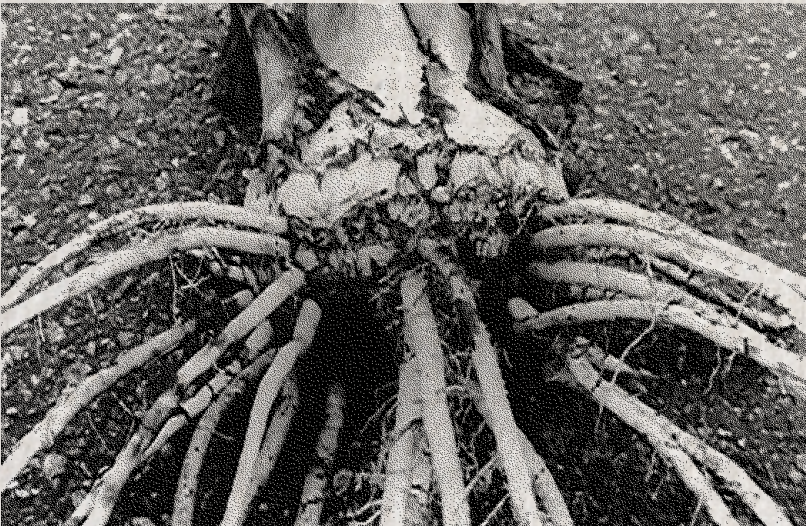


Progress in understanding the roots of *Musa* spp.

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Figure 1. The *Musa* root system



relying on detailed knowledge of the root system size and development.

A comprehensive study of the root system of the entire gene pool is required to complete the ideotype of a *Musa* plant and to support the genetic improvement of plantains and bananas. Such studies have been carried out at the IITA and at the *Université Catholique de Louvain* (UCL). Experiments conducted at IITA focussed on elucidating relationships between root and shoot traits, assessing variability in root system size, assessing the biophysical effects on root development and devising alternative methods for root evaluation (Blomme 2000). At UCL, research has been carried out primarily on lateral root initiation, aluminium toxicity effects on roots, cation exchange capacity of roots and interaction with mycorrhizae. In addition, the effects and interactions of nematodes and endomycorrhizae on root growth are currently being assessed at K.U.Leuven.

The considerable size of the *Musa* root system

The number of cord roots (i.e. adventitious roots) varies considerably depending upon the health status of the plant. A healthy corm (i.e. the true stem) can bear 200 to 400 primary cord roots with a total length of 230 m (Summerville 1944, Robin and Champion 1962, Beugnon and Champion 1966). Fawcett (1913) noted that growth rates of the tips may reach 60 cm per month, which is in agreement with later studies of the AAA variety 'Poyo' in Côte d'Ivoire where growth rates of 2 to 3.5 cm a day were recorded (Lassoudière 1978). Roots generally spread over 2 to 3 m and may extend up to 5 m from the plant, but most of the root system occurs within a 60 cm radius from the stem (Avilán *et al.* 1982, Gousseland 1983). Root distribution down the soil profile is mainly limited to the upper 40 cm but is, however, strongly influenced by soil type (Irizarry *et al.* 1981) and drainage. Compact soils, impermeable soil layers, high clay content and saturated soil conditions

The *Musa* root system (Figure 1) is a complex structure that supports multiple plant functions. For example, it ensures the optimal uptake of water and nutrients, provides anchorage to the plant and supposedly produces plant growth regulators (De Langhe *et al.* 1983, Swennen *et al.* 1984, Stover and Simmonds 1987, Price 1995). Although research on *Musa* roots started some 70 years ago (Skutch 1932), this focussed predominantly on the high value export dessert bananas, such as the variety 'Gros Michel' (Moreau and Le Bourdelles 1963) and later on the 'Cavendish' varieties (Beugnon and Champion 1966, Lassoudière 1978, Avilán *et al.* 1982).

While extensive breeding efforts have been devoted to improve shoot traits of *Musa*, comparatively little has been done for roots, despite the interdependence of shoot growth and root development. For example, nematodes reduce root growth, which often results in yield decline in *Musa* (Swennen *et al.* 1988, Gowen and Quénehervé 1990). While the nematode pest has been considered an important priority in breeding programmes at International Institute of Tropical Agriculture (IITA 1997, 1998), CRBP and FHIA, no systematic effort has been devoted to develop root systems that are less prone to nematode damage, thereby

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prevent or reduce root growth (Beugnon and Champion 1966, Champion and Sioussaram 1970, Godefroy 1969, Lassoudière 1971).

