Original article

Effect of aluminium on bananas (*Musa* spp.) cultivated in acid solutions. I. Plant growth and chemical composition

Gervais Rufyikiri
Didier Nootens
Joseph E. Dufey
Bruno Delvaux*

Unité des sciences du sol,
Université catholique
de Louvain,
Place Croix-du-Sud 2/10,
B-1348 Louvain-la-Neuve
Belgium

* *Correspondence and reprints*

Received 19 May 2000
Accepted 4 September 2000

Fruits, 2000, vol. 55, p. 367–379

RESUMEN ESPAÑOL, p. 379

Effect of aluminium on bananas (*Musa* spp.) cultivated in acid solutions. I. Plant growth and chemical composition.

Abstract — Introduction. Although aluminium (Al) is a major limiting growth factor for most cultivated plants in acid soils, no detailed studies were reported so far for banana (*Musa* spp.) despite of its importance in the tropics. This paper aims at providing a scientific baseline on the effect of Al on young banana plants. **Materials and methods**. Five banana cultivars (Grande Naine, Agbagba, Obino l'Ewaï, Igitsiri and Kayinja) were grown in nutrient solutions without and with 78.5 µM Al (10 µM Al^{3+} activity) in a phytotron at temperatures close to that of their cropping areas. The pseudostem height and the leaf surface area were determined once a week. Biomass production and mineral content were measured in different plant parts after 40 d. **Results and discussion**. Though Al did not affect the rate of appearance of new leaves, it decreased the total biomass, pseudostem height, leaf surface area, growth of lateral roots, number and diameter of root axes. Aluminium induced Mg-like deficiency symptoms on Kayinja leaves after one week of treatment. Similar symptoms appeared on Grande Naine after 10 d and later on the other cultivars. In all plant parts for all cultivars, Al reduced Ca and Mg contents, increased K and P contents, and did not change significantly N content. For most parameters, the two plantains Agbagba and Obino l'Ewaï appeared more Al-resistant and Kayinja more Al-sensitive than both Grande Naine and Igitsiri. Without Al, acidification was first noticed with all cultivars. For the cultivars Grande Naine, Kayinja and Agbagba, alcalinisation then occurred after about 4 weeks. With Al, only little changes of pH were observed, because of the acidity of the input solutions (pH 4.2) and the inhibition of plant metabolism. © Éditions scientifiques et médicales Elsevier SAS

***Musa* / edaphic factors / aluminium / growth / mineral content**

Effet de l'aluminium sur les bananiers (*Musa* spp.) cultivés en solutions acides. I. Croissance et composition chimique des plantes.

Résumé — Introduction. Bien que l'aluminium (Al) soit l'un des principaux facteurs limitant la croissance de la plupart des plantes cultivées sur sols acides, aucune étude détaillée n'avait été rapportée jusqu'ici pour le bananier en dépit de son importance dans les tropiques. Cet article vise à définir une ligne de base scientifique sur l'effet de Al sur de jeunes bananiers. **Matériel et méthodes**. Cinq cultivars de bananiers (Grande Naine, Agbagba, Obino l'Ewaï, Igitsiri et Kayinja) ont été cultivés en solutions nutritives sans et avec 78,5 µM Al (activité de 10 µM Al^{3+}), en phytotron, à des températures proches de celles trouvées dans leurs aires de culture. La taille du pseudotronc et la surface des feuilles ont été déterminées une fois par semaine. La production de biomasse et la teneur en éléments minéraux ont été mesurées sur différentes parties de la plante après 40 d de culture. **Résultats et discussion**. Bien que Al n'ait pas affecté le taux d'apparition des nouvelles feuilles, il a diminué la biomasse, la taille du pseudotronc, la surface des feuilles, la croissance des racines latérales, ainsi que le nombre et le diamètre des axes racinaires. Sur feuilles de Kayinja, après une semaine de traitement, l'aluminium a induit des symptômes de déficience proches de ceux dus au magnésium. Des symptômes semblables sont apparus sur Grande Naine après 10 d et plus tard pour les autres cultivars. Pour toutes les parties de la plante et chez tous les cultivars, Al a réduit les teneurs en Ca et en Mg, augmenté celles en K et P, et n'a pas changé de manière significative la teneur en N. Pour la plupart des paramètres, les deux plantains Agbagba et Obino l'Ewaï ont semblé plus résistants à Al et Kayinja plus sensible que Grande Naine et Igitsiri. Sans Al, une acidification a été tout d'abord notée pour tous les cultivars. Pour les cultivars Grande Naine, Kayinja et Agbagba, une alcalinisation est apparue ensuite, après environ 4 semaines de culture. En présence de Al, les pH ont peu changé en raison de l'acidité des solutions de départ (pH 4,2) et de l'inhibition du métabolisme de la plante. © Éditions scientifiques et médicales Elsevier SAS

***Musa* / facteur édaphique / aluminium / croissance / teneur en éléments minéraux**

1. introduction

In acid soils with low organic matter content, aluminium (Al) limits plant growth and yield of cultivated crops, and, additionally, in natural ecosystems, acidity and soluble aluminium determine to a large extent the type of spontaneous vegetation [1].

Aluminium (Al) tolerance varies among plant species and, also, among varieties or cultivars of a same plant species [2, 3]. Intensive research efforts have long been devoted to Al sensitivity of cultivated plants, especially tropical crops. Breeding programs were developed to select Al resistant cultivars for sustainable agriculture on acid soils [4]. Although bananas (*Musa* spp.) are among the most important crops in the tropics, only very limited studies were reported so far on the sensitivity of these plant species to Al toxicity [5]. However, some authors have observed that the growth and the yield were low for bananas cultivated on mineral acid soils [6, 7]. Plantains, a subgroup of bananas, have been reported to be more resistant to soil acidity than other banana cultivars. Spain et al. [8] consider plantains as suitable crops for acid soils and Rodriguez-Garcia et al. [9] observed that plantains can tolerate up to 77 % Al on the effective cation exchange capacity.

Systematic studies on this topic are needed because bananas represent an important food source for the populations in the tropics as only 13 % of the world banana production is exported [10].

The purpose of our research was to assess the Al sensitivity of young banana plants in controlled nutrient solutions in order to provide a scientific baseline for further applied studies. This paper reports results on growth and chemical composition of roots and shoots of five banana cultivars. A second paper [11] will deal specifically with water and nutrient uptake.

