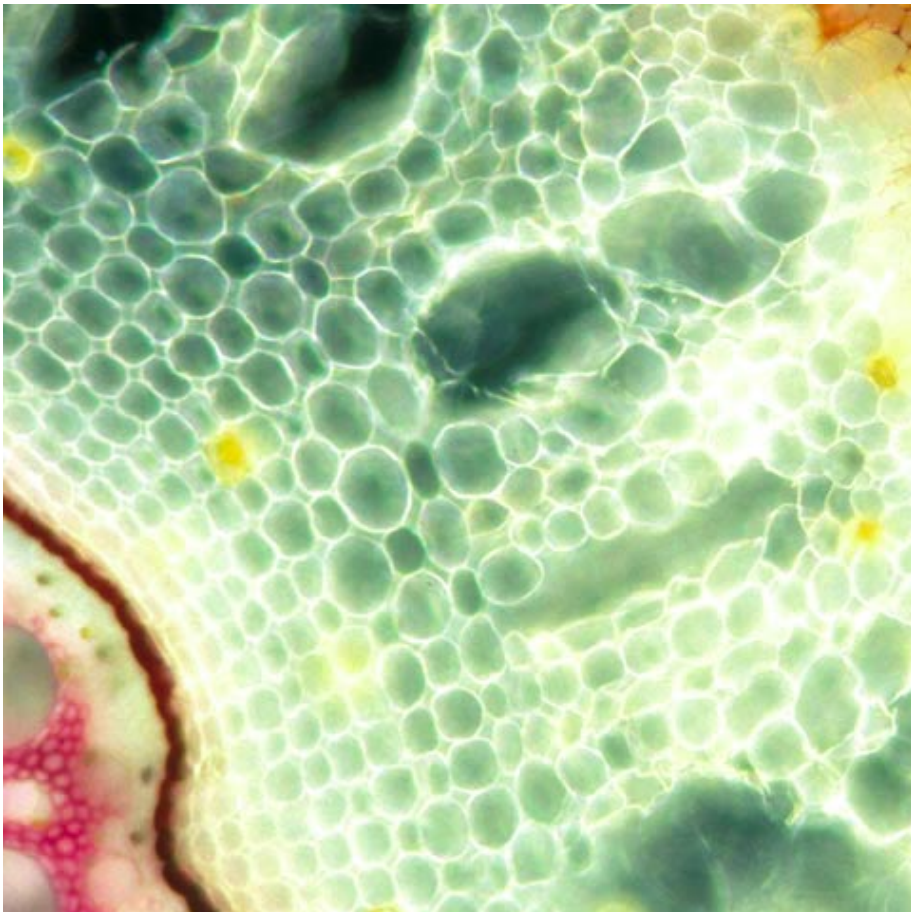
Banana Root System: towards a better understanding for its productive management

Proceedings of an international symposium held in San José, Costa Rica, 3-5 November 2003

Sistema Radical del Banano: hacia un mejor conocimiento para su manejo productivo

Memorias de un simposio internacional, San José, Costa Rica, 3-5 noviembre 2003

David W. Turner and Franklin E. Rosales, editors



INIBAP – International Network for the Improvement of Banana and Plantain

The mission of INIBAP is to sustainably increase the productivity of banana and plantain grown on smallholdings for domestic consumption and for local and export markets.

The Programme has four specific objectives:

- To organize and coordinate a global research effort on banana and plantain, aimed at the development, evaluation and dissemination of improved cultivars and at the conservation and use of *Musa* diversity
- To promote and strengthen collaboration and partnerships in banana-related research activities at the national, regional and global levels
- To strengthen the ability of NARS to conduct research and development activities on bananas and plantains
- To coordinate, facilitate and support the production, collection and exchange of information and documentation related to banana and plantain.

INIBAP is a network of the International Plant Genetic Resources Institute (IPGRI), a Future Harvest centre.

