.5 µM Al (10 µM Al^{3+} activity) (+Al) (mean values of three replicates). For a same parameter, means between the –Al and +Al treatments are all significant (p = 0.05).

Cultivar	Ca			Mg			K		
	–Al	+Al	[+Al / –Al][3]	–Al	+Al	[+Al / –Al][3]	–Al	+Al	[+Al / Al][3]
Grande Naine[1]	881 a	402 a	46	92 a	18 a	19	2154 a	1160 a	54
Kayinja[1]	591 b	92 e	16	84 a	12 b	14	2345 a	647 c	28
Agbagba[1]	408 c	271 b	66	26 c	11 bc	42	1550 bc	846 b	55
Obino l'Ewaï[1]	339 cd	192 d	57	25 c	10 c	40	1632 b	842 b	52
Igitsiri[2]	367 c	246 c	67	33 b	12 b	36	1471 c	665 c	45
Kayinja[2]	301 d	100 e	33	34 b	11 bc	32	1054 d	349 d	33

Cultivar	P			NO_3–N			NO_4–N		
	–Al	+Al	[+Al / –Al][3]	–Al	+Al	[+Al / –Al][3]	–Al	+Al	[+Al / –Al][3]
Grande Naine[1]	95 a	71 a	75	1217 a	522 a	41	187 a	104 a	56
Kayinja[1]	99 a	54 b	55	1035 b	202 d	20	182 a	39 c	21
Agbagba[1]	52 c	26 c	50	632 c	206 d	33	102 c	79 b	77
Obino l'Ewaï[1]	73 b	34 c	47	594 c	317 b	53	105 c	77 b	73
Igitsiri[2]	66 b	32 c	48	627 c	266 c	42	181 a	80 b	44
Kayinja[2]	71 b	32 c	45	347 d	140 e	40	154 b	45 c	29

Cultivar	Water			Al	
	–Al	+Al	[+Al / –Al][3]	–Al	+Al
Grande Naine[1]	18.7 a	9.2 a	49	–	14.2 b
Kayinja[1]	18.5 a	3.4 b	18	–	4.1 c
Agbagba[1]	6.7 b	3.5 b	52	–	19.5 a
Obino l'Ewaï[1]	6.8 b	3.6 b	52	–	18.7 a
Igitsiri[2]	4.0 c	2.6 c	65	–	14.0 b
Kayinja[2]	3.5 c	2.0 d	57	–	5.6 c

a, b, c in the same column: significant difference groups (p = 0.05, Scheffé's multiple range test).
[1] Day / night temperature 28 / 25 °C.
[2] Day / night temperature 24 / 20 °C.
[3] [+Al / –Al] is expressed in %.

uptake was the most affected by Al. Among the cultivars, Kayinja at 28/25 °C had the lowest uptake except for P.

Aluminium uptake remained low for the five cultivars as compared to the Al quantities (196 µmol or 5.3 $mg \cdot d^{-1}$) supplied daily in nutrient solutions (*figure 4*). Marked differences in Al absorption were observed among cultivars (*table I*). Three groups distinctly discriminate: (i) the two plantains Agbagba and Obino l'Ewaï, (ii) Grande Naine and Igitsiri, and (iii) Kayinja at both temperatures with the highest, intermediate and lowest uptake, respectively. A comparison of *figures 1–4* suggests that the greatest Al detrimental effect on water and nutrient uptake was obtained at the lowest Al uptake (*i.e.*, for Kayinja at 28/25 °C). This

Table II.
Time (days) from which significant differences (p = 0.05) were observed in water and nutrient uptake rates between banana plants grown without Al or with 78.5 µM Al (10 µM Al^{3+} activity).

Cultivars	Water	Ca	Mg	K	P	NO_3–N	NH_4–N
Grande Naine[1]	14	10	7	10	21	18	10
Kayinja[1]	7	7	10	10	14	10	10
Agbagba[1]	10	14	7	10	14	10	21
Obino l'Ewaï[1]	10	14	7	10	14	7	14
Igitsiri[2]	18	10	7	7	14	10	10
Kayinja[2]	14	3	14	3	3	7	10

[1] Day / night temperature 28 / 25 °C.
[2] Day / night temperature 24 / 20 °C.

observation suggests that Al toxicity did not result from a simple antagonistic mechanism between Al and the essential nutrient cations.

3.3. Net H^+/OH^- release and cation/anion uptake balance

Net H^+/OH^- release was calculated from pH using the buffering curves of the nutrient solutions. On the other hand, cation/anion balance of plant uptake was calculated from the detailed analysis of solutions. A strong correlation (r = 0.99) appears, close to the 1:1 line, between the difference $[OH^-]$-$[H^+]$ released by roots and the difference $[mol_{c+}]$-$[mol_{c-}]$ of uptake (*figure 5*).

