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Assessment of genotypic variation in the root architecture of *Musa* spp. under field conditions

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The *Musa* root system consists of adventitious roots, or cord roots, which are formed on the underground true stem, called rhizome or corm. These roots are predominantly found in the upper 40 cm of soil and may spread 2 to 3 m from the rhizome (Gousseland 1983, Araya *et al.* 1998). A healthy corm can bear 200 to 300 primary cord roots which can total 230 m in length (Beugnon and Champion 1966). These cord roots are mainly responsible for anchorage and transport of water and nutrients (Price 1995).

On these cord roots, first-order, second-order and occasionally third-order lateral roots are formed (Riopel 1966). Many first-order lateral roots usually emerge 12-15 cm behind the root tip of a cord root and may be as long as 15 cm (Laville 1964). When the apex of a primary *Musa* cord root is damaged, due to biotic or abiotic factors, two or three of these first-order laterals may develop into long secondary cord roots (Lassoudière 1977, Swennen *et al.* 1986).

The initiation and development of lateral roots provide important means of constructing a root system, thereby increasing its absorptive area and the volume of substrate exploited (Charlton 1996). However, lateral roots tend to be short lived. In banana, cord roots were observed to be functional for 4-6 months, whereas first-order and second-order laterals were functional for 8 and 5 weeks, respectively (Robinson 1988). Root elongation rates depend on root diameter: extension rates of 2-4 cm per day and 0.33 cm per day were reported for cord roots and first-order lateral roots, respectively (Lavigne 1987).

In a study on 10 *Musa* landraces grown in a nutrient solution, Swennen *et al.* (1986) observed variations in the total root length, the relative proportions of cord roots, first-order and second-order lateral roots, and the proportion of cord roots covered by lateral roots. The differences in these components were attributed to genetic differences.

Unlike plants grown in hydroponics, the root environment in the soil is heterogenous. Microsite conditions (e.g. pore size, fertility) influence lateral root development (Box 1996). Considerable modifications are exerted on the number of lateral roots per unit length of root and on their length. Thus, the part of a root axis developing in a more favourable zone exhibits a localized proliferation of lateral roots (Drew 1975, Russell 1977, Robinson 1994; Forde 2002).

It can be assumed that lateral root development will differ whether grown under field conditions or hydroponics. The objective of this study was to quantify the lateral root development of eight genotypes grown under field conditions.

Materials and methods

This study was carried out at the IITA High Rainfall station at Onne in south-eastern Nigeria (4°43' N, 7°10' E, 5 masl). The soil is an ultisol derived from coastal sediments, well drained, poor in nutrients, with the exception of available P, and with a pH of 4.3 in 1:1 H₂O. The average annual rainfall is 2400 mm and is distributed monomodally from February until November. The site has been described by Ortiz *et al.* (1997).

Eight genotypes were used for this study (Table 1). Vigorous sword suckers were prepared as recommended by Swennen (1990) and planted on 17 August 1998. Evaluation was done at 12 weeks after planting.

The experimental site, which had been under grass fallow for 8 years, was harrowed and ploughed to a depth of 25 cm to soften the soil, to allow optimum root growth, and to facilitate root excavation. Plant spacing was 2 m x 2 m to avoid overlapping between the root systems of adjacent plants. The experimental area was treated with the nematicide Nematicur (fenamiphos) at a rate of 15 g/plant (3 treatments/year). Fertilization was done at a rate of 200 g/plant with muriate of potassium (K₂O, 60% K) and at a rate of 100 g/plant with Urea (47% N), split over 2 equal applications: at planting and 8 weeks after planting. No mulch was applied. The fungicide Bayfidan (triadimenol) was applied 4 weeks after planting, to control black leaf streak disease.

Shoot, corm and root traits were assessed for all plants. The complete root system was excavated. The excavation was carefully done to avoid breaking the roots. Roots were washed on a large sieve to remove soil particles.

Table 1. Genotypes evaluated.