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*MUSA*LAC was created under the umbrella of FORAGRO on 6 June 2000 in Cartagena de Indias, Colombia, following the signing of a Constitution Agreement. *MUSA*LAC is composed of 15 national research and development institutions representing their respective country (Bolivia, Brazil, Colombia, Costa Rica, Cuba, Ecuador, Honduras, Jamaica, Mexico, Nicaragua, Panama, Peru, Puerto Rico, Dominican Republic and Venezuela) and 4 regional/international institutions (CATIE, CIRAD, IICA and INIBAP). The main objective of *MUSA*LAC is to increase the productivity and competitiveness of the plantain and banana commodity chain through scientific and technological development by strengthening national research and development programmes, facilitating exchanges between stakeholders and prioritizing and coordinating actions in Latin America and the Caribbean. *MUSA*LAC is led by a Steering Committee composed of one representative from each member country; one President and two Vice-presidents and an Executive Coordinator, which is INIBAP-LAC, headquartered at CATIE in Turrialba, Costa Rica.

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- To increase banana productivity at a minimum environmental risk.
- To promote programmes on cost reduction
- To provide services in research, technical assistance and information on prices and markets.
- To facilitate an equal relationship between national producers and export companies.
- To establish jointly with the Costa Rican Government, banana policies to help maintaining the industry on the long term.
- To centralize banana information to promote and facilitate the participation of the banana sector in research and technological development of the banana sector.

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Cover illustration: Transverse section of a mature root of 'Williams' (*Musa* AAA, Cavendish) showing aerenchyma development in the mid cortex. (Credit: Michael W. Shane).

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La Red Internacional para el Mejoramiento del Banano y el Plátano (INIBAP) y la Corporación Bananera Nacional (CORBANA, S.A.), organizadores del Symposium Internacional "Sistema radical del banano: hacia un mejor conocimiento para su manejo productivo", agradecen a los patrocinadores y colaboradores quienes, con su contribución, hicieron posible el desarrollo de este evento tan importante para el beneficio del sector bananero mundial.

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Preface

The fruit of bananas and plantains (*Musa* spp.) being delicious and the aerial parts of the plant spectacular, it is easy to overlook the root system that supports them. Many scientists have commented on our limited knowledge of banana and plantain roots. However, those who work on root systems, especially in plantations, are aware that a huge effort is needed to extract even a small piece of information.

This volume contains papers presented during the International symposium on the 'Banana Root System: towards a better understanding for its productive management' held in San José, Costa Rica, in November 2003. Although root health is a universal preoccupation, the idea to hold a symposium on the topic follows from concerns expressed by the banana producing/exporting sector, especially Romano Orlich, President of the National Banana Corporation from Costa Rica. CORBANA asked INIBAP to work with them in exploring solutions to the problems of the banana root system. This Symposium shows that the private and public sector can share a research agenda.

The objective of the symposium was to present the state of the art knowledge on the functioning of the *Musa* root system and its interrelationships with micro-organisms and pests, and to propose ways to improve root health. The demand for this kind of information is increasing because of the need to prevent deterioration of root health, which contributes to a steady decline in production in many commercial farms of Latin American and the rest of the world. The papers present work done on cells as well as whole plants, and short-term studies as well as ones that cover many years and multiple locations. An appreciation of these differences in scale is important because knowledge gained about root tissues in short-term experiments, for example, needs to be integrated with our knowledge at higher levels of plant organization and over longer time scales. Similarly, laboratory results on root structure and function, and on roots and microbes, need to be compared with results from field experiments. Only by facilitating interactions between people working at different scales, will we increase our understanding of banana and plantain root systems, in the laboratory as well as in the field. This is exciting in its own right, and provides the basis for sound management decisions needed to sustain our markets and our environment.

Work on banana and plantain root systems is usually done within the broader international framework of research on root systems in plants. This is a valuable approach. Good progress is being made on evaluating the impact of the pests that attack the root system. We are learning about the importance of having a soil that is amenable to management, such as drainage, irrigation and fertilization. We should not push this knowledge aside as we explore other aspects of root performance. On the other hand, we are making slow progress in understanding the role of genetics in the functioning and architecture of the banana root system. Indeed, we have yet to ask the question: what sort of root system do we want for banana plants? The answer may be somewhat different, according to the local situation, but there will be some general principles as the plants will always need water, nutrients and being able to stay upright! These answers may help us see clearly what is important and help us focus on how best to achieve our objectives. In the final session of the symposium, the participants produced an outline on the way ahead. These points reflect a consensus following the diversity of ideas and information presented during the symposium.