3.4. Statistical ranking of cultivars

The relative Al resistance or sensitivity among cultivars was studied by an analysis of variance (*table I*). For most parameters, the amounts absorbed by the two plantains, Agbagba and Obino l'Ewaï, cultivated with Al were representing more than 50% of those absorbed by the same cultivars grown without Al. For other cultivars, and especially for Kayinja, the [+Al / –Al] ratios were less than 50% for most parameters. So, the two plantains, Agbagba and Obino l'Ewaï, appeared more resistant to Al; Kayinja more sensitive.

4. Discussion

4.1. Water and nutrient uptake

The reduction of water and nutrient uptake for bananas grown with Al corroborates with previous studies involving different plant species [12, 15, 20, 21]. It seems well established that the detrimental Al effect on ion uptake does not result from a straightforward and unique mechanism (*figure 6*).

In the short term, Al binds mainly to the pectic substances in the root cell walls [2, 22] and in the root cell plasma membranes [20, 23] as a result of the high affinity of Al to negative exchange sites [21, 24]. This results in an impairment of root elongation (25, 26) and most ion transport processes through the plasmalemma [27–29]. Therefore, the root growth and the water and mineral uptake are reduced. The decrease of water uptake could affect the mineral element absorption by decreasing its mass-flow component. Cation uptake can also be directly inhibited by the competition of Al for exchange sites in root cell walls [2, 4, 8, 14]. Different authors found relationships between the uptake of given cations and their loading rate on root exchange capacity, especially for Mg [21].

In the long term, the low water and nutrient uptake by plants grown with Al, as compared to plants grown without Al, can mainly be explained by the differences in