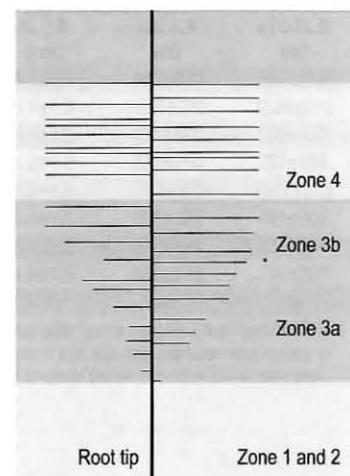
Name	Ploidy level	Genome	Type
Valery	3	AAA	Dessert banana
Yangambi km5	3	AAA	Dessert banana
Agbagba	3	AAB	Plantain
Obino l'ewai	3	AAB	Plantain
Fougamou	3	ABB	Cooking banana
Cardaba	3	ABB	Cooking banana
TMPx 1658-4	4	AAB x AA	Hybrid plantain (Obino l'ewai x Pisang lilin)
TMPx 548-9	4	AAB x AA	Hybrid plantain (Obino l'ewai x Calcutta 4)

The shoot characteristics measured included: plant height, circumference of the pseudostem at soil level, number of leaves, leaf area and total number of leaves produced from planting until assessment. Leaf length and leaf widest width were measured and the leaf area calculated according to Obiefuna and Ndubizu (1979). Corm fresh weight and corm height were measured. Root characteristics included the number and length of cord roots, root dry weight and average basal cord root diameter. The length of cord roots was estimated according to Tennant (1975) and their average diameter was measured, at 5 cm from their insertion point on the rhizome, with a Vernier calliper. Similar shoot and root traits were also assessed for the suckers and the mat (i.e. mother plant crop and suckers).

Two large mature cord roots per plant were evaluated for lateral root development. Cord roots were subdivided into 4 morphological zones (Swennen *et al.* 1986) (Figure 1). Zone 1 and 2 comprise the elongation zone and the distal zone without lateral roots. Zone 3a is the zone with growing lateral roots, while zone 3b is the zone with mature lateral roots. Finally, zone 4 comprises the bare proximal end of the cord root. The length of these zones was measured. The number and length of first-order lateral roots were measured on a 5-cm section of zone 3b, and the number and length of second-order lateral roots were measured on a 1-cm section of a first-order lateral root in zone 3b. The length and density of root hairs were not considered even though they are probably very important in nutrient and water uptake. The contribution of first-order lateral roots, second-order lateral roots and cord roots to the total estimated root length was calculated. The contribution of cord roots and the lateral roots to the total dry weight was also measured.

The experimental layout was a randomized complete block design with two replications of two plants per genotype. Statistical analysis

Figure 1. Schematic view of the different zones on a cord root.



was carried out using the SAS statistical package. The shoot and root traits were square root transformed prior to analysis (Gomez and Gomez 1984). Linear correlations between shoot and root traits and between different root traits were assessed using the PROC corr in SAS. The data were subjected to a mixed model ANOVA: Growth trait= μ +genotype(group)+error(μ =general mean). Groups nested in genotype were considered fixed effects, while residuals or error were random effects. Variability of the different growth characteristics was assessed and total phenotypic variance was partitioned according to the following sources of variation: genotype and replication.

Results

The shoot and root system were very healthy and no dead cord roots were observed at the time of assessment. Linear correlations between leaf area, corm fresh weight, number

of cord roots, cord root length and root dry weight were positive and in nearly all cases highly significant (Table 2).

The genotype had a significant effect on most shoot, corm and cord root traits whether they measured on mother plants, suckers or mats. 'Yangambi km5,' 'Cardaba' and 'TMPx 1658-4' had the highest values for leaf area and plant height, and 'Yangambi km5' and 'Cardaba' had the highest values for cord root length and root dry weigh (Table 3).