We would like to thank the contributing authors for their insights into the problem, and INIBAP and CORBANA for bringing us together and making this publication available worldwide. We hope that these proceedings will stimulate readers into exploring how this knowledge might be translated into improved management practices.

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Prefacio

El fruto de los bananos y plátanos (*Musa* spp.) es delicioso y su parte aérea espectacular, por lo que es fácil olvidarse del sistema radical que lo sostiene. Existen muchos comentarios sobre el limitado conocimiento acerca de las raíces de banano y plátano y de su ambiente. Sin embargo, quienes trabajan con los sistemas radicales, especialmente en la plantación, conocen el enorme esfuerzo que generalmente es necesario para extraer aún una pequeña cantidad de información.

Este volumen contiene los trabajos presentados en el Simposio internacional "Sistema Radical del Banano: hacia un mejor conocimiento para su manejo productivo", realizado en San José, Costa Rica en noviembre de 2003. Aún cuando la salud de las raíces es una preocupación generalizada, la idea de realizar un simposio sobre este tema surgió como resultado de las inquietudes expresadas por el sector productor/exportador de banano, especialmente del señor Romano Orlich, Presidente de la Corporación Bananera Nacional de Costa Rica. CORBANA solicitó a INIBAP trabajar juntos para explorar soluciones a los problemas del sistema radical del banano. Este Simposio muestra que los sectores público y privado pueden compartir una agenda de investigación.

El objetivo del simposio fue presentar el conocimiento sobre el estado del arte del funcionamiento del sistema radical del género Musa y sus interrelaciones con microorganismos y plagas y proponer vías para mejorar la salud de la raíz. La demanda por este tipo de información aumenta cada vez más, debido a la necesidad de prevenir el deterioro en la salud del sistema radical que contribuye a una disminución constante en la producción de muchas fincas comerciales en América Latina y el resto del mundo. Las presentaciones cubren un amplio rango de niveles, desde células hasta plantas completas, y desde estudios de corto plazo hasta aquellos que reúnen información recolectada por muchos años y en muchos lugares. La apreciación de estas diferencias es importante ya que, por ejemplo, el conocimiento obtenido sobre los tejidos de las raíces en experimentos de corto plazo, debe ser integrado con el conocimiento a niveles más altos de organización en la planta y sobre escalas mayores de tiempo. De igual manera, el conocimiento obtenido en el laboratorio sobre la estructura y función de la raíz, o sobre las raíces y los microbios, debe ser comparado con los resultados obtenidos a nivel de campo. La única forma de incrementar nuestro conocimiento sobre los sistemas radicales del banano y el plátano, tanto en el laboratorio como en el campo, es facilitar las interacciones entre personas que trabajan a diferentes niveles. Esto es fascinante en sí mismo y además suministra las bases para tomar decisiones de manejo correctas, necesarias para mantener nuestros mercados y nuestro ambiente.

El trabajo sobre los sistemas radicales de banano y plátano se realiza usualmente como parte del amplio marco internacional de la investigación en sistemas de raíces de plantas. Este es un enfoque valioso. Se han logrado progresos significativos en cuando a evaluar el impacto de las plagas que atacan el sistema radical. Estamos aprendiendo sobre la importancia de tener un suelo sensible al manejo, tal como el drenaje, la irrigación y la fertilización. No debemos dejar este conocimiento de lado a medida que exploramos otros aspectos del desempeño de la raíz. Por otra parte, el progreso obtenido en el conocimiento del papel que juega la genética en el funcionamiento y la arquitectura del sistema radical del banano es poco. Efectivamente, aún debemos preguntarnos: ¿que clase de sistema radical queremos para las plantas de banano? La respuesta puede ser un tanto diferente, dependiendo de la situación local, pero hay algunos principios generales ya que las plantas siempre necesitarán agua, nutrientes y la habilidad de sostenerse en pie!. Estas respuestas pueden ayudarnos a ver claramente lo que es importante y a enfocarnos en cómo alcanzar nuestros objetivos. Durante la sesión final del simposio, los participantes elaboraron un perfil de lo que resta por hacer. Estos puntos representan el consenso de la diversidad de ideas e información presentados en el simposio.

Deseamos agradecer a todos los autores contribuyentes por su conocimiento del problema, a INIBAP y a CORBANA por reunirnos a todos y de esa forma hacer disponible esta publicación a escala mundial. Esperamos que estas Memorias estimularán a los lectores a explorar de que manera éste conocimiento podría traducirse en prácticas mejoradas de manejo.