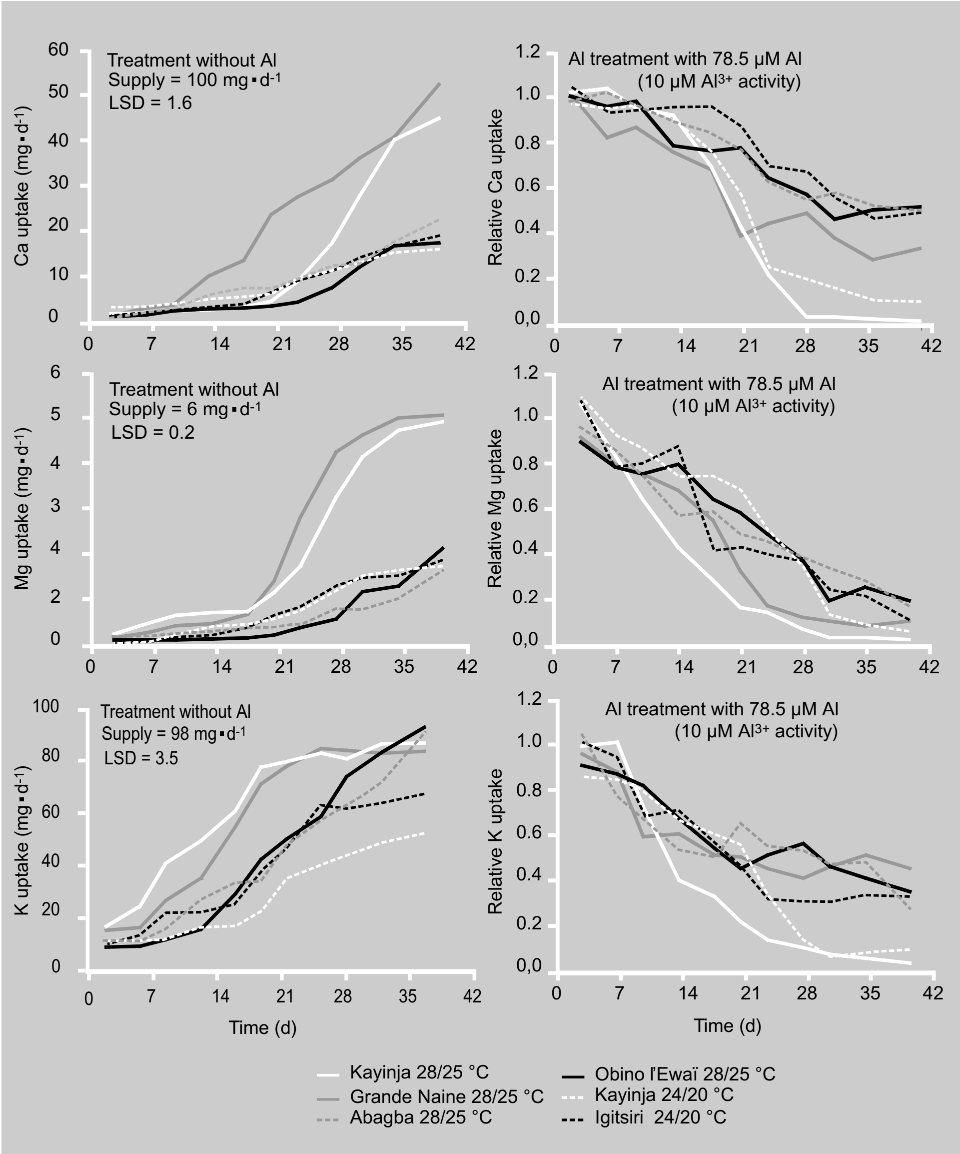


Figure 2.
Evolution of Ca, Mg and K uptake by five cultivars of *Musa* during 40 d of culture at two temperatures. Absolute values with LSD are given for the control treatment without Al. Relative values, *i.e.*, ratio of values with and without Al, are given for treatments with Al (average values of three replicates).

the absorbing surface area. In fact, the root biomass production has been shown to be reduced by Al for many plant species [4, 8, 30], including bananas [17].

As the plant transpiration is considered as the driving force for water upward movement in the plant tissues [31], the low development of the leaf surface area and the presence of necrotic spots on leaves of banana plants grown with Al [17] can reduce the water uptake which may thus affect the absorption and the upward movement of nutrients. Moreover, as mentioned above, other direct and indirect Al effects on mineral element uptake exist and can also affect the water uptake by alteration of the plant metabolism.

As observed in *figures 1–3*, water and nutrient uptake curves have similar shapes in both control and Al treatments. In *figure 7* where nutrient uptake are plotted against water uptake, the straight lines correspond to the calculated uptake resulting only from convective transport in water

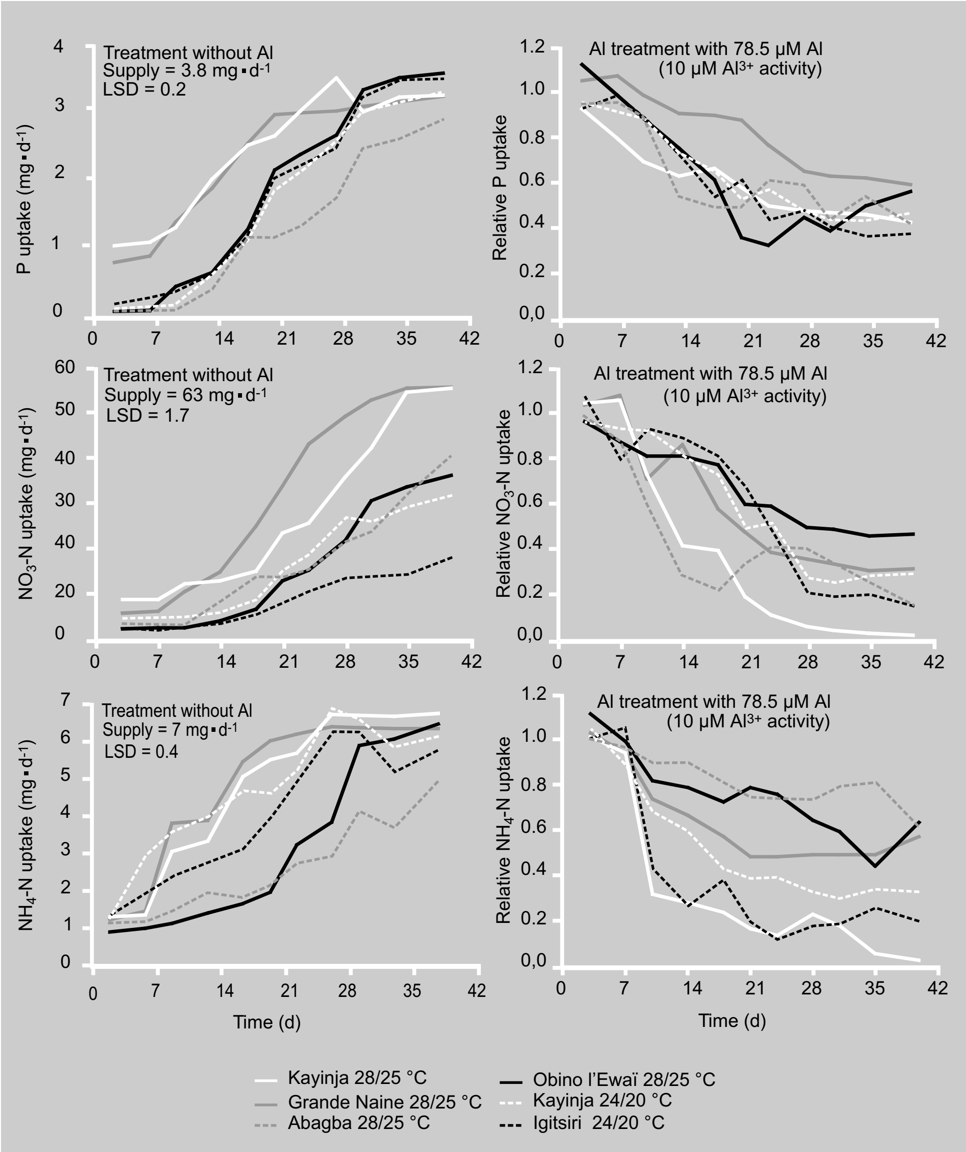
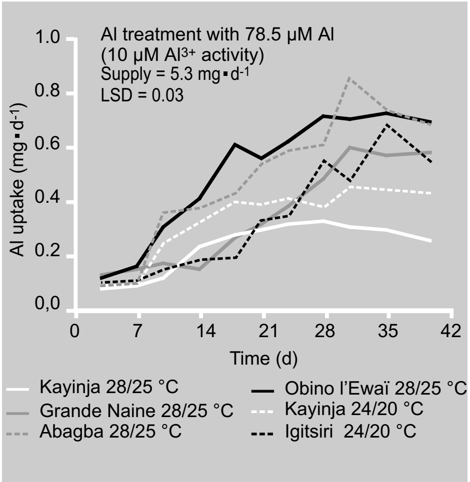