The genotype had a significant effect on the length of zone 4 ($P=0.05$) but not on the length of the other zones (Table 4). The length of zones 1 and 2 ranged from 15 to 21 cm, whereas the length of zone 3, with growing and mature lateral roots, ranged from 72 to 112 cm and accounted for 60 to 80% of total cord root length (Table 4).

The genotype had a significant effect on the number and length of second-order lateral roots on a 1-cm section of a zone 3b first-order

Table 2. Correlations between shoot and root traits measured on mother plants 12 weeks after planting.

	LA (cm ²)	CW (g)	NR	LR (cm)	DW (g)	AD (mm)	PL-NR	PL-LR (cm)	SL-NR	SL-LR (cm)	DWcord (g)	DWlat (g)
PH	0.77***	0.83***	0.23	0.48**	0.46**	-0.36	-0.08	-0.13	0.15	0.01	0.06	0.13
LA		0.82***	0.67***	0.80***	0.82***	-0.11	-0.02	-0.03	0.24	-0.02	0.11	0.04
CW			0.57***	0.76***	0.76***	-0.21	-0.09	-0.14	0.12	-0.05	0.25	0.18
NR				0.85***	0.84***	0.15	-0.09	-0.01	0.20	-0.01	0.29	0.17
LR					0.97***	0.09	0.01	-0.01	0.19	-0.03	0.32	0.18
DR						0.13	0.03	0.03	0.23	-0.01	0.38	0.21
AD							-0.20	0.37	0.19	0.28	0.52**	0.54**
PL-NR								0.71**	0.51**	0.37	-0.42*	-0.20
PL-LR									0.65***	0.52**	-0.12	0.16
SL-NR										0.84***	0.25	0.42*
SL-LR											0.32	0.57**
DW cord												0.81***

PH: plant height; LA: leaf area, CW: corm weight, NR: number of cord roots, LR: cord root length, DW: root dry weight, AD: average basal diameter of the cord roots, PL-NR: number of first-order lateral roots on a 5-cm section of zone 3b, PL-LR: length of first-order lateral roots on a 5-cm section of zone 3b, SL-NR: number of second-order laterals on a 1-cm section of a zone 3b first-order lateral root, SL-LR: length of the second-order laterals on a 1-cm section of a zone 3b first-order lateral root, DWcord: dry weight of cord roots, DWlat: dry weight of lateral roots.

* significant at $p<0.05$ ** significant at $p<0.01$ *** significant at $p<0.001$.

Table 3. Characteristics of the shoot, corm and cord root measured on the mother plants of 8 genotypes 12 weeks after planting (mean \pm s.e.).

Genotype	LA (cm ²)	PH (cm)	CW (g)	NR	LR (cm)	DW (g)
Valery	22 773 \pm 4212	77.8 \pm 10.2	2110 \pm 815	116.3 \pm 12.7	1909 \pm 277	59.2 \pm 8.9
Yangambi km5	32 868 \pm 4212	97.1 \pm 10.2	4074 \pm 815	133.8 \pm 12.7	2658 \pm 277	83.1 \pm 8.9
Agbagba	18 054 \pm 4864	88.8 \pm 11.8	2821 \pm 942	83.0 \pm 14.6	1766 \pm 320	43.9 \pm 10.3
Obino l'ewai	15 015 \pm 4212	84.0 \pm 10.2	1796 \pm 815	98.8 \pm 12.7	1322 \pm 277	38.0 \pm 8.9
Fougamou	18 168 \pm 4212	82.8 \pm 10.2	2173 \pm 815	83.3 \pm 12.7	1635 \pm 277	56.2 \pm 8.9
Cardaba	38 049 \pm 4212	142.8 \pm 10.2	7659 \pm 815	81.0 \pm 12.7	2454 \pm 277	77.4 \pm 8.9
TMPx 1658-4	30 030 \pm 4212	107.8 \pm 10.2	2973 \pm 815	97.3 \pm 12.7	1623 \pm 277	47.2 \pm 8.9
TMPx 548-9	22 678 \pm 4212	88.0 \pm 10.2	2762 \pm 815	113.5 \pm 12.7	1843 \pm 277	54.3 \pm 8.9
p	0.05	0.05	0.01	ns	0.05	0.05

LA: leaf area, PH: plant height, CW: corm weight, NR: number of cord roots, LR: cord root length, DW: root dry weight.
ns: nonsignificant.

lateral root (Table 5). In contrast, there was no significant effect of the genotype on the characteristics of first-order lateral roots. 'Valery', 'Cardaba' and 'TMPx 1658-4' had poor first-order lateral root development but the high variability within a genotype may explain why the differences between genotypes were not statistically significant.