2. materials and methods

2.1. plant material and culture conditions

This study concerned five banana cultivars: Grande Naine (AAA, dessert banana) [12], Agbagba (AAB, medium false horn plantain) [13] and Obino l'Ewaï (AAB, French plantain) [13] which are very common in low altitude areas of West Africa, and Igitsiri (AAA-EA, 'beer variety') [14] and Kayinja (ABB, a 'cooking variety', but known in the Eastern Africa as a 'beer variety') [15] which 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 for 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 were supplied by Vitropic (Montpellier, France) for Grande Naine. The other four cultivars were produced by ourselves in the *Musa* Germplasm Transit Centre (Heverlee, Belgium) of the International Network for Improvement of Banana and Plantain (INIBAP). They were weaned for 3 weeks in an aerated nutrient solution. Among 50 vitroplants per cultivar, the six tallest but homogeneous individuals were selected. The average height was 7.5 cm for Grande Naine, 17.1 cm for Agbagba, 17.1 cm for Obino l'Ewaï, 8.0 cm for Igitsiri and 15.0 cm for Kayinja.

The vitroplants were transferred to 2.5 L pots (one plant per pot). Nutrient solution was 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 [16]. This device allowed to use input solutions with known chemical composition and to sample output solutions at 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; in microelements (µM), 80 H_3BO_3, 80 FeEDTANa, 8 $MnCl_2$, 0.8 $ZnSO_4$, 0.8 $CuSO_4$, 5.6 $(NH_4)_6Mo7O_{24}$. This composition was determined from (i) the nutrient requirements and the mineral equilibria as established for young bananas [17, 18] and (ii) the realistic ion concentrations in solutions of tropical acid soils [19]. The other banana plants were supplied with the same solution to which 78.5 µM Al was added as $Al_2(SO_4)_3$ $18H_2O$. The two treatments were noted '–Al' and '+Al' respectively.

The reference Al concentration was fixed as a plausible value in soil solution at pH 4.2 assuming that monomeric Al^{3+} activity should obey the thermodynamic relationship $\log (Al^{3+}) = A - 3$ pH in mineral soil horizons, where A is a constant ranging between 6.73–8.03 [20] corresponding to Al^{3+} activity ranging between $10^{-5.87}$–$10^{-4.57}$ M, respectively. We chose an Al^{3+} activity of 10^{-5} M (corresponding to $A = 7.6$). The Al concentration was computed as the value of total Al which gave this fixed Al^{3+} activity, in the presence of other elements given above, with the program SPECIES [21]. The pH of the nutrient solutions was not adjusted but was the one which naturally resulted from the preparation of the solutions: pH 5.2 for the –Al treatment and pH 4.2 for the +Al treatment. All experiments were carried out in triplicates.

2.2. measurements

Measurements of pH values of output solutions were taken three times a week using specific electrodes. Different plant growth measurements were carried out once a week: pseudostem height from the top of the corm to the crossing point of the last two unfurled leaves, length (l) and width (w) of the last unfurled leaf which made it possible to calculate leaf surface area (LS) as $LS = \alpha \times l \times w$. Accurate LS measurements on three leaves of each cultivar using computer scanning and surface calculation gave a mean value of 0.7 for α. Particular disorder symptoms were noted on leaves. At the end of the experiment, i.e. after 40 d, the plants were cut in different parts: root axis, lateral root, pseudostem, lamina, midrib. The length and diameter (at 1 cm from root to bulb inserting point) of all root axes were measured. All plant parts were dried at 60 °C for 1 week, weighed, then calcinated at 450 °C for 1 d. Ashes were dissolved with concentrated nitric acid (HNO_3). Calcium (Ca), magnesium (Mg), phosphore (P) and aluminium (Al) were measured by plasma emission spectroscopy (DCP), potassium (K) by flame absorption spectrophotometry. The nitrogen (N) was determined by Kjeldahl distillation.

2.3. statistical analyses

The General Linear Models (GLM) procedure of the statistical software SAS [22] 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.

3. results and discussion

3.1. pH changes

The pH values measured in the output solutions during the culture, compared with those of the input solutions, i.e. 5.2 without Al, and 4.2 with Al, showed that, without Al, the pH dropped quickly in the output solutions to values depending on cultivars and temperature (*figure 1*). Less acidification was noted for Igitsiri and Kayinja at 24 / 20 °C. With other cultivars, pH changed from 5.2 in input solution to about 4 or less in output solutions until about 21–28 d. This acidification phase was followed by an alcalinisation phase with pH rising up to about 6.5 for Grande Naine, Kayinja, and Agbagba. These varieties were cultivated at 28 / 25 °C. Only one low altitude cultivar, Obino l'Ewaï, grown at 28 / 25 °C, did not give rise to alcalinisation before 40 d. Apparently, Igitsiri grown at 24 / 20 °C started alcalinisation by the end of the culture. With Al, only small pH changes were observed compared to the input solution which was already quite acidic. No alcalinisation phase occured for any cultivar.