Figure 3.
Evolution of P, NO_3–N and NH_4–N uptake by five cultivars of *Musa* during 40 d of culture at two temperatures. Absolute values with LSD are given for the control treatment without Al. Relative values, *i.e.*, ratio of values with and without Al, are given for treatments with Al (average values of three replicates).

flow, *i.e.*, the product of water uptake by input nutrient concentration. In our experiments, these straight lines would correspond to identical concentrations in both output and input solutions. It was the case for Ca uptake by bananas cultivated without Al. Potassium, NO_3–N, NH_4–N and P uptake were larger than the calculated uptake by massflow. For Mg, values were identical to the calculated uptake when water uptake was low, whereas they were larger when water uptake was large. These results on banana corroborates with established characteristics for many other plant species [32–35].

As far as Al treatments are concerned, nutrient uptake was reduced to values which were similar to those observed in control treatments at the same water uptake rate. In other words, water and nutrient uptake seem to be related by a single relationship which is independent of metabolism inhibition by Al toxicity. The question is therefore twofold: (i) does the nutrient uptake with Al mainly decrease due to

Figure 4.
Evolution of Al uptake by five cultivars of *Musa* during 40 d of culture with Al, at two temperatures (average values of three replicates).



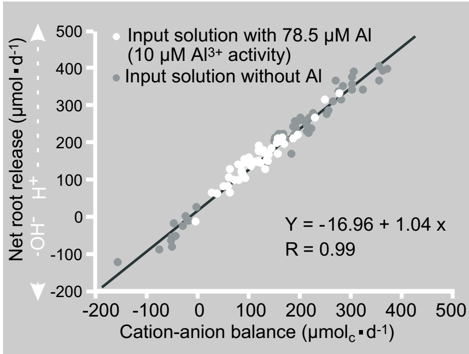


Figure 5.
Relationship between net H^+/OH^- release by roots and cation-anion balance of uptake for banana cultivars.

water uptake impairment or (ii) does water uptake mainly decrease due to nutrient uptake inhibition by Al? It is likely that, whether Al induces a decrease in root growth and mineral uptake that induces a decrease in water uptake in the short term, in long term, water uptake decrease induced by Al becomes the main cause for decreasing both growth and mineral uptake by plants. That may be in good agreement with field data which show that water stress of plant is frequently observed as among the first symptoms of soil acidity and Al toxicity. However, this aspect is complex and should be more documented to elucidate causal relationships.