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Objective

Present and discuss actual knowledge about and new insights into the functioning of the *Musa* root system, the interrelation with micro-organisms and pests, and propose alternatives to improve root health.

Objetivo

Presentar y discutir el conocimiento actual y nuevos puntos de vista sobre el funcionamiento del sistema radical de *Musa*, la interrelación con microorganismos y plagas, y presentar alternativas para mejorar la sanidad del sistema radical.

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1

Banana root deterioration and impacts on production

Deterioro radical del banano y sus impactos en la produccion

The problem of banana root deterioration and its impact on production: Latin America's experience

Carlos A. Gauggel[1], Francisco Sierra[2] and Gloria Arévalo[1]

Abstract

The deterioration of the banana root system and its effect on production is due to climatic, edaphic (physical and chemical) and biological factors. There are two kinds of root deterioration processes: 1) a fast one with accelerated collapse of the root system (days to months) due to site specific characteristics such as limited effective depth of soil, very high sand, gravel or clay content, high water table, and high soluble salt and sodium content; and, 2) a slow and gradual collapse which is due to the degradation of soil physical and chemical conditions, deterioration of soil biological activity, inefficient drainage (design, construction, management and maintenance) and poor crop management practices (disease control, nematodes, insects and weeds). The interaction between rainfall and topography ranks among the main climatic factors that can cause a fast or gradual collapse of the banana root system. On the other hand, corm rot (due to several causes), nematodes, and decrease in the soil biological activity are identified among the most important biological factors. The various physical, chemical and biological factors that cause deterioration of the root systems in Latin America are examined from the production point of view and experience of the authors. The application of new concepts and procedures (Soil Quality and Health) will make it possible to quantify the impact of the soil physical, chemical and biological properties in root performance and in banana production. This will also make it possible to determine, with precision, the production potential of the soils of the various banana zones and to manage them within the concepts and goals of sustainable production. The need to undertake more basic and applied research on the various factors that determine banana root performance are highlighted in order to design and implement more economically efficient production practices.

Resumen - La problemática del deterioro radical del banano y su impacto en la producción: Experiencia en América Latina

El deterioro del sistema radical del banano y su efecto adverso en la producción se debe a factores climáticos, edáficos (físicos y químicos) y biológicos. Se presentan dos tipos de deterioro del sistema radical: 1) uno rápido con colapso acelerado del sistema radical (días a meses) debido a condiciones especificas al sitio tales como limitada profundidad efectiva del suelo, excesos de arena, grava o arcilla, nivel freático alto, y elevados contenidos de sales solubles y sodio; 2) un deterioro lento y gradual debido a la degradación paulatina de las propiedades físicas y químicas del suelo, deterioro de la actividad biológica, sistemas de drenajes deficientes (diseño, implementación, manejo y mantenimiento) y prácticas pobres de manejo del cultivo (control de enfermedades, nemátodos, insectos y malezas). Entre los factores climáticos se debe destacar la interacción de la precipitación y la topografía, la cual resulta en condiciones que pueden generar el colapso rápido o paulatino de la raíz. Por otro lado, entre los biológicos se destacan la podredumbre de los cormos (por diferentes causas), nemátodos y disminución de la actividad biológica del suelo. Las propiedades físicas, químicas y biológicas que comúnmente resultan en deterioro del sistema radical del banano en las diferentes áreas productoras de banano de América Latina son examinadas a la luz de la experiencia práctica de los autores realzando su impacto en la producción. La aplicación de nuevos conceptos y procedimientos (Calidad y Salud de Suelos) permitirán cuantificar el efecto de las propiedades físicas, químicas y biológicas del suelo en el desempeño de las raíces y en la producción. Esto también permitirá determinar con precisión el potencial productivo de los suelos de las diferentes

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zonas bananeras y manejarlos dentro del concepto de producción sostenible. Se realza la necesidad de hacer más investigación básica y práctica en los diferentes factores que determinan el desempeño radical para poder diseñar e implementar prácticas de producción más económicamente eficientes.