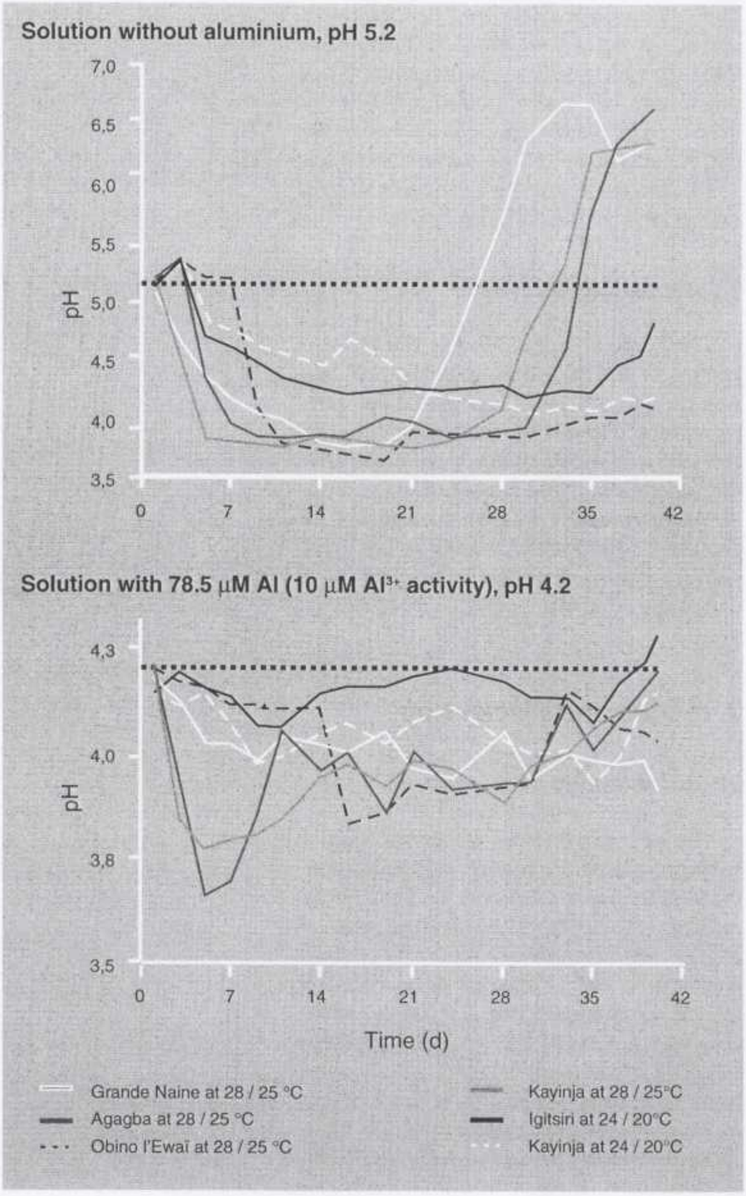

Figure 1.
Evolution of pH in output solutions for five banana cultivars at two temperatures.

Such pH changes showed that, in our experimental conditions, the pH of the input solutions are of a little importance in interpreting mineral uptake which could be influenced by the changes in proton activity. In this experiment, although nutrient solutions were not adjusted and maintained at the same pH by the addition of acid or basic solution as it was done in other studies [23, 24], the acidification induced by the roots maintained the pH values of the solution in contact with roots in the range 3.75–4.25 for both cultivars grown with or without Al during a period of 22–33 d depending on cultivar. Without Al, although the pH values were almost as low as those observed with Al, the plants grew well as shown by the evolution of the pseudostem height and the last expanded leaf surface with time (see below). On the contrary, the plant growth decreased with Al. This indicated that all differences observed between banana plants grown without Al and with Al were mainly related to Al toxicity rather than to the low pH naturally due to the presence of Al or due to proton excretion by the roots.

3.2. shoot growth

Without Al, the pseudostem height of all the cultivars increased by about 30 cm in 40 d, except for Kayinja that grew more slowly at 24 / 20 °C (*figure 2*). New leaves were formed at a rate of one per 4–5 d at 28 / 25 °C and one per 6 d at 24 / 20 °C, and each of them had a larger surface area than the previous one. The recent leaves were larger than the previous ones. The effect of temperature was marked for Kayinja: pseudostem height and leaf surface area were twice the size at 28 / 25 °C in comparison to 24 / 20 °C.

With Al, the pseudostem height increased by about 15 cm in 40 d for all cultivars, except for Kayinja that grew only by 3–5 cm. Cumulative detrimental effects were observed on leaf surface area. The differences with the control without Al increased with time, more particularly for Kayinja. Reduced leaf size is a typical response of banana to water deficit [25]. Unlike the other growth parameters described above, the rate of new leaf formation did not change with Al, so that leaf choked throat was observed at the top of the pseudostem. Choking resulting in a rosette-like foliage insertion was particularly marked for Kayinja and Grande Naine. Similar symptoms of choking resulting in a rosette-like foliage insertion are known to appear in water stressed plants [25]. Such a stunted growth might therefore result from

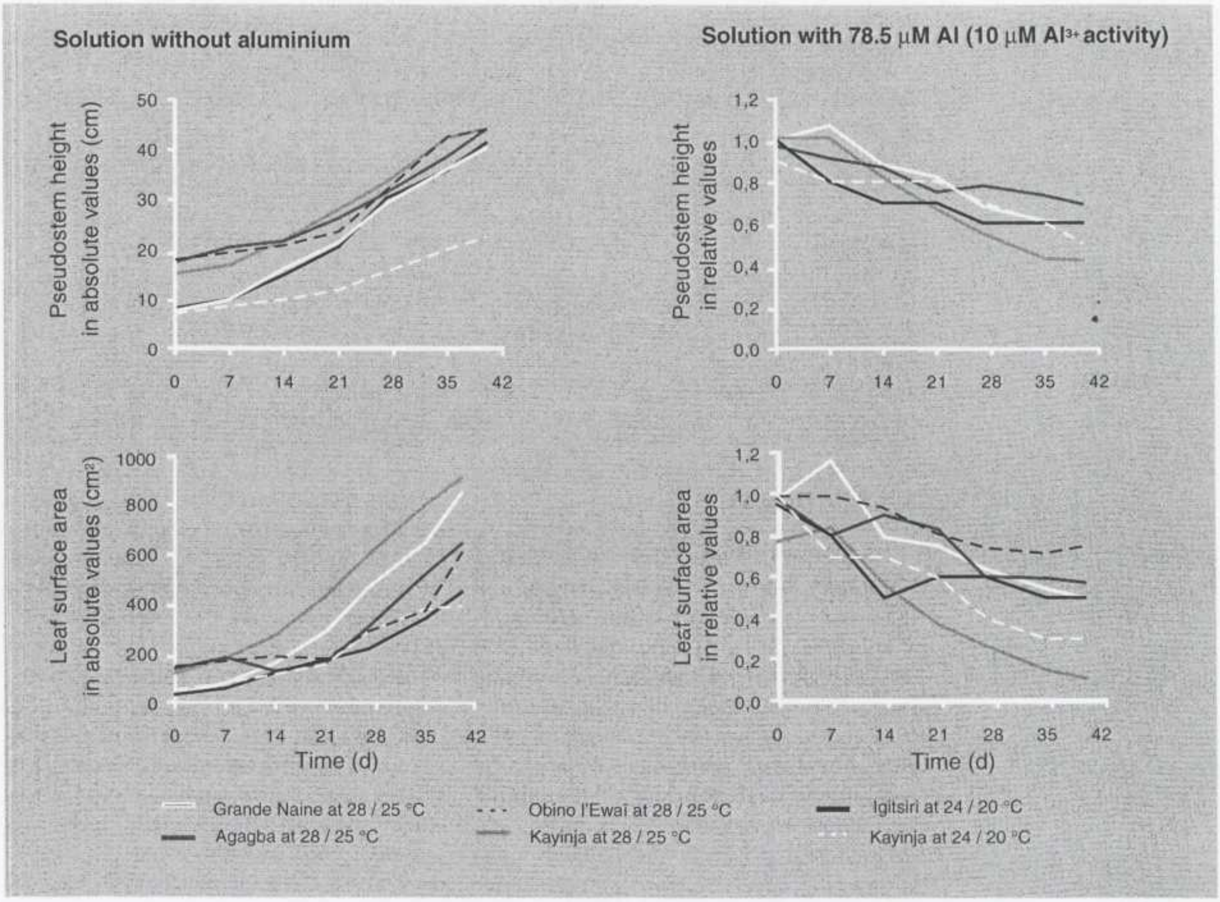

Figure 2.
Evolution of the pseudostem height and the surface area of the last unfurled leaf of five banana cultivars during the culture at two temperatures (average values of three replicates). The relative values correspond to the ratio of values with and without Al.