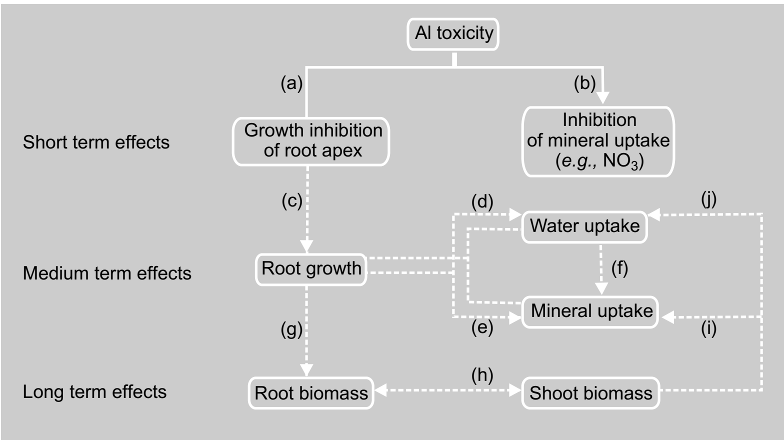


Figure 6.
Schematic representation of mechanisms of Al toxicity for plants. The full arrows indicate the inhibiting effects of Al and the broken arrows indicate the relationship between processes. In the short-term, Al may inhibit the growth of the root apex (a) and, simultaneously, decrease the uptake of mineral uptake, e.g., nitrate (b). The medium term effects are the inhibition of the root growth (c) which results in decreasing water (d) and mineral uptake (e). The decrease in water uptake may also affect the mineral uptake by decreasing its massflow component (f). In the long term, root (g) and shoot (h) biomass production must be consequently reduced. The reduced development of the leaf surface area of plants grown with Al are other possible causes of the low mineral (i) and water (j) uptake.

4.2. Net H^+/OH^- release and cation/anion uptake balance

Our results show that the net H^+/OH^- release by roots was in close relation to the balance in cations-anions taken up by plants (*figure 5*). The net H^+ release was displayed by a decrease of pH in output solutions and the net OH^- release was displayed by an increase of this pH [17]. Numerous studies showed similar effects of plant nutrition on pH changes in the rhizosphere [35–39]. These changes were mostly related to N nutrition. Indeed, nitrogen is the only nutrient which can be supplied either as a cation (NH_4^+) or as an anion (NO_3^-). In our experiments, both N forms were supplied to banana at concentrations 1.8 mM NO_3–N and 0.2 mM NH_4–N. This can explain that both acidification and alcalinisation were observed [17] for some cultivars in the control treatments. Despite NH_4–N represented only 10% of the available N, all bananas were found to prefer