Total first-order lateral root development for the mother plant was estimated by multiplying the number and length of first-order lateral roots on a 1-cm section of zone 3b with the total length of zone 3. The length of first-order lateral roots might have been over-estimated as zone 3a was regarded as a zone with mature lateral roots. The number and length of second-order lateral roots on a 1-cm section of first-order lateral roots were multiplied with the estimated length of first-order lateral roots (Table 5). The estimated total root length of mother plants ranged from 297 m to 1529 m and comprised cord root length and estimated first-order and second-order lateral root lengths. According to the ANOVA analysis, the genotype had no significant effect on the estimated root traits. 'Yangambi km5' and 'Fougamou' had the longest roots. Even though 'Fougamou' had a relatively low proportion (60%) of its cord roots covered with lateral roots (Table 4), its lateral roots were well developed (Table 5), resulting in a high total estimated root length.

The genotype had no significant effect on the proportion of first-order lateral root length, second-order lateral root length and cord root length to the total estimated root length. The second-order laterals made the largest contribution to total root length, 70 to 87%, compared to 1.7 to 5.3% for cord roots (Figure 2).

Table 4. Length of cord root morphological zones measured on the mother plants of 8 genotypes 12 weeks after planting (mean ± s.e.).

Genotype	Zone 1 & 2 (cm)	Zone 3a (cm)	Zone 3b (cm)	Zone 4 (cm)	LCR (m)	CR (%)
Valery	20.0±3.5	46.9±12.5	48.0±13.0	15.8±8.8	14.6±3.3	74.7±7.8
Yangambi km5	19.6±3.5	46.5±12.3	54.0±12.7	6.9±8.7	20.5±2.9	78.4±6.8
Agbagba	15.9±3.1	55.2±10.7	45.4±10.6	5.6±7.9	14.4±3.9	80.0±9.1
Obino l'ewai	18.0±3.0	39.9±10.4	47.4±10.6	12.7±7.5	6.0±2.6	64.8±6.0
Fougamou	20.7±3.3	41.5±11.5	49.9±11.8	24.3±8.2	11.9±2.9	60.2±6.9
Cardaba	20.4±3.5	40.9±12.6	71.2±13.0	20.7±8.8	18.5±3.3	78.1±7.8
TMPx 1658-4	15.8±3.4	36.3±11.9	35.6±12.2	8.5±8.4	12.2±3.0	74.4±7.2
TMPx 548-9	15.5±3.1	29.7±11.0	51.6±11.2	12.5±7.8	11.7±2.7	73.3±6.4
p	ns	ns	ns	0.05	-	-

Zone 1 & 2: Elongation zone and bare distal zone without lateral roots, Zone 3a: zone with growing lateral roots, Zone 3b: zone with mature lateral roots, Zone 4: bare proximal end of the cord root, LCR: length of cord root with lateral roots (i.e. length of zone 3a & 3b), CR: percentage of cord root length with lateral roots.

ns: non significant.

-: not available.

Although they contributed to >94% of the total root length, lateral roots accounted for only 14 to 27% of the total dry weight. This illustrates the fineness of the lateral roots compared to the thicker cord roots.