The effect of soil and climate

Studies on the effects of soil and climate on root growth conducted at IITA stations in Nigeria revealed significant influences of substrate type and climate on root growth (Blomme, 2000). Also, field-grown plants had a relatively larger root system (i.e. lower shoot-root ratio) under low nutrient conditions. These plants might have invested more dry matter in the root system in order to explore a larger soil volume to produce a vigorous shoot. In addition, a reduction in soil bulk density (during the first months after ploughing and harrowing) significantly enhanced root and shoot growth.

Root branching: the lateral roots

Due to their considerable surface in contact with the soil, lateral roots are often thought to be responsible for the major part of nutrient and water uptake. Lateral root growth, however, is highly influenced by micro-environmental conditions (Blomme, 2000) and genotype (Swennen *et al.* 1986). As a rule, lateral roots are generally abundant on cord roots growing in organic layers in the topsoil, and absent from cord roots growing deeper in the soil.

An in-depth study of lateral root development and growth is greatly facilitated under controlled conditions. Young plants were grown in hydroponics using a flowing standard nutrient solution, or in large tanks filled with sand supplied with the same flowing nutrient solution. All water-grown cord roots produce laterals while many of the sand-grown cord roots are devoid of laterals, suggesting a possible role of mechanical impedance in the presence/absence of laterals. The few sand-grown cord roots which carry lateral roots, show lateral root densities and lateral root lengths that are very similar to those of water-grown plants. Hence, at least a few root growth parameters might be estimated legitimately on plants grown under controlled conditions, despite many controversial aspects of nutrient solution experiments.

Lateral root initiation has been further investigated under the microscope (Draye *et al.* 1999) on field-grown cord roots. Neither the environment, nor the genotype affected the initiation of laterals: the production of lateral root

primordia appeared to be constitutive and followed a rigid pattern of differentiation and cell division in the root tip. Under certain circumstances, however, those primordia entered a dormant phase, giving rise to bare cord roots. Discovering the conditions prevailing in the rhizosphere that lead, directly or indirectly, to the developmental arrest of lateral root growth in the soil constitutes the challenge for future research conducted at UCL.

Allocation of dry matter to the shoot and root system

The percentage dry matter allocated to the shoot and the root portion of a *Musa* plant depends on the developmental stage and planting material (Figure 2). For example, juvenile *in vitro*-derived 'Calcutta 4' (AA genome group) and 'FHIA-03' (AAAB genome group) plants allocated up to 45% of dry matter to the root system just after field establishment. Subsequently, the percentage root dry matter declined during the further growth stages to about 10-15% at flowering. In contrast, less than 20% of plant dry matter was allocated to the roots of juvenile sucker-derived 'Mbi Egome' (AAB genome group) plants, while the corm contained up to 70% of the plant dry matter (Figure 2).

Percentage dry matter invested in the mat root system decreased gradually towards flower emergence (Figure 2). For example, there was a clear increase in the shoot-root ratio with increasing age for the *in vitro*-derived 'FHIA-03' mat. The shoot-root ratio of juvenile sucker-derived 'Mbi Egome' plants was relatively high, compared to the *in vitro*-derived plants and was caused by the large corm size of the planting material. As for the *in vitro*-derived plants, the highest shoot-root ratio was observed during the late vegetative phase.

Genetic variability in root growth and relationships with shoot growth: refining the ideotype

Strong positive correlations between shoot and root development of a mat (i.e. mother plant and lateral shoots) are observed during the vegetative and reproductive phase. For example, the vigorous shoot growth of most plantains and cooking bananas is associated with a large root system growth. In contrast, the semi-dwarf dessert

Figure 2. Dry matter partitioning between roots, corm, pseudostem (including bunch) and leaves in unthinned mats of 'Calcutta 4', 'Mbi Egome' and 'FHIA-03' from planting until harvest (FL: flower emergence). (source: Blomme, 2000)