an Al-induced water uptake decrease as shown by Rufyikiri et al. [11].

3.3. leaf symptoms

Without Al, bananas showed leaf yellowing which started at the lamina margin extending throughout the leaf in about 1 d without affecting the midrib. Marginal necrosis further developed. These Al-related symptoms started to affect young leaves 3 d after unfurling. However, they progressed at different speeds and with distinct severity depending on the cultivar (*table I*). Kayinja was most affected: the symptoms appeared after 7 d culture with Al, both at 28 / 25 °C and at 24 / 20 °C. The leaves withered progressively, except the youngest ones. Severe symptoms were also observed on Grande Naine after 10 d with Al. Less serious symptoms appeared after 13, 27, and 35 d on Igitsiri, Agbagba and Obino l'Ewaï, respectively. A large part of the surface of each leaf remained green till the end of the culture. These Al-related symptoms observed on young bananas are similar to those reported for young coffee plants grown in nutrient solutions with Al [26]. Increased leaf yellowness is also one of the banana responses to water deficit [27]. However, both marginal yellowing extending close to the midrib and marginal necrosis are considered by Martin-Prével [28] and Lahav [18] as leaf symptoms of Mg deficiency in banana. Magnesium deficiency symptoms were also observed on leaves of inbred Oh40B maize grown at high Al levels (370 and 740 µM) [29].

Table I.
Appearance and severity of symptoms on leaves of five banana cultivars grown in a nutrient solution with 78.5 μM Al (10 μM Al^{3+} activity).

Day / night temperature (°C)	Cultivar	Symptoms on leaves	
		Delay of appearance (d)	Severity level
28 / 25	Grande Naine	10	Medium
	Kayinja	7	High
	Agbagba	27	Low
	Obino l'Ewaï	35	Low
24 / 20	Igitsiri	13	Low
	Kayinja	7	High

3.4. root growth

The growth of root axes was evaluated by considering their number, length, and diameter after 40 d of culture (*table II*). Without Al, Grande Naine and Kayinja at 28 / 25 °C had more root axes with greater length than the other cultivars; root diameters were not much different among cultivars. Aluminium particularly reduced the root number and diameter in all cultivars; root length was significantly reduced only for Kayinja at 28 / 25 °C. Visual observations showed that lateral roots were much shorter with Al than without Al for all cultivars.

Most reports on Al toxicity conclude to significant impairment of root elongation [30–32]. With bananas, we clearly noticed such effect only for one cultivar (Kayinja) at the highest temperature regime (28 / 25 °C). According to Foy et al. [30, 33], reduction of root elongation by Al might be due to a competition with Ca, leading to Ca deficiency in roots. In our experiment, it is possible that Ca concentration in the nutrient solution was large enough to avoid Ca deficiency, whereas, in acid soils, increasing soluble Al concentrations eventually involve decreasing Ca concentrations. Rhue and Grogan [31] also noticed that increasing Ca

Table II.
Growth parameters of root axes of five banana cultivars grown for 40 d in nutrient solutions without (–Al) and with 78.5 μM Al (10 μM Al^{3+} activity) (+Al) (mean values of three replicates).

Day / night temperature (°C)	Cultivars	Number			Length (cm)			Diameter (mm)			Ratio root lenght (+Al) / (– Al)
		–Al	+Al	T-test significance¹	–Al	+Al	T-test significance¹	–Al	+Al	T-test significance¹	
28 / 25	Grande Naine	25 a	16 a	**	45 b	49 a	ns	4.6 a	3.0 b	**	11
	Kayinja	24 a	13 bc	**	65 a	28 b	**	4.1 a	2.3 c	**	4
	Agbagba	18 bc	13 b	**	22 d	21 c	ns	4.4 a	3.7 a	**	10
	Obino l'Ewaï	20 bc	14 b	**	18 d	17 d	ns	3.6 b	2.8 b	**	9
24 / 20	Igitsiri	14 d	13 bc	ns	33 c	39 ab	ns	3.4 b	2.2 c	**	12
	Kayinja	17 cd	11 c	**	31 c	26 b	ns	3.4 b	2.8 b	**	8

1 Differences between –Al and +Al treatments ($p = 0.05$, T-test paired method). ns: not significant; ** significant.
a, b, c: in the same column, means not significantly different ($p = 0.05$, Scheffé's multiple range test).

Table III.
Root and shoot dry matter production (g) and shoot/root ratio of five banana cultivars cultivated for 40 d without (–Al) and with 78.5 µM Al (10 µM Al^{3+} activity) (+Al) (mean values of three replicates) for roots and shoots.

a) Roots. For a same parameter, significant differences between –Al and +Al treatments (p = 0.05, T-test paired method) were observed for all cultivars.

Day / night temperature (°C)	Cultivars	Root axes		Lateral roots		Total roots	
		–Al	+Al	–Al	+Al	–Al	+Al
28 / 25	Grande Naine	6.4 a	2.6 a	8.4 a	0.8 c	14.8 a	3.3 b
	Kayinja	6.5 a	0.5 e	5.3 b	0.1 e	12.9 a	0.6 d
	Agbagba	3.4 b	2.2 b	4.1 c	2.1 e	7.5 b	4.2 a
	Obino l'Ewaï	3.1 b	1.7 c	3.3 d	1.4 b	6.4 b	3.1 b
24 / 20	Igitsiri	1.9 c	0.6 d	1.5 e	0.2 d	3.4 c	0.8 c
	Kayinja	1.8 d	0.2 e	1.5 e	0.1 e	3.3 c	0.3 e

a,b, c, d, e in the same column: means not significantly different (p = 0.05, Scheffé's multiple range test).

b) Shoots. For a same parameter, significant differences between –Al and +Al treatments (p = 0.05, T-test paired method) were observed for all cultivars.