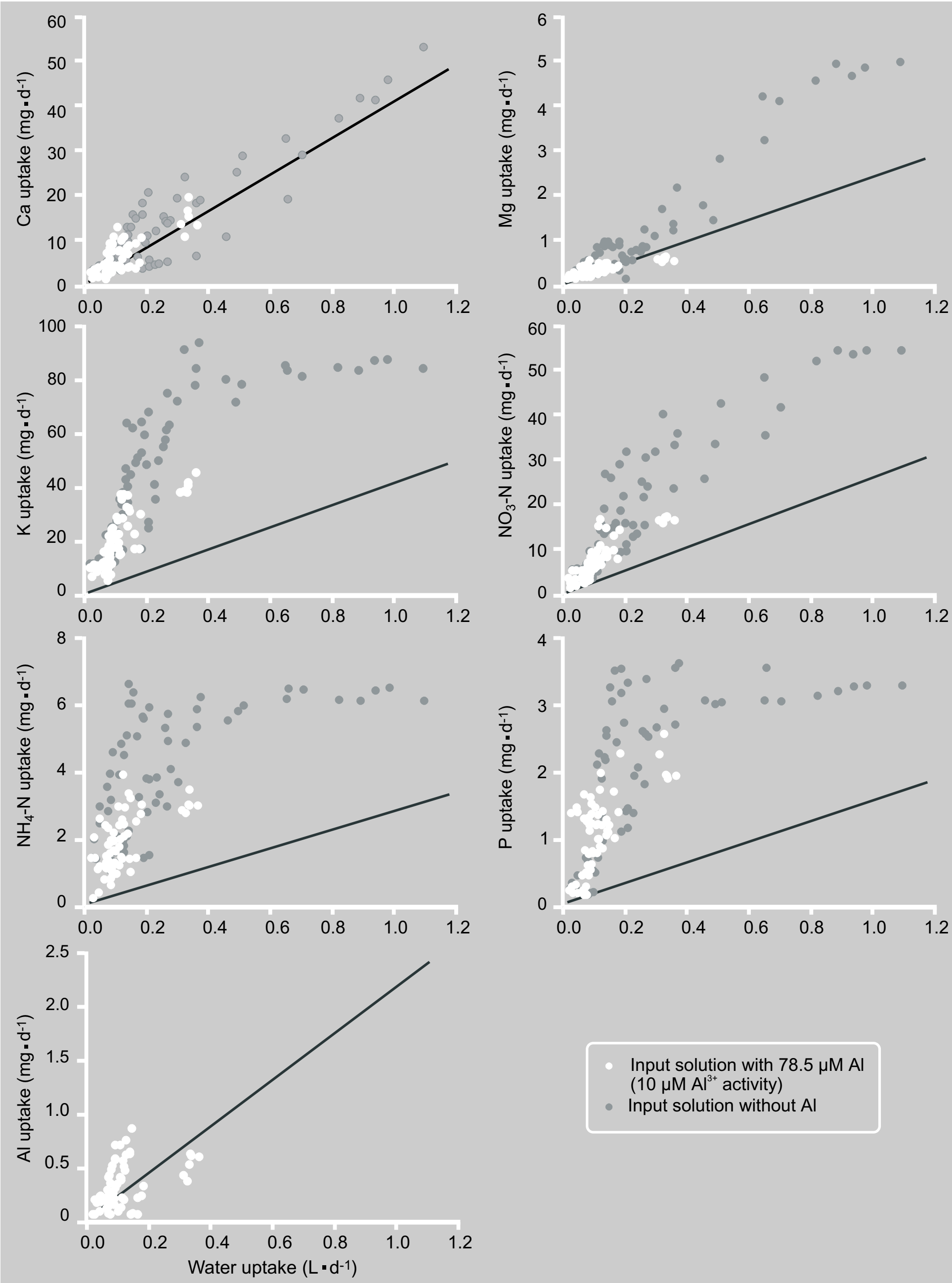


Figure 7.
Relationship between ion uptake and water uptake for banana cultivars cultivated without or with Al.

this N form, *i.e.*, as far as the N needs remained lower than the supplied NH_4–N quantities, the NH_4/NO_3 uptake ratio was greater than the input NH_4/NO_3 ratio, until NH_4–N was depleted in the nutrient solution. Knowing that NH_4–N was supplied at a rate of 6.7 mg·d^{-1}, one notices in *figures 2* and *3* that complete uptake of this N form was reached for some cultivars on and after about 28 d. Therefore increasing absolute and relative NO_3–N uptake rate resulted in excess anion uptake and consequently in the net OH^- release by the roots in solutions, except for the two cultivars grown at 24/20 °C.

No such pH changes were observed when Al was added to input solutions [17]. These solutions were more buffered than the control solutions due to Al hydrolysis; as the input pH was lower, identical H^+/OH^- release would have resulted in smaller pH changes than in control solutions because of the logarithmic scale between H^+ activity and pH. Anyway, if a small acidification occurred in two cases during the first week [17], alcalinisation was not expected because the metabolic inhibition caused by Al was reducing N needs and, as shown for control treatments, pH increased only at high N demand.

4.3 Statistical ranking of cultivars

It must be recalled that any conclusion on the relative Al resistance or sensitivity among cultivars is only valid for the growth conditions imposed in the experiments, and for the parameters that were measured. Therefore, no hasty conclusion about the effect of Al on banana yield under field conditions can be drawn from this basic research conducted with young plants in nutrient solutions of fixed composition. Moreover, the picture is complicated because differences already existed in the control treatments: for example, *table I* shows that Grande Naine was absorbing more water and nutrients during 40 d than any other cultivar, whereas the two cultivars grown at 24/20 °C showed lower water uptake and also often lower nutrient uptake. Therefore, the effect of Al can only be assessed in relative terms with respect to controls.

5. Conclusion

Young bananas, as most cultivated plant species, are sensitive to Al. Water and nutrient uptakes were drastically reduced for banana plants grown with Al. This Al effect seems to result from many mechanisms which interact. In the long term, the decrease in the root absorbing surface area was thought to be the main cause of the decrease of the water and nutrient uptake for plants grown with Al. Statistical analysis indicates that the plantains Agbagba and Obino l'Ewaï are generally more resistant to Al than the other cultivars, at least for the nutrient uptake rates reported in this paper. On the other hand, Kayinja was the most sensitive. Changes of temperature are likely to modify Al sensitivity: indeed one cultivar, Kayinja, showed greater Al sensitivity at 28/25 °C than at 24/20 °C.

Acknowledgements

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References

[1] Foy C.D., Physiological effects of hydrogen, aluminum and manganese toxicities in acid soils, in: Adams F. (Ed.), Soil acidity and liming, 2nd edition, ASA, CSSA, SSSA, Madison, WI, USA, 1984, pp. 57–97.

[2] Horst W.J., The role of the apoplast in aluminium toxicity and resistance of higher plants: a review, Z. Pflanz. Bodenkunde 158 (1995) 419–428.

[3] Von Uexküll H.R., Mutert E., Global extent, development and economic impact of acid soils, Plant Soil 171 (1995) 1–15.

[4] Dufey J.E., Drimmer D., Lambert I., Dupont Ph., Composition of root exchange sites in acidic soil solutions, in: McMichael B.L., Persson H. (Eds), Plant roots and their environment: proceedings of an ISRR-symposium, August 21–26, 1988, Uppsala, Sweden, Elsevier, Amsterdam, The Netherlands, 1991, pp. 31–38.