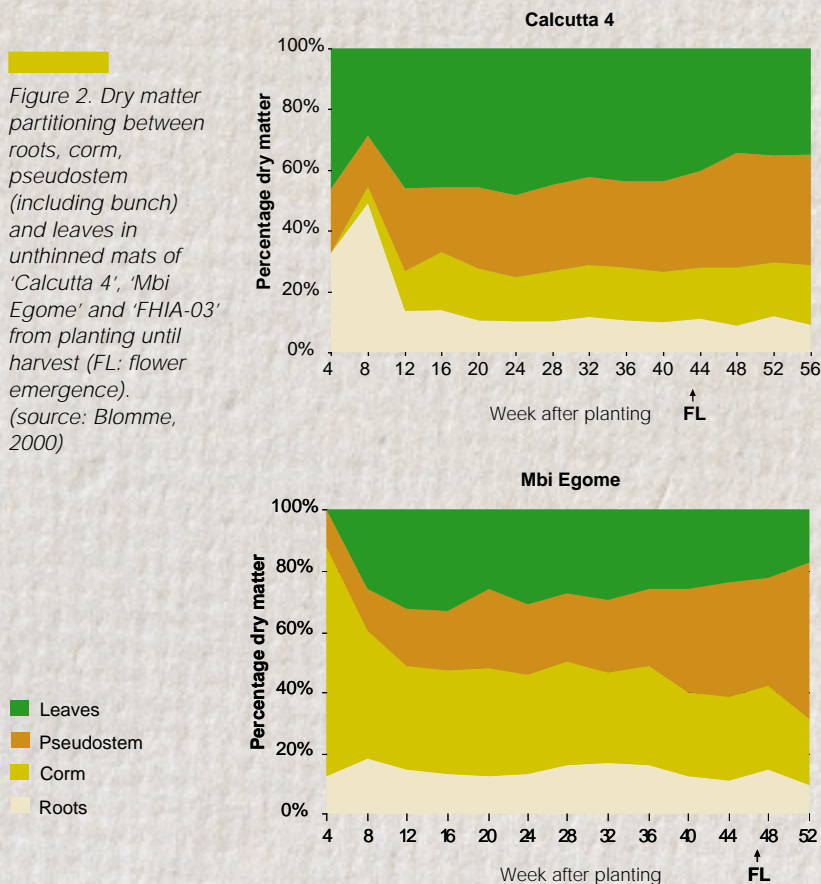
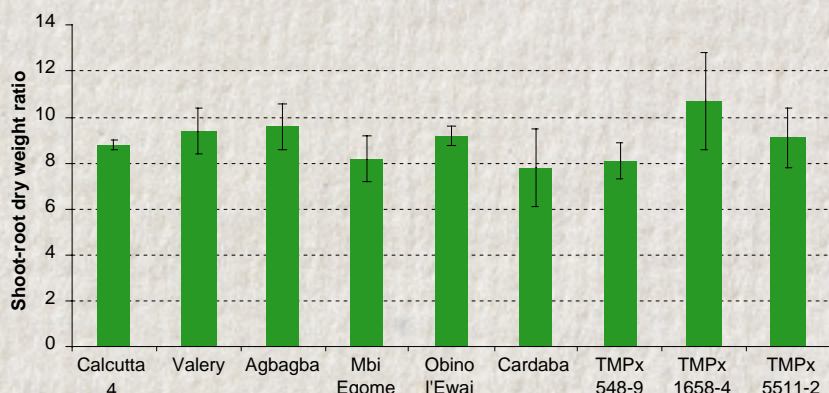


Figure 3. Shoot-root ratio for the mat of nine *Musa* genotypes at flower emergence of the plant crop. {Calcutta 4 (AA); Valery (AAA); Agbagba, Mbi Egome and Obino l'Ewai (AAB); Cardaba (ABB); TMPx 548-9, TMPx 1658-4 and TMPx 5511-2 (tetraploid plantain hybrids)} (source: Blomme, 2000)



banana variety 'Valery' (AAA genome group) has a small root system. Despite the observed variability in root system size between genotypes, shoot-root dry weight ratios are similar for mats of a wide variety of genotypes (Figure 3). These results indicate that breeding for an increased root system size, in addition to being cumbersome, goes along with breeding for a larger aerial part. The study of segregating populations should however be considered as different shoot-root relationships may be observed at the within-population level.

Strong positive relationships between shoot and root traits are also observed for the lateral shoots (i.e. suckers) (IITA 1999, Blomme 2000). Therefore, breeding for a regulated suckering (2 to 3 well-developed lateral shoots present during the reproductive phase) may prove to be more beneficial for plant anchorage and productivity of the crop than breeding for a modified shoot-root ratio or root system size of the main plant. Under regulated suckering, lateral shoots will have a vigorous shoot as well as root development. In addition, their large corm size will give stability to the mat. For example, plantain hybrids with a regulated suckering will be less susceptible to toppling compared to plantain landraces, which predominantly exhibit an inhibited suckering.