Day / night temperature (°C)	Cultivars	Lamina		Midrib		Pseudostem		Total shoots	
		–Al	+Al	–Al	+Al	–Al	+Al	–Al	+Al
28 / 25	Grande Naine	20.6 a	8.6 a	7.2 a	2.8 a	17.1 a	4.6 a	44.9 a	16.2 a
	Kayinja	18.7 a	2.9 d	5.7 b	0.8 c	15.4 a	1.4 c	39.8 a	5.2 c
	Agbagba	9.1 c	5.3 c	3.9 c	2.4 b	7.8 b	3.9 b	20.8 c	11.4 b
	Obino l'Ewaï	12.3 b	6.3 b	4.0 c	2.2 b	9.0 b	4.5 a	25.3 b	12.9 b
24 / 20	Igitsiri	8.4 cd	2.9 d	2.3 d	0.8 c	8.7 b	1.6 c	19.4 c	5.0 c
	Kayinja	7.3 d	2.2 e	1.9 c	0.5 d	4.9 c	0.7 d	14.1 d	3.4 d

c) Shoot / root ratio.

Day / night temperature (°C)	Cultivars	Shoot / root ratio		
		–Al	+Al	T-test significance[1]
28 / 25	Grande Naine	2.9 c	5.0 d	**
	Kayinja	3.1 c	8.7 b	**
	Agbagba	2.8 c	2.7 f	ns
	Obino l'Ewaï	4.0 b	4.3 e	ns
24 / 20	Igitsiri	5.6 a	6.4 c	ns
	Kayinja	4.4 b	11.4 a	**

[1] Differences between –Al and +Al treatments (p = 0.05, T-test paired method). ns: not significant; ** significant.

concentration (i) reduced the detrimental Al effect on Al-sensitive maize cultivars, and (ii) alleviated it completely for Al-resistant cultivars. Noble et al. [34], Cronan and Grigal [35], and Sanzonowicz et al. [36] also reported that Al toxicity is more related to [Ca/Al] balance than to absolute Al concentrations. However, the mechanisms are still far from fully elucidated [37] even though Ca-Al competition for root exchange sites, mainly located in cell walls, has been demonstrated [38, 39]. The inhibition of lateral root growth observed for all banana cultivars was also reported for white clover [40] and maize [41].

3.5. biomass production

Without Al, the total biomasses of Grande Naine and Kayinja at 28 / 25 °C were greater than those of the other cultivars (*table III*). A marked effect of temperature was observed for Kayinja, especially for roots: indeed root dry weight was four times smaller at 24 / 20 °C than at 28 / 25 °C, whereas shoot dry weight was reduced by a factor of 3.

With Al, the total biomass was severely reduced in all bananas. However, Agbagba and Obino l'Ewaï were more Al-resistant than the other cultivars. In all cultivars, Al particularly reduced the pseudostem biomass relatively to the other shoot parts, as well as the weight of lateral roots relative to root axes. These observations on biomass production after 40 d confirm those reported for the other growth parameters.

3.6. element concentrations in roots and shoots

For all banana cultivars grown without Al, Ca was more accumulated in the midrib, Mg in the root, K in the pseudostem and the midrib, and N in the lamina; P contents were similar in all plant parts (*table IV*). In addition, significant differences were noticed between cultivars for most element contents in most plant parts. Nitrogen content was less cultivar dependent than any other nutrient.

Aluminium reduced Ca and Mg contents in all plant parts for all cultivars, but increased K and P, whereas it did not significantly affect N content. As far as Al is concerned, translocation from root to shoot was obviously very limited for all cultivars, so that Al concentrations were at least 30 times larger in roots than in shoots.

Nevertheless some differences were observed among cultivars: Kayinja exhibited the largest Al contents in roots, at both temperatures. Igitsiri, cultivated at 24 / 20 °C, also showed higher Al content than those of the cultivars grown at 28 / 25 °C. It is possible that a low temperature increased the Al accumulation in roots as judged from the results in Kayinja. Indeed, Turner and Lahav [42] have shown that temperature can strongly affect the content of most mineral elements in most banana tissues.

Aluminium accumulation in roots has been observed in many plant species [2, 29, 43, 44]. Aluminium ions have a strong affinity for root exchange sites and can precipitate as hydroxides, Al-phosphate and Al-oxalate in roots [44, 45] so that their transfer to the aerial parts remains limited, except for Al accumulator plant species such as tea (*Camellia sinensis*) [46], *Richeria grandis* [47] and *Melastoma* (*Melastoma malabathricum*) [48] which have a high Al uptake ability and internal mobility.

Noteworthy is the fact that Al decreased the content of elements such as Ca and Mg, whereas it did not affect or even increased the content of other elements such as K, P and N. Especially, the Mg content in young bananas grown with Al (0.44–0.95 $g \cdot kg^{-1}$) was smaller than the Mg critical content (2–3 $g \cdot kg^{-1}$) reported by Lahav and Turner [49] in distinct parts of banana (*Musa* spp. AAA group, cv. Dwarf Cavendish, 'fully grown sucker' stage). As young micropropagated bananas usually show higher levels of most elements than mature field banana, one can conclude that severe Mg deficiency was affecting the bananas grown with Al in this study. Therefore the Al-induced leaf symptoms described above are likely Mg deficiency symptoms. Such deficiency is likely strengthened by the relative excess of K, the uptake of which is controlled mostly by an active mechanism. In this respect, it is worth noting that both direct Mg defi-

Table IV.
Element contents ($g \cdot kg^{-1}$ dry weight) in dry matter of different parts of banana plants cultivated for 40 d without Al (–Al) and with 78.5 µM Al (10 µM Al^{3+} activity) (+Al) (mean values of three replicates).