[5] Vo Dinh Quang, Tang Van Hai, Tombo Kanyama E., Dufey J.E., Effets combinés de l'aluminium, du fer, et du phosphore sur l'absorption d'ions et le rendement du riz (*Oryza sativa* L.) en solution nutritive, Agronomie 16 (1996) 175–186.

[6] Costa de Macedo C., Kinet J.M., Van Sint Jan V., Effects of duration and intensity of aluminium stress on growth parameters in four rice genotypes differing in aluminium sensitivity, J. Plant Nutr. 20 (1997) 181–193.

[7] Bernal J.H., Clark R.B., Mineral acquisition of aluminum-tolerant and -sensitive sorghum genotypes grown with varied aluminum, Commun. Soil Sci. Plant Anal. 28 (1997) 49–62.

[8] Godbold D.L., Jentschke G., Aluminium accumulation in root cell walls coincides with inhibition of root growth but not with inhibition of magnesium uptake in Norway spruce, Physiol. Plantarum 102 (1998) 553–560.

[9] Voigt P.W., Godwin H.W., Morris D.R., Effect of four acid soils on root growth of clover seedlings using a soil-on-agar procedure, Plant Soil 205 (1999) 51–56.

[10] Zhao X.J., Sucoff E., Stadelmann E.J., Al^{3+} and Ca^{2+} alteration of membrane permeability of *Quercus rubra* root cortex cells, Plant Physiol. 83 (1987) 159–162.

[11] Kruger E., Sucoff E., Aluminium and the hydraulic conductivity of *Quercus rubra* L. root systems, J. Exp. Bot. 40 (1989) 659–665.

[12] Ishikawa S., Wagatsuma T., Plasma membrane permeability of root-tip cells following temporary exposure to Al ions is a rapid measure of Al tolerance among plant species, Plant Cell Physiol. 39 (1998) 516–525.

[13] Tang Van Hai, Truong Thi Nga, Laudelout H., Effect of aluminium on the mineral nutrition of rice, Plant Soil 114 (1989) 173–185.

[14] Galvez L., Clark R.B., Nitrate and ammonium uptake and solution pH changes for Al-tolerant and Al-sensitive sorghum (*Sorghum bicolor*) genotypes grown with and without aluminium, Plant Soil 134 (1991) 179–188.

[15] Calba H., Jaillard B., Effect of aluminium on ion uptake and H^+ release by maize, New Phytol. 137 (1997) 607–616.

[16] Sharrock S., Frison E., Musa production around the world – trends, varieties and regional importance, in: INIBAP (Ed.), Networking banana and plantain: INIBAP annual report 1998, International Network for the Improvement of Banana and Plantain, Montpellier, France, 1999, pp. 42–47.

[17] Rufyikiri G., Nootens D., Dufey J.E., Delvaux B., Effect of aluminium on bananas (*Musa* spp.) cultivated in acid solutions. I. Plant growth and chemical composition. Fruit 55 (6) (2000) 367–379.

[18] Declerck S., Laloux S., Sarah J.L., Delvaux B., Application of a flowing solution culture technique to study the parasitic fitness of the nematode *Radopholus similis* on banana plantlets under two different nitrogen nutrient regimes, Plant Pathol. 47 (1998) 580–585.

[19] SAS institute, Inc., SAS user's guide: statistics, 5th ed., SAS Inst., Cary, NC, USA, 1985.

[20] Arp P.A., Strucel I., Water uptake by black spruce seedlings from rooting media (solution, sand, peat) treated with inorganic and oxalated aluminum, Water Air Soil Poll. 44 (1989) 57–70.

[21] Keltjens W.G., Magnesium uptake by Al-stressed maize plants with special emphasis on cation interactions at root exchange sites, Plant Soil 171 (1995) 141–146.

[22] Wagatsuma T., Characterization of absorption sites for aluminum in the roots, Soil Sci. Plant Nutr. 29 (1983) 499–515.

[23] Wagatsuma T., Ishikawa S., Obata H., Tawaraya K., Katohda S., Plasma membrane of younger and outer cells is the primary specific site for aluminium toxicity in roots, Plant Soil 171 (1995) 105–112.

[24] Tice K.R., Parker D.R., De Mason D.A., Operationally defined apoplastic and symplastic aluminum fractions in root tips of Al-intoxicated wheat, Plant Physiol. 100 (1992) 309–318.

[25] Foy C.D., Fleming A.L., Armiger W.H., Aluminum tolerance of soybean varieties in relation to calcium nutrition, Agron. J. 61 (1969) 505–511.

[26] Krizek D.K., Foy C.D., Mirecki R.M., Influence of aluminum stress on shoot and root growth of contrasting genotypes of coleus, J. Plant Nutr. 20 (1997) 1045–1060.