Towards alternative methods for root system assessment

Two man-days are needed to excavate, wash and assess the root system of one mature *Musa* plant. Also, attempts to correlate root growth of juvenile plants with that of adult plants have been inconclusive, indicating that an early assessment of root system growth of juvenile plants may not give sufficient information about the root system size and development of mature plants (Blomme 2000). Therefore, methodologies for fast and non-destructive root system assessment have been developed (IITA 1999, Blomme 2000).

Due to the strong relationships between shoot and root traits, regression models were obtained to estimate root traits from easily measurable shoot traits (Table 1). More than 90% of the variability in root traits could be explained by the variability observed in shoot traits. However, as the shoot-root ratio is dependent on the developmental stage of a plant and on environmental conditions (Blomme, 2000), fine-tuning of these models is still needed for assessing plants grown under different environments.

Core root samples taken around a plant can also provide adequate information on the variability in mat root system size (Blomme 2000).

Table 1. Regression models to predict root system characteristics of 20 weeks old plants, using aerial growth characteristics and ploidy level as independent variables (source: Blomme, 2000).

Trait#	Trait#				R ²
	LA [^]	PC	HS	PL	
DR	0.001628***	0.596934**			0.93
NR	0.001459***	1.255633***			0.930
LR	0.066704***	23.476717**			0.94
AD		0.093835***		0.681434***	0.97
TL	0.099478***		14.69139***		0.92
TD	0.002066***	0.426590	0.17142*		0.93

#: LA: leaf area (cm²); PC: pseudostem circumference (cm); HS: height of the tallest sucker (cm); PL: ploidy level; DR: root dry weight (g); NR: number of cord roots; LR: cord root length (cm); AD: average basal diameter of the cord roots (mm); TL: cord root length of the mat (i.e. mother plant and suckers) (cm); TD: root dry weight of the mat (g).

*, **, *** Significant at P<0.05, 0.01 and 0.001, respectively.

[^]: independent variables.

Table 2. Root cation exchange capacity and exchangeable cations (cmol_c kg⁻¹ dry wt) of five banana cultivars grown in nutrient solution without (-Al) and with 78.5 μM Al (+Al), and in soils (Andisol and Oxisol). The values are the means ± SE of triplicate (source: Rufyikiri, 2000).

	Nutrient solution		Soil <i>in situ</i>		Andisol	Oxisol
	-Al	+Al	-Al	+Al		
	Cord roots	Lateral roots	Cord roots	Lateral roots		
CECR						
Grande Naine	21.7±2.3	34.4±1.9	27.5±1.1	ND [§]	23.0±3.5	25.0±1.0
Kayinja	29.5±1.6	37.5±2.9	34.1±1.5	47.7±1.6	25.1±1.7	30.2±1.6
Agbagba	22.1±1.5	33.2±2.8	35.6±2.2	ND	23.2±1.0	23.8±1.9
Obino l'Ewai	22.9±2.7	35.3±7.8	35.0±1.1	ND	22.5±1.1	24.6±2.6
Igitsiri	18.8±1.1	29.4±1.6	31.0±5.8	34.9±1.1	20.3±2.1	21.2±1.9
Exchangeable cations (mean values of five cultivars)						
Aluminium	ND	ND	8.8±0.8	ND	4.9±1.8	3.3±0.9
Calcium	15.1±1.3	ND	13.8±1.1	ND	15.2±3.0	7.9±1.4
Magnesium	9.8±1.7	ND	1.6±0.5	ND	12.4±2.3	3.5±0.7

[§] Not determined.

This method only takes about 5% of the time needed to excavate and assess the root system of a mature plant.

These alternative methods may provide breeders and especially nematologists with adequate information on the roots of a *Musa* plant.