Cultivars	Ca			Mg			K			P			N			Al		
	–Al	+Al	Sign.[3]	–Al	+Al	Sign.[3]	–Al	+Al	Sign.[3]	–Al	+Al	Sign.[3]	–Al	+Al	Sign.[3]	–Al	+Al	Sign.[3]
Roots																		
Grande Naine[1]	4.6 a	3.5 b	**	2.9 a	0.9 b	**	45 c	81 b	**	2.9 b	4.3 d	**	25 a	25 ab	ns	–	2.9 d	–
Kayinja[1]	4.9 a	3.4 b	**	2.6 a	0.7 c	**	53 c	74 b	**	2.3 c	6.8 c	**	27 a	28 a	ns	–	7.8 b	–
Agbagba[1]	5.2 a	3.9 a	**	1.8 b	1.0 a	**	60 b	121 a	**	3.9 a	9.0 b	**	24 a	23 b	ns	–	4.3 c	–
Obino l'Ewaï[1]	5.1 a	3.4 b	**	2.1 b	0.9 b	**	53 c	64 c	**	4.1 a	4.7 d	ns	26 a	29 a	ns	–	3.8 c	–
Igitsiri[2]	4.9 a	3.9 a	**	1.4 c	0.9 b	**	71 a	84 b	**	3.0 b	9.1 b	**	24 a	24 b	ns	0.20 b	6.9 b	**
Kayinja[2]	4.2 b	3.6 ab	**	1.4 c	0.5 d	**	59 b	47 c	ns	3.6 a	13.1 a	**	26 a	25 b	ns	0.30 a	10.6 a	**
Pseudostem																		
Grande Naine[1]	14.2 ab	12.5 a	**	1.4 a	0.7 a	**	71 c	115 b	**	2.7 c	5.1b	**	19 a	22 a	ns	–	0.24 b	–
Kayinja[1]	15.6 a	8.5 bc	**	1.2 a	0.6 b	**	63 d	156 a	**	2.1 c	6.4 a	**	21 a	24 a	ns	–	0.16 c	–
Agbagba[1]	13.3 b	8.9 b	**	0.8 c	0.5 b	**	80 b	93 c	**	4.3 a	5.1 b	**	20 a	16 b	**	–	0.13 c	–
Obino l'Ewaï[1]	11.9 c	9.6 b	**	0.9 c	0.6 b	**	91 a	116 b	**	3.4 b	6.5 a	**	22 a	21 a	ns	–	0.13 c	–
Igitsiri[2]	13.8 b	7.9 c	**	1.1 b	0.7 ab	**	82 b	121 b	**	3.6 b	4.8 b	**	21 a	18 ab	**	0.09 a	0.19 b	ns
Kayinja[2]	14.6 a	7.6 c	**	1.0 bc	0.6 b	**	83 b	120 b	**	4.3 a	5.0 b	**	19 a	22 a	**	0.22 a	0.30 a	ns
Lamina																		
Grande Naine[1]	16.2 a	15.6 a	ns	1.6 b	0.9 a	**	37 d	67 c	**	2.5 c	5.5 b	**	36 b	38 b	ns	–	0.13 ab	–
Kayinja[1]	10.1 c	6.2 d	**	1.5 b	0.5 c	**	45 c	108 a	**	1.6 d	8.3 a	**	41 a	45 a	**	–	0.08 b	–
Agbagba[1]	15.1 ab	11.3 b	**	1.1 c	0.8 a	**	53 b	51 d	**	4.1 a	4.9 bc	ns	40 ab	40 b	ns	–	0.11 b	–
Obino l'Ewaï[1]	11.9 c	8.7 c	**	1.2 c	0.8 a	**	46 c	68 c	**	3.5 ab	5.5 b	ns	46 a	39 b	**	–	0.11 b	–
Igitsiri[2]	14.9 b	14.6 a	ns	1.9 a	0.7 b	**	33 e	79 b	**	2.8 c	4.3 c	**	38 b	39 b	ns	0.06 b	0.16 a	**
Kayinja[2]	11.5 c	8.5 c	**	0.9 d	0.6 bc	**	58 a	69 c	**	3.1 b	4.6 c	**	43 a	42 ab	ns	0.19 a	0.11 b	ns
Midrib																		
Grande Naine[1]	24.8 a	18.6 a	**	0.92 b	0.71 a	**	62 c	108 b	**	2.9 b	5.5 c	**	14 c	22 a	ns	–	0.16 bc	–
Kayinja[1]	17.3 c	7.7 d	**	0.95 b	0.56 b	**	59 c	143 a	**	2.1 c	5.8 bc	**	15 bc	24 a	**	–	0.13 c	–
Agbagba[1]	19.4 b	11.7 c	**	0.83 b	0.68 a	ns	87 b	138 a	ns	4.1 a	8.6 a	**	16 b	13 b	**	–	0.22 b	–
Obino l'Ewaï[1]	18.2 b	12.6 bc	**	0.68 c	0.66 ab	**	90 ab	118 b	**	2.8 b	6.4 b	**	20 a	22 a	ns	–	0.13 c	–
Igitsiri[2]	16.8 c	14.2 b	**	1.14 a	0.63 ab	**	87 b	109 b	**	3.9 a	4.7 c	ns	17 b	15 b	ns	0.12 b	0.35 a	**
Kayinja[2]	18.6 b	10.0 c	**	0.84 b	0.44 c	**	101 a	96 c	ns	2.8 b	3.1 d	ns	16 b	21 a	**	0.22 a	0.19 bc	ns

a, b, c in the same column and for a same plant part: means not significantly different ($p = 0.05$, Scheffé's multiple range test).
[1] Day / night température 28 / 25 °C.
[2] Day / night température 24 / 20 °C.
[3] Mean significance according to the T-test paired method used to compare the –Al and +Al treatments ($p = 0.05$). ns: not significant; ** Significant.

ciency and K excess-induced Mg deficiency (with symptoms known as 'banana blue') are promoted by a low soil pH [5]. A decrease of Mg concentration in plants grown with Al rather than other macroelements was also obtained in other studies [29, 50]. The forest decline in acid soils was related to leaf Mg deficiency in many regions [51, 52]. Possibly, in these acid soils, Mg deficiency was induced or aggravated by the presence of soluble Al.

4. conclusion

As far as the general effects of Al on growth indices are concerned, this study showed that Al decreased pseudostem height and leaf surface area but did not affect the rate of new leaf emission. Aluminium reduced the number and the diameter of root axes as well as the length of lateral roots, but had a limited effect on the root axis length, except for Kayinja. The chemical composition changes of plant tissues in the presence of Al exhibited some general tendencies for all cultivars: Ca and Mg contents were depressed, K and P were increased, and N was not affected. Magnesium content in plant parts was lower than the deficiency threshold concentrations reported in literature; consequently, leaf yellowing and marginal necrosis developing on Al-treated bananas is attributed to Mg deficiency. These symptoms appeared in all cultivars, but less rapidly on the two plantains Agbagba and Obino l'Ewaï.