No significant correlations were observed between the first-order and second-order lateral root traits on one hand and the aerial, corm and cord root parameters on the other (Table 2). However, mostly significant positive correlations were observed between individual lateral root traits (Table 2). For example, the number and length of first-order laterals measured on a 5-cm section of zone 3b were respectively correlated with the number and length of second-order laterals observed on a 1-cm section of zone 3b first-order lateral root. This indicates that the development of second-order lateral roots depends on the development of first-order lateral roots. The number of first-order lateral roots was not correlated with the diameter of the cord root.

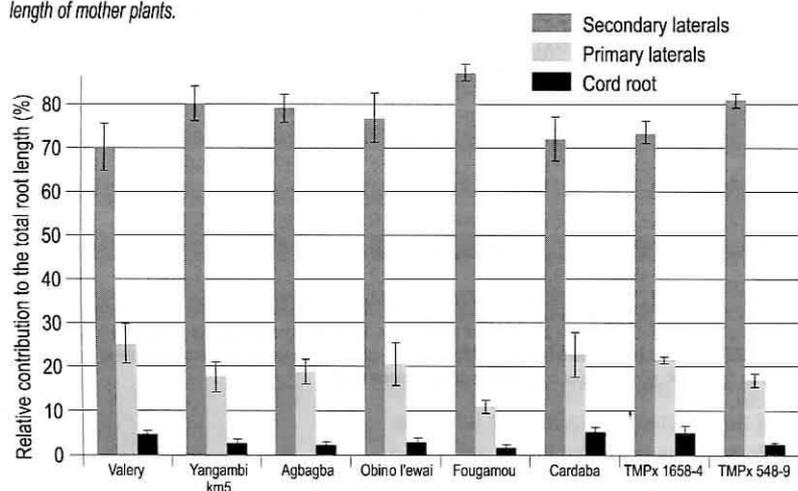
Table 5. Characteristics of first-order and second-order lateral roots measured on the mother plants of 8 genotypes 12 weeks after planting (mean ± s.e.).

Genotype	PL-NR	ePL-NR	PL-LR (cm)	ePL-LR (m)	SL-NR	eSL-NR	SL-LR (cm)	eSL-LR (m)	eTOT-LR (m)
Valery	13.0±5.6	2639±2374	54.9±14.6	118±48	7.4±1.9	92 177±62 256	3.1±1.5	466±320	610±359
Yangambi km5	17.6±5.5	5742±2084	62.3±14.5	206±43	11.1±1.9	246 648±55 097	5.7±1.5	1295±282	1529±315
Agbagba	17.6±5.0	8115±2794	36.9±13.5	133±57	9.9±1.7	144 053±73 237	5.0±1.3	438±377	596±422
Obino l'ewai	19.5±4.7	1598±1875	64.8±12.7	61±39	7.8±1.6	43 200±49 889	4.2±1.2	224±254	297±283
Fougamou	24.2±5.8	4651±2132	68.2±15.1	145±44	12.4±2.0	201 625±56 143	8.5±1.5	1342±288	1511±322
Cardaba	11.5±5.4	3359±2401	41.9±14.2	128±49	7.1±1.8	101 340±63 496	3.4±1.4	498±325	661±363
TMPx 1658-4	13.2±5.1	2323±2212	41.5±13.5	62±45	5.3±1.7	33 166±58 454	3.2±1.3	278±299	364±334
TMPx 548-9	18.8±4.9	4177±1992	68.3±13.3	132±41	9.1±1.7	135 384±52 890	4.9±1.3	645±270	796±301
p	ns	ns	ns	ns	0.01	ns	0.05	ns	ns

PL-NR: number of first-order lateral roots on a 5-cm section of zone 3b, ePL-NR: estimated total number of first-order lateral roots, PL-LR: length of first-order lateral roots on a 5-cm section of zone 3b, ePL-LR: estimated total length of the first-order lateral roots, SL-NR: number of second-order laterals on a 1-cm section of a zone 3b first-order lateral root, eSL-NR: estimated total number of second-order lateral roots, SL-LR: length of the second-order laterals on a 1-cm section of a zone 3b first-order lateral root, eSL-LR: estimated total length of the second-order lateral roots and eTOT-LR: estimated total (cord and lateral) root length.

ns: non significant.