Aluminium toxicity, cation exchange capacity of roots and mycorrhizal interaction in bananas

An increase in soil acidity may enhance the content of exchangeable aluminium (Al) in the soil. Research at UCL is focusing on Al toxicity in relation to cation exchange capacity of the roots. Plant roots have cation exchange sites resulting from dissociated free carboxyl groups of organic components in the root cell wall. In bananas, the cation exchange capacity of roots (CECR), as measured in nutrient solution and in soil, can largely vary between cultivars but also between types of roots (Table 2) (Rufyikiri 2000). The values of CECR reported here range between 19 and 48 cmol_c kg⁻¹. These values are much larger than the ones reported by Bhattacharyya and Madhava Rao (1988), which ranged from 6.8 to 13.5 cmol_c kg⁻¹ in 'Robusta' (AAA genome group) banana roots. Significant differences are related to the root order (Table 2): firstly the CECR values are larger for the lateral roots than for the cord roots. Secondly, the CECR of 'Kayinja' (Pisang Awak, ABB genome group) cultivar is larger than any other cultivar. All cultivars show a positive correlation between the Al concentration in the roots and the CECR (Figure 4), resulting from the high affinity of carboxyl groups of root cell walls for aluminium. The preference for Al is further shown in Table 2: the fixation of Al on root exchange sites

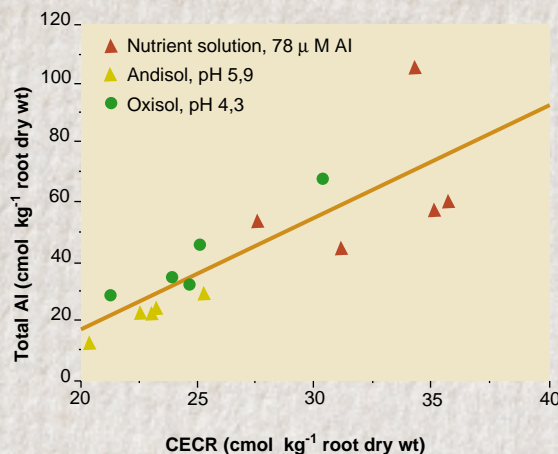


Figure 4. Relationship between total Al concentration and cation exchange capacity of banana roots. Values are means of five banana cultivars. (source: Rufyikiri, 2000)

occurred at the expense of other cations, especially Mg which leads to Mg-deficiency symptoms and a reduced plant biomass (Rufyikiri 2000).

The proportion of Mg in the sum of exchangeable Al, Ca and Mg dropped from 40% to 6% with increasing Al saturation on roots. Therefore cation absorption may be inhibited by Al competition on root exchange sites and this is considered as one of the numerous mechanisms involved in Al toxicity. The cultivar Kayinja with a large CECR has the largest Al concentration in its roots and is the most sensitive to Al toxicity (Rufyikiri 2000). The presence of Al strongly reduced the dry matter of lateral roots, because these roots have relatively large CECR.

In acid soils depleted of

Table 3. Shoot dry weight (g/plant) for the non-mycorrhizal (-AMF) and mycorrhizal (+AMF) banana plants grown without Al (Al₀) and with 78.5 μM Al (Al₁) and 180 μM Al (Al₂) added to the nutrient solution. Values are means of four replicates. For each parameter, values in the same column (-AMF and +AMF) followed by identical letter are not significantly different (P ≤ 0.05, Scheffé's multiple range test). For each parameter and Al concentration, the effect of AMF is indicated by NS if not significant or * if significant at P ≤ 0.05 (t-test paired method) (source: Rufyikiri, 2000).

Al treatments	- AMF	+AMF	AMF effect
Al ₀	29.6 a	30.7 a	NS
Al ₁	22.6 b	26.3 b	*
Al ₂	18.8 c	21.8 c	*