This paper paints a broad picture of the effect of Al on five banana cultivars. As for other plant species, noticeable differences of Al resistance were observed among the banana cultivars. Kayinja was shown to be the most sensitive to Al both at 28 / 25 °C and 24 / 20 °C; the Grande Naine cultivar which produced the greatest biomass without Al at 28 / 25 °C can also be considered as really sensitive to Al. The biomass of Igitsiri (cultivated at 24 / 20 °C) was drastically reduced in the presence of Al, and this raises the question of possible temperature effect on Al toxicity. The other two cultivars, Agbagba and Obino l'Ewaï, grown at 28 / 25 °C produced less biomass when cultivated without Al, they were less affected by Al than the other cultivars. It is interesting to note that these two more resistant cultivars are plantains whereas the other three cultivars are bananas sensu stricto. This observation is in agreement with Spain et al. [8] who considered plantains as suitable crops for acid soils.

acknowledgements

This work was supported by the EU contract INCO-DC CEE CT 970208 "Alleviating abiotic and biotic soil constraints by combining arbuscular mycorhizal fungi with banana and plantain micropropagation systems" and by the research programme N° 2.4595.98 of the Belgian *Fonds de la Recherche Fondamentale et Collective* (FNRS-FRFC). We thank P[r]. Charles Renard for stimulating discussions and suggestions, Inès Van den Houwe of the INIBAP Transit Centre at the Katholieke Universiteit Leuven for advice and services during the in vitro culture phase of bananas, Patrick Populaire and Anne Iserentant for their technical support during the experiments and for the chemical analyses.

references

[1] Foy C.D., Effects of aluminum on plant growth, in: Carson E.W. (Ed.), The plant root and its environment, Univ. Press of Virginia, Charlottesville, 1974, pp 601–642.

[2] Tang Van Hai, Houben V., Nzok Mbouti C., Dufey J.E., Diagnostic précoce de la résistance de cultivars de riz (*Oryza sativa* L.) à la toxicité aluminique, Agronomie 13 (1993) 853–860.

[3] Zhang X.G., Jessop R.S., Analysis of genetic variability of aluminium tolerance response in triticale, Euphytica 102 (1998) 177–182.

[4] Van Sint Jan V., Costa de Macedo C., Kinet J.M., Bouharmont J., Selection of Al-resistant plants from a sensitive rice cultivar, using somaclonal variation, in vitro and hydroponic cultures, Euphytica 97 (1997) 303–310.

[5] Delvaux B., Soils, in: Gowen S. (Ed.), Bananas and Plantains, Chapman & Hall, London, UK, 1995, pp. 230–257.

[6] Wilson G.F., Swennen R., De Langhe E., Effects of mulch and fertilizer on yield and longevity of a medium and giant plantain and a banana cultivar, in: IARPB (Ed.), International Cooperation for effective plantain and banana research, Proceedings of the third meeting, 27–31 May 1985, International Association for Research on Plantains and Bananas, Abidjan, Côte d'Ivoire, 1987, pp. 109–111.

[7] Blomme G., The interdependence of root and shoot development in banana (*Musa* spp.) under field conditions and the influence of different biophysical factors on this relationship, Dissertationes de Agricultura No. 421, Faculteit Landbouwkundige en Toegepaste Biologische Wetenschappen, K.U.Leuven, Belgium, Ph. D. Thesis, 2000, 183 p.

[8] Spain J.M., Francis C.A., Howeler R.H., Calvo F., Differential species and varietal tolerance to soil acidity in tropical crops and pastures, in: Bornemisza E., Alvarado A. (Eds), Soil management in tropical America, North Carolina State Univ., Raleig, 1975, pp. 308–329.

[9] Rodriguez-Garcia J., Rivera E., Abruna F., Crop response to soil acidity factors in ultisols and oxisols in Puerto Rico. 14. Plantains and bananas, J. Agric. Univ. Puerto Rico 69 (1985) 377–382.

[10] 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.

[11] Rufyikiri G., Nootens D., Dufey J.E., Delvaux B., Effect of aluminium on bananas (*Musa* spp.) cultivated in acid solutions. II. Water and nutrient uptake, Fruits 56 (2000) (accepted).

[12] Champion J., Le Bananier, Techniques Agricoles et Productions Tropicales, G.-P. Maisonneuve & Larose, Paris, 1963.

[13] Swennen R., Vuylsteke D., Morphological taxonomy of plantain (*Musa* cultivars AAB) in West Africa, in: Persley G.J., De Langhe E.A. (Eds), Banana and plantain breeding strategies: proceedings of International Workshop held at Cairns, Australia, 13–17 October 1986, ACIAR Proceedings No. 21, Cairns, Australia, 1987, pp. 165–171.

[14] Sebasigari K., Principaux caractères de détermination dans la caractérisation morphologique des bananiers triploïdes *acuminata* d'Afrique de l'Est, in: Jarret R.L. (Ed.), Identification of genetic diversity in the genus *Musa*, Proceedings of an international workshop held at Los Baños, Philippines, 5–10 September 1988, Inibap, France, 1990, pp. 124–139.

[15] Sebasigari K., Morphological taxonomy of '*Musa*' in Eastern Africa, in: Persley G.J., De Langhe E.A. (Eds), Banana and plantain breeding strategies, Proceedings of International workshop held at Cairns, Australia, 13–17 October 1986, ACIAR Proceedings No. 21, Cairns, Australia, 1987, pp. 172–176.

[16] 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.

[17] Marchal J., Mallessard R., Comparaison des immobilisations minérales de quatre cultivars de bananiers à fruits pour cuisson et de deux « Cavendish », Fruits 34 (1979) 373–392.

[18] Lahav E., Banana nutrition, in: Gowen S. (Ed.), Bananas and plantains, Chapman & Hall, London, UK, 1995, pp 258–316.

[19] Roose E., Dynamique actuelle des sols ferrallitiques et ferrugineux tropicaux d'Afrique occidentale. Étude expérimentale des transferts hydrologiques et biologiques de matières sous végétations naturelles ou cultivées, Travaux et Documents de l'Orstom, n° 130, Orstom, Paris, 1981.

[20] Lindsay W.L., Chemical equilibria in soils, John & Wiley, New York, USA, 1979, 449 p.

[21] Barak P., Species: a spreadsheet program for modeling chemical speciation of soil solution, J. Agron. Educ. 19 (1990) 44–46.

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

[23] 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.