Figure 2. Relative proportion (%) of cord roots, first-order lateral roots and second-order lateral roots to the total root length of mother plants.



Discussion

The size of the root system was related to corm size and aerial growth, confirming observations made by Blomme and Ortiz (1996) and Blomme (2000) who reported strong relationships between the aerial parts of the plant, corm and cord root system growth during the vegetative stage.

Compared to the present study, the densities of first-order and second-order lateral roots were more homogenous under hydroponic conditions (Swennen *et al.* 1986). In addition, significant differences between genotypes were detected for both first-order and second-order lateral roots characteristics. It could be that hydroponic conditions lower the variance within a genotype and are more suitable to assess variability in lateral root growth between genotypes.

The length of zone 1 and 2 observed in this study confirms observations made by Riopel (1966) and Laville (1964). Lecompte *et al.* (2001) found a positive relationship between daily root growth rate and the length of these zones. The values of 15 to 20 cm observed in the present study were found on fast-growing cord roots (>2 cm/day) in their study.

Under hydroponic conditions, the proportion of a cord root occupied with lateral roots ranged from 94 to 97% (Swennen *et al.* 1986), which is larger than in this study (60 to 80%), and is most probably due to the excellent condition of the roots and optimal fertilization.

Swennen *et al.* (1986) compared plants of the same height (154 cm) and estimated that the total length of the root system (root hairs excluded) was 9.2 km for 'Agbagba' (a plantain) and 41.3 km for 'Robusta' (a dessert

banana). In our study, 'Cardaba', which is the only genotype with a similar height, had an estimated total root length of only 0.66 km.

Under hydroponic conditions, the proportion of cord roots to the total estimated root length ranged from 0.32 to 1.45% (Swennen *et al.* 1986), a result which indicates more developed lateral roots compared to field conditions. Swennen *et al.* (1986) also reported a shift in the proportion of total root length from second-order lateral roots in favour of first-order laterals and from first-order lateral roots in favour of cord roots under less favourable conditions (Wecks 1982, Swennen *et al.* 1986), a result which is confirmed by our observations.

Swennen *et al.* (1986) reported that the capacity to form second-order lateral roots was greater in dessert bananas than in plantains. The proportion of first-order and second-order lateral roots to total root length were respectively 53% and 46% in plantain compared to 22% and 77% in dessert bananas (Swennen *et al.* 1986). The same authors postulated that the lower total root length of plantains, especially due to the lower proportion of second-order lateral roots, could be a contributing factor to the lower productivity of plantains compared to dessert bananas. On the contrary, in the present study, the contribution of first-order and second-order lateral roots to the total root length was similar for the plantains ('Agbagba' and 'Obino l'ewai') and the dessert bananas ('Valery' and 'Yangambi km5').

Conclusion

Plants growing under field conditions were observed to have a smaller total root length than plants growing in hydroponics. The proportion of lateral roots to the total root length was higher for plants growing under hydroponic conditions. In addition, lateral root growth was more homogenous under hydroponic conditions, making it easier to detect genotypic effects on lateral root traits.

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Agronomic performance and resistance to black leaf streak of the hybrid 'CRBP-39'

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Plantain, one of the main food sources for the people of central Africa, is subject to numerous production constraints due largely to numerous pests and diseases, including black leaf streak disease (BLSD, caused by the ascomycete fungus *Mycosphaerella fijiensis* Morelet). This is regarded as the most serious leaf spot disease of bananas throughout the world (Pasberg-Gauhl *et al.* 2000) and can

cause very heavy yield losses depending on the epidemiological situation (Stover 1983, Fouré *et al.* 1984, Mobambo *et al.* 1993). In commercial plantations, its control requires the intensive use of fungicides which are very harmful to the environment and which increase production costs. Hence it is impossible to use this method in low-income smallholdings. As cultural techniques such as deleafing do not provide effective control, the development

Evaluation