Introduction

It can be stated without a doubt that climate and soils determine the success of banana production enterprises. In most cases, climatic factors are easier to determine; however, the soil component is much more difficult to characterize due to the variation of the soil morphological, physical and chemical properties within a given area (large or small) under the same climate. The effect on banana root performance of the various components of these two factors has not been fully understood mainly due to the interactions that occur among them. However, the effect of some soil properties on root performance has been understood to a considerable extent after the experience gained during the great expansion of the banana industry in the 1990s.

From an historical point of view, the understanding of the banana soil-plant relationship can be divided into periods before and after 1990. Before 1990, the banana industry in general was very respectful of soil quality; only soils with optimum morphological, physical and chemical conditions were placed under banana production. However, after 1990 the lack of suitable soils for banana production, very high prices for the few available soils, decisions made without adequate soil studies, and dangerous speculation typical of new and unknown markets, led many investors (large and small) to develop areas with undesirable soil conditions. This resulted in deterioration of the banana root systems in those areas, some gradual and some fast. In most cases these "experiments" associated with unfavorable market conditions had disastrous consequences for many investors. However, it also generated the need to better understand the causes and interrelations of the climate-soil-root complex in banana production. The level of knowledge of such a complex problem has increased significantly in the last thirteen years as a consequence of past experiences and the advent of new and promising technologies. Thus, the objective of this paper is to undertake a general review of the production experience in Latin America as a consequence of banana root system deterioration in light of the lessons learned from the past and the opportunities offered by the future.

Causes of banana root system deterioration

In general, the causes of banana root system deterioration are the same as those determining yield. They can be classified as climatic, soil-related, and biological (diseases and insects affecting banana roots). The degree to which root deterioration occurs will be determined by the intensity of the predominant factors involved under the specific site conditions. In this way, the deterioration of the banana root system can be slow or fast - frequently too slow to be detected immediately.

Factors that cause a fast deterioration of the banana root system

These factors are usually directly related to climatic conditions or soil properties and have drastic negative impacts on the banana plant. They are of major geographic importance in Latin America and strongly influence the banana root system (Table 1).

Table 1. Important factors involved in banana root deterioration and poor development

Factors	Effects in the banana root system
Soil factors	
Restricted soil effective depth	Weak development of the root system, shallow and thin roots
Extreme textures (massive clay, sand and burden)	Weak root system, many dead roots, few live roots
Poor internal soil drainage.	Short, weak and rotten roots, abundant dead roots
Soil compaction inherited from previous land uses	Short, shallow and horizontal roots
High exchangeable and soluble sodium contents	Few short functional roots with frequent injuries; many dead roots
High soluble salt concentrations	Similar to above
Climatic and topographic factors	
High water table	Many dead roots, shallow root system
Frequent water logging of the upper soil horizons (rain and poor surface drainage)	Many dead roots, many accidental roots, superficiaroot system
Frequent flooding	Many dead and rotted roots, many adventitious roots
Phytopathological factors	
Rotten roots	Many dead roots, also corms with lesions

Climate and topography

Rainfall is the most important factor involved in banana root system deterioration. It interacts with topographic factors that may result in severe adverse conditions for banana root development. The most important of the possible interactions are flooding, puddles after rains, shallow water tables (permanent or frequently fluctuating), and areas too close to sea level to be effectively drained.

In areas with rainy and humid climates, whose soils have high organic matter contents with high water retention, bananas generally experience root and corm rot. This results in a collapse of the plantation during the first crop and in an irreversible deterioration of the root system. Such cases are common on the Atlantic coasts of Costa Rica, Panama and Colombia (specifically the Urabá zone) in areas previously used either for pasture, secondary forest or left fallow for long periods.

Soils

The fast deterioration of the banana root system takes place when the soil has one or more of the following characteristics:

1. More than 60% coarse fragments by volume, high sand content (loamy sand or sand of coarse and very coarse size), very high clay content without soil structure (massive) or with coarse and very coarse blocks and prisms.
2. Effective soil depth less than 30 cm, restricted by continuous rock, massive clay or a shallow permanent water table.
3. High soluble salt concentrations with electrical conductivity greater than 4 dS/m.