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

[25] Turner D.W., The response of the plant to the environment, in: Gowen S. (Ed.), Bananas and plantains, Chapman & Hall, London, UK, 1995, pp. 493–508.

[26] Pavan M.A., Bingham F.T., Toxicity of aluminum to coffee seedlings grown in nutrient solution, Soil Sci. Soc. Am. J. 46 (1982) 993–997.

[27] Stover R.H., Simmonds NW., Bananas, Tropical agriculture series, third edition, Longman Scientific and Technical, 1987, 468 p.

[28] Martin-Prével P., La nutrition minérale du bananier dans le monde. Première partie, Fruits 35 (1980) 503–518.

[29] Clark R.B., Effect of aluminum on growth and mineral elements of Al-tolerant and Al-intolerant corn, Plant Soil 47 (1977) 653–662.

[30] 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.

[31] Rhue R.D., Grogan C.O., Screening corn for Al tolerance using different Ca and Mg concentrations, Agron. J. 69 (1977) 755–760.

[32] 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.

[33] Foy C.D., Fleming A.L., Gerloff G.C., Differential aluminum tolerance in two snapbean varieties, Agron. J. 64 (1972) 815–818.

[34] 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.

[35] Cronan C.S., Grigal D.F., Use of calcium/aluminum ratios as indicators of stress in forest ecosystems, J. Environ. Qual. 24 (1995) 209–226.

[36] Sanzonowicz C., Smyth T.J., Israel D.W., Calcium alleviation of hydrogen and aluminum inhibition of soybean root extention from limed soil into subsurface solutions, J. Plant Nutr. 21 (1998) 785–804.

[37] Marschner H., Mineral nutrition of higher plants, 2nd ed., Academic Press, London, UK, 1995.

[38] 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, Elsevier Sci. Publ., Amsterdam, 1991, pp. 31–38.

[39] 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. Plant. 102 (1998) 553–560.

[40] Care D.A., The effect of aluminium concentration on root hairs in white clover (*Trifolium repens* L.), Plant Soil 171 (1995) 159–162.

[41] Calba H., Action des racines sur la mobilisation de l'aluminium – Analyse du fonctionnement d'un système modèle, thèse, Ensam, France, 1996.

[42] Turner D.W., Lahav E., Temperature influences the distribution of some nutrients in young banana plants independently of its effect on dry matter, Scientia Hortic. 28 (1985) 47–58.

[43] Alam S.M., Adams W.A., Effects of aluminum on nutrient composition and yield of oats, J. Plant Nutr. 1 (1979) 365–375.

[44] Haynes R.J., Ludecke T.E., Yield, root morphology and chemical composition of two pasture legumes as affected by lime and phosphorus applications to an acid soil, Plant Soil 62 (1981) 241–254.

[45] Dahlgren R.A., Vogt K.A., Ugolini F.C., The influence of soil chemistry on fine root aluminium concentrations and root dynamics in a subalpine spodosol, Washington State, USA, Plant Soil 133 (1991) 117–129.

[46] Matsumoto H., Hirasawa E., Morimura S., Takahashi E., Localisation of aluminium in tea leaves, Plant Cell Physiol. 17 (1976) 627–631.

[47] Cuenca G., Herrera R., Mérida T., Distribution of aluminium in accumulator plants by X-ray microanalysis in *Richeria grandis* Vahl leaves from a cloud forest in Venezuela, Plant Cell Environ. 14 (1991) 437–441.

[48] Watanabe T., Osaki M., Yoshihara T., Tadano T., Distribution and chemical speciation of aluminium in the Al accumulator plant, *Melastoma malabathricum* L., Plant Soil 201 (1998) 165–173.

[49] Lahav E., Turner D.W., Banana nutrition, Bull. 7. International Potash Institute, Worblaufen-Bern, Switzerland, 1983.

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

[51] Roberts T.M., Skeffington R.A., Blank L.W., Causes of type 1 spruce decline in Europe, Forestry 62 (1989) 179–222.

[52] Van Praag H.J., Weissen F., Dreze P., Cogneau M., Effects of aluminium on calcium and magnesium uptake and translocation by root segments of whole seedlings of Norway spruce (*Picea abies* Karst), Plant Soil 189 (1997) 267–273.

Efecto del aluminio en bananos (*Musa* spp.) cultivados en soluciones ácidas. I. Crecimiento y composición química de las plantas.

Resumen — Introducción. Aunque el aluminio es uno de los factores que limita el crecimiento de las plantas cultivadas en suelos ácidos, no se había reportado todavía ningún estudio detallado sobre el banano a pesar de su importancia en los trópicos. Este artículo intenta definir una línea de base científica sobre èl afecto de Al en bananos jóvenes. **Material y métodos**. Se cultivaron cinco cultivares de banano (Grande Naine, Agbagba, Obino l'Ewaï, Igitsiri y Kayinja) en una solución nutritiva sin y con 78,5 µM Al (actividad de 10 µM Al^{3+}), en fitotrón, a temperaturas próximas de las de sus zonas de cultivo. El diámetro del pseudotallo y la superficie foliar se determinaron una vez por semana. La producción de biomasa y el contenido en elementos minerales se midieron en diferentes partes de la planta tras 40 d de cultivo. **Resultados y discusión**. Aunque Al no afectó la tasa de aparición de nuevas hojas, disminuyó la biomasa, el diámetro del pseudotallo, la superficie foliar, el crecimiento de las raíces laterales y el número y diámetro de los ejes radiculares. En hojas de Kayinja, después de una semana de tratamiento, el aluminio indujo síntomas de deficiencias parecidos a los que provoca el magnesio. Síntomas similares se produjeron en Grande Naine tras 10 d y más tarde en los demás cultivares. En todas las partes de la planta y en todos los cultivares, Al disminuyó los contenidos en Ca y Mg, aumentó los contenidos en K y P, y no afectó de forma significativa al contenido en N. Los dos plátanos Agbagba y Obino l'Ewaï se mostraron más resistentes al Al en la mayoría de los parámetros, Kayinja se mostró más sensible que Grande Naine e Igitsiri. Sin Al, se observó, primeramente, una acidificación en todos los cultivares. Seguidamente, se produjo una alcalización tras 4 semanas de cultivo. Con Al, los pH cambiaron poco debido a la acidez inicial de las soluciones (pH 4,2) y la inhibición del metabolismo de la planta.

***Musa* / factores edáficos / aluminio / crecimiento / contenido mineral**