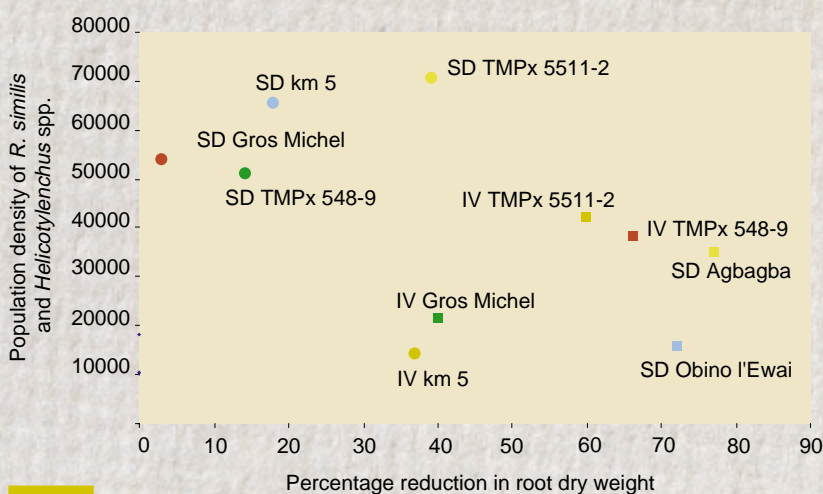


Figure 5. Reduction in root dry weight (g) of flowering mother plants of four Musa genotypes plotted against the nematode population density per 100 g fresh roots of *R. similis* and *Helicotylenchus* spp. for in vitro (IV) and sucker-derived (SD) plants. 'km5' and 'Gros Michel' are AAA dessert bananas; 'Agbagba' and 'Obino l'Ewai' are AAB plantains; 'TMPx 548-9' and 'TMPx 5511-2' are tetraploid plantain hybrids. The in vitro-derived plants of 'Agbagba' and 'Obino l'Ewai' died due to the nematode infection. (source: Blomme, 2000)

colonization of banana roots in the presence of Al. The mycorrhizal plants produced more shoot dry matter than the non-mycorrhizal plants grown in the same conditions with Al (Table 3). Mycorrhization also caused a delay of appearance of Mg-deficiency symptoms, the increase of the concentration of most mineral elements in plant tissues and the decrease of the Al concentration in roots (Rufyikiri 2000). Since no differences were observed between mycorrhizal and non-mycorrhizal bananas grown in the absence of Al stress, it appears that the arbuscular mycorrhizal fungi could be effective in alleviating Al toxicity for banana plants.

The effect and interaction of nematodes and endomycorrhizae

As there is a functional equilibrium in plant growth, the high reduction in root growth, due to nematode infection, is accompanied by a moderate reduction of above ground growth characteristics. A study conducted by Blomme (2000) showed that the host plant response to a

nematode infection depended on the type of planting material (Figure 5). Sucker-derived plants were observed to be less sensitive to nematode infestation compared to *in vitro*-derived plants, confirming observations made by De Waele *et al.* (1998). For example, the root system of the sucker-derived dessert bananas tolerated higher nematode population densities than the *in vitro*-derived propagules. The plantains were observed to be highly sensitive to nematodes since moderate population densities caused a severe reduction in root system size. *In vitro*-derived plants of the plantains 'Obino l'Ewai' and 'Agbagba' (both AAB genome group) were highly susceptible to nematode infection and died during the late vegetative development. This is in accordance with reports by Swennen and Vuylsteke (1988), Price (1994), Binks and Gowen (1996) and Fogain *et al.* (1996). The fragile roots produced by the juvenile *in vitro*-derived plants may be less resistant to nematodes compared to the more robust and thicker roots produced by young sucker-derived plants.

In field experiments in Costa Rica, De Waele *et al.* (1998) have shown that at least during the first 12 weeks, *in vitro*-derived banana plants can be severely damaged by *Radopholus similis* and *Helicotylenchus multicinctus* even at relatively low nematode densities and that the adverse effects were so great that the damaging symptoms can be expected to continue indefinitely.

The effect of endomycorrhizae on *Radopholus similis* population densities in banana plants was studied under greenhouse conditions by Umesh *et al.* (1988). They observed a reduction of the nematode population in both the roots and the soil. Moreover, nematode damage to the roots (necrotic lesions in the cortex) was reduced in the presence of endomycorrhizae. For *Meloidogyne* spp. and *Pratylenchus goodeyi*, also important banana nematodes, similar results were obtained (Jaizme-Vega and Pinochet 1997, Jaizme-Vega *et al.* 1997, Pinochet *et al.* 1997). The suppressive effect of endomycorrhizae (*Glomus intraradices*) on *R. similis* was also demonstrated under *in vitro* conditions using Ri-DNA transformed carrot roots as host tissue (Elsen *et al.* 2000).

In Uganda, differences in nematode population densities and root damage (number of functional roots, percentage of dead roots and necrosis) were observed between 2-to-3-month-old plants grown from sword suckers and the sword suckers of established mats. This suggests a different host plant response to nematode attack by young root systems compared to older root systems (Speijer *et al.* 1999).

Conclusions

Considerable advancements have been made over the past years in understanding the *Musa* root system. However, such research still has a long way to go. Future efforts are required in order to gain a greater understanding of root-shoot relationships and lateral root growth, while methodologies for easy assessment (e.g. genetic markers for root traits) need further development and more studies are required in the areas of nematode resistance/tolerance, and the effect of endomycorrhizae on root growth.

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