4. High exchangeable sodium (PSI > 30%) and soluble sodium (RAS > 30) contents.

It is important to point out that these conditions can be devastating for the plant depending upon the characteristics of rainfall and cultural practices. Severe dehydration of the plant occurs in areas with an intense and long dry season. This can be worse in plantations with poor irrigation systems on light-textured soils. On the other hand, soils with heavy, massive clays at shallow depths cause the quick collapse of the root system in climates with intense and long rainfall episodes. The damage is more severe if the drainage systems (surface and subsurface) are deficient. High soluble salt content is devastating for banana root systems in areas where evapotranspiration exceeds rainfall most of the year and water quality and availability are poor, such as in the banana zones of Santa Marta, Colombia, the Dominican Republic and the Southern Maracaibo Lake of Venezuela. In several cases, exceptionally good climatic conditions or costly efforts to supply excess irrigation water for leaching of salts, may temporarily delay the collapse. However, when the weather returns to normal or efforts to avoid the problem diminish, the collapse of the roots occurs rapidly. Great efforts to improve this situation are only possible during times of favorable markets. The first half of the 1990s is a good example of this.

Biological factors

Areas with high nematode populations, other banana root parasitic microorganisms and insects can cause fast banana root deterioration, especially when the areas have been previously planted with bananas.

Factors that cause the gradual deterioration of the banana root system

These factors can also be classified as climatic, soil-related (edaphic) and biological with very complex interrelations depending upon specific site conditions. Their impact on yields depends on the intensity at which the limiting factor occurs at the given site (Table 2).

Climatic factors

Extreme climatic conditions (severe drought or heavy rainfall), without effective measures to protect the banana root system, can result in its gradual deterioration. In areas subject to severe drought, the deterioration of the root system is a consequence of either a lack of, or an inadequate, irrigation system and an insufficient supply of good quality water. This condition is very frequent in the Santa Marta banana zone. If these conditions are light to moderate the root system deterioration is gradual; however, under severe conditions the collapse is fast.

In areas with high and fairly even rainfall patterns (Atlantic coasts of Costa Rica, Panama, and Urabá, Colombia) the deterioration of the banana plant root system is gradual. Such conditions occur where there is an inefficient drainage system, the depth to the water table is less than 0.9 m (this condition may occur also in dry areas) or perched water tables within the upper 0.9 m as a consequence of impermeable soil horizons. This latter condition is very common in high rainfall areas. It can also occur in dry areas as a consequence of applying irrigation water at higher volumes than required.

Table 2. Important factors involved in the gradual deterioration on the banana root system.

Factor	Effect in the root	Potential reduction of maximum performance (%)
Soil factors		
Organic matter loss	Poorly developed root system	Variable
Soil erosion	Poorly developed root system	Variable
Soil salinization by saline irrigation water	Poorly developed root system with injuries	30-80
Acidification by excessive fertilizer use	Poorly developed root system with injuries	10-50
Loss due to porosity and soil compaction	Few, short and thin roots	10-60
Low fertilizer rates	Poorly developed root system	Variable
High permanent and perched water tables	Short, rotten roots and high root mortality	10-60
Poor surface drainage	Rotten and high mortality and adventitious roots	10-70
Nutrient imbalances	Poorly developed root system	Variable
Inversion of soil profile	Poor developed root system, adventitious roots	0-50
Biological factors		
Increase in nematode population		70
Decrease in soil micro and macroorganism populations	Poorly developed root system	Variable

During long and intense rainfall (cold fronts in the Atlantic coasts of Central America), despite adequate drainage systems, the amount and duration of rainfall saturates the soil causing anaerobic conditions in the root zone. Such conditions result in the formation of abundant adventitious roots, deterioration of the underground root system, and temporary reductions in yield and fruit quality.

Soil factors

Effective soil depth and soil texture

Limitations in effective soil depth between 30 and 90 cm usually result in gradual deterioration of the root system depending upon what constitutes the limiting physical barrier (coarse fragments, sand or massive clay) and the texture of the horizon itself. If massive heavy clay is limiting, rainfall or excessive irrigation can cause temporary water logging in the root zone resulting in damage to the root system. On the other hand, predominantly sandy textures result in frequent water deficits or nutrient leaching that in turn, weaken the root system.

Soil erosion, organic matter loss and soil compaction

To varying degrees, the soils of the banana farms are subject to water erosion. The main causes are high intensity rainfall and sprinkler irrigation (under and above tree). Soil

cover is of paramount importance to prevent significant soil losses. Weeds under proper control can be a great ally in this task. Soil erosion causes substantial losses of soil organic matter, since soil colloids (humus and clays) are the most vulnerable to loss. Compaction of the topsoil horizon is an almost unavoidable process due to frequent human traffic for various agricultural practices. Such compaction never reaches deeper than 15 cm, although, the loss of porosity at the soil surface reduces oxygen supply and soil infiltration rate. These processes take place slowly over months, and even years, and the effect is not noticeable in the short-term. Likewise, root deterioration takes place gradually over time resulting in weak root systems that eventually affect yields. Depending on the time elapsed, and the intensity of the causal factor, the reduction in yield can be severe.

Soil management practices (fertilization, irrigation and drainage)

The production experience indicates that poor agricultural practices can cause deterioration of the banana root system. Inadequate (too low or too high) and inefficient irrigation and drainage should be highlighted. These factors cause a significant deterioration of the banana root system and in general are a consequence of restricted budgets, the lack of proper diagnostic techniques and poor maintenance of the irrigation and drainage systems. Inadequate fertilization practices cause nutritional deficiencies and imbalances that, in turn, also cause root deterioration.

Inversion of the soil profile

The frequent maintenance of the drainage system requires spreading the sediment dug out from the bottom of drainage canals on the soil surface. Most of this sediment comes from the walls of the drainage canals and the lower soil horizons. Over time, the sediment spread on the surface reaches significant thickness, greater than 50 cm. In cases where the sediment is too clayey or sandy, soil quality diminishes substantially. In clayey soils the infiltration rate decreases substantially as a result of the loss of porosity in this new soil horizon with intense human traffic. This condition presents an obstacle to the flux of water and gases between the atmosphere and the soil and also for water infiltration, thus aggravating surface drainage conditions (Table 2).

Biological factors

Nematodes

Increases in nematode population and other banana root pathogens are, without a doubt, one of the most critical factors affecting the gradual deterioration of the banana root system. Such conditions can become chronic and very serious if not managed. To maintain a vigorous root system in banana plantations requires careful pest and disease control, taking into consideration innovative alternatives that promote biological diversity and healthy activity of beneficial microorganisms in the soil environment.

Beneficial soil microorganisms

The excessive, but sometimes necessary, use of pesticides, poor irrigation water quality, excessive use of fertilizers, soil erosion, loss of soil organic matter and soil compaction, all upset the soil population of beneficial microorganisms. This is a field that is recognized, at least conceptually, by the banana industry to be very important but has lacked scientific research in banana plantations. It is very important for the

banana industry to undertake vigorous research in this area to determine the effect of the decrease and changes in the populations of soil organisms, especially micro-organisms, on yields.

Interrelation between production and the deterioration of the banana root system

Soil physical properties

The production experience through time indicates that those physical properties that limit the development and performance of the banana root system, have considerable impact on yields and in many instances lead to production lower than that required for profitable returns (Table 3). As previously indicated, the intensity of the specific limiting factor will determine the crop yield. Some of these limiting factors cannot be significantly improved, for example soil texture. In other cases, however, the improvement will depend on the cause of the limiting factor. For example, effective soil depth can be improved by soil rehabilitation practices. The cost of rehabilitation will depend on the characteristics of the soil-limiting factor (for example, rock, gravel, sand, clay).

Table 3. Common banana crop yields in areas with physical properties that affect the performance of the banana root system. Mean yields for different areas of Latin America.

Physical factors restrictive for banana root development	Mean annual production boxes ha^{-1} $year^{-1}$
Effective soil depth	1200-2000
Texture	1100-2200
Shallow soil compaction	1200-1800
Low available water	1000-1900
Poor soil internal drainage	900-1700
Flooding	1200-2000

Soil chemical properties

Of the range of chemical properties that restrict the development and performance of banana roots, the best understood are the percentage of exchangeable sodium, the sodium absorption ratio and the soluble salt content. These conditions generally occur in areas where evapotranspiration exceeds rainfall significantly, as in the banana zones of Santa Marta, Colombia, some areas of the Dominican Republic or where elevation above sea level and the effect of tides do not allow efficient leaching of soluble salts and sodium. In the cases where the concentrations of soluble salts and sodium are high enough, the collapse of the banana root system is very fast; these areas are usually abandoned after the first few crops. Some small areas that are affected by high soluble and exchangeable sodium occur within large non-affected areas, and they are kept under production. Such areas have low yields and are kept under production at a very high cost and constitute a burden for the farm that contains them.

Areas with soils with high iron and manganese concentrations and exchangeable aluminum usually have low yields (Table 4). Field observations indicate short and thin roots with dark brown and black lesions on the epidermis. Whether this is a direct effect of elemental toxicity on the roots or the effect of interactions with multiple factors, has not been determined since the soils with these characteristics are very low in phosphorus, cations, zinc and boron. In most cases, areas with these characteristics are kept under production at high cost. Lime and dolomite applications have given partially effective results, probably due to application rates that are too low for the soil requirements.

Table 4. Common banana plantation yields in areas severely affected by soil chemical factorsthat affec root performance. Average yield ranks for different areas of Latin America.

Restrictive factors for root development	Annual average yield boxes ha^{-1} $year^{-1}$
Exchangeable sodium percentage	900-1500
Soluble salts	700-1200
Soluble iron and manganese	1200-1700
Exchangeable aluminium	1200-1700

Soil quality and health

These are two very important concepts that have been developed in the last decade in Soil Science and without doubt will help us to better understand and quantify the interrelation of the soil properties and the banana root system and production under the perspective of sustainable agriculture.

Soil quality

Soil quality is defined as the capability of the soil to function effectively in the present and future. This integrates physical, chemical and biological soil processes establishing the most relevant for the production of biomass of sustainable quality necessary to generate good plant and animal health (Doran and Parkin 1994). The quantification of the effect of soil in biomass production will depend on the impact of each individual soil property on the performance of the crop of interest. The concept applied by Karlen and Stott (1994), to assign weightings to the relevant soil properties involved in the effects of soil erosion, was applied to evaluate the effect of these properties in the production of crops other than bananas (Barahona 2000). The success of the practical application of these concepts (Fernandez 2003, Cueva 2003, Orellana 2003) and their usefulness to predict the performance of several crops has lead to the application of these concepts to banana cultivation. Considering the soil requirements for the adequate performance of the banana root system and its impact on crop production, weights can be assigned to the key soil characteristics according to their role in banana production (Table 5). Such an approach makes it possible to quantify the effect of these key soil properties and to correlate them with yields in a quantitative manner. According to their importance in

Table 5. Soil quality indices of morphological, physical and chemical soil properties that determine banana production.

Physical /morphological property	Weight (0-1) for plant development	Chemical property	Weight (0-1) for plant development
Effective soil depth	0.70	pH	0.25
Texture	0.60	Base saturation	0.20
Structure	0.35	Organic matter	0.40
Internal soil drainage	0.35	Exchangeable aluminum	0.40
Resistance to penetration	0.35	Soluble salts	0.60
Hydraulic conductivity	0.35	Sodium absorption ratio (SAR)	0.60
Bulk density	0.35	Exchangeable sodium percentage	0.60
Available water	0.50	Cation exchange capacity	0.40

determining banana plant yield, soil effective depth, soil texture, soluble salt concentrations, and the various forms of sodium in the soil, have the highest weights.

Soil health

Besides the soil morphological, physical and chemical characteristics, soil health emphasizes the biological activities in the soil (Roming *et al.* 1996). In Latin America, the application of this concept makes it possible to create a system to develop the potential of the soil that is more adapted to the technical expertise of small farmers, emphasizing the sustainability of the soil resource. These are methods adapted for use by farmers with little formal education and technical knowledge. These methods will allow simple but effective field evaluations of the interrelations between soil and plants in a continuous way at a low cost (Roming *et al.* 1996, the Cornell University, Zamorano and Soil Working Group 2002). With some modifications, these methods will be of much help for banana and plantain producers focusing efforts on the continuous improvement of the root environment.

Conclusions

Banana plantation yield is a direct function of the physical, chemical and biological conditions under which the banana plant roots develop and the interrelations that occur between climate and cultural practices. The deterioration of the banana root system can be quick or slow, often imperceptible in the short term. The intensity of the various factors involved in the deterioration of the banana root system varies throughout the different banana producing zones of Latin America. These conditions are usually the same in the different geographic locations except where climate and elevation above sea level are the main causes.

Among the most important soil factors that