[27] Rengel Z., Robinson D.L., Competitive Al^{3+} inhibition of net Mg^{2+} uptake by intact *Lolium multiflorum* roots. I. Kinetics, Plant Physiol. 91 (1989) 1407–1413.

[28] Huang J.W., Shaff J.E., Grunes D.L., Kochian L.V., Aluminum effects on calcium fluxes at the root apex of aluminum-tolerant and aluminum-sensitive wheat cultivars, Plant Physiol. 98 (1992) 230–237.

[29] Durieux P.P., Jackson W.A., Kamprath E.J., Moll R.H., Inhibition of nitrate uptake by aluminium in maize, Plant Soil 151 (1993) 97–104.

[30] Noble A.D., Fey M.V., Sumner M.E., Calcium-aluminum balance and the growth of soybean roots in nutrient solutions, Soil Sci. Soc. Am. J. 52 (1988) 1651–1656.

[31] Mengel K., Kirkby E.A., Principles of plant nutrition, 3rd edition, International Potash Institute, Bern, Switzerland, 1982.

[32] Higinbotham N., The mineral absorption process in plants, Bot. Rev. 99 (1973) 15–69.

[33] Cheeseman J.M., Hanson J.B., Energy-linked potassium influx as related to cell potential in corn roots, Plant Physiol. 64 (1979) 842–845.

[34] Sentenac H., Grignon C., Effect of pH on orthophosphate uptake by corn roots, Plant Physiol. 77 (1985) 136–141.

[35] Haynes R.J., Active ion uptake and maintenance of cation-anion balance: a critical examination of their role in regulating rhizosphere pH, Plant Soil 126 (1990) 247–264.

[36] Moorby H., Nye P.H., White R.E., The influence of nitrate nutrition on H^+ efflux by young rape plants (*Brassica napus* cv. Emerald), Plant Soil 84 (1985) 403–415.

[37] Gijsman A.J., Rhizosphere pH along different root zones of douglas-fir (*Pseudotsuga menziesii*), as affected by source of nitrogen, in: van Beusichem M.L. (Ed.), Plant nutrition-physiology and applications, Kluwer Academic Publishers, Dordrecht., 1990, pp. 45–51.

[38] Loss S.P., Robson A.D., Ritchie G.S.P., H^+/OH^- excretion and nutrient uptake in upper and lower parts of lupin (*Lupinus angustifolius* L.) root systems, Ann. Bot. 72 (1993) 315–320.

[39] Hinsinger P., Gilkes R.J., Root–induced dissolution of phosphate rock in the rhizosphere of lupins grown in alkaline soil, Aust. J. Soil Res. 33 (1995) 477–489.

Efecto del aluminio en bananos (*Musa* spp.) cultivados en soluciones ácidas. II. Absorción de agua y de elementos nutritivos.

Resumen — **Introducción**. En un artículo anterior, se mostró que el aluminio (Al) introducido en la solución de elementos nutritivos afectaba al crecimiento, producción de biomasa y composición química de los bananos (*Musa* spp.). El presente estudio está dirigido a proporcionar resultados complementarios relativos al efecto de Al sobre la absorción de agua y elementos nutritivos. **Material y métodos**. Se cultivaron las vitroplantas de cinco cultivares de banano (Gran Enana, Agbagba, Obino l'Ewaï, Igitsiri y Kayinja) durante 40 días en fitotrón a temperaturas próximas de las que se dan en sus áreas de cultivo. Las plantas recibieron aportes continuos, mediante bombas peristálticas, de soluciones nutritivas sin y con 78,5 µM Al. Se efectuaron mediciones de la absorción diaria de agua y de elementos nutritivos dos veces una semana. También se controló la acidificación o alcalinización de la rizosfera. **Resultados y discusión**. El aluminio redujo la absorción de agua por las plantas y se observaron efectos nocivos acumulativos. Tras 40 días, la absorción de agua era sólo de un 30 al 40% con respecto a la de los testigos. Sin Al, la absorción de elementos nutritivos (Ca, Mg, K, NO_3–N, NH_4–N) aumentó progresivamente, mientras que la presencia de Al impidió la absorción de todos estos elementos, especialmente la del magnesio. Al igual que con el agua, se observaron efectos acumulativos: tras 40 días, la mayoría de las tasas de absorción de los elementos nutritivos se redujeron más de un 50% con respecto a los testigos. Los plátanos (Agbagba y Obino l'Ewaï) se mostraron más resistentes a Al que los demás cultivares. Las variaciones de temperatura pueden modificar la sensibilidad a Al; en efecto, el cultivar Kayinja mostró una mayor sensibilidad a Al a 28/25 °C que a 24/20 °C.

***Musa* / aluminio / absorción de agua / absorción de sustancias nutritivas / pH del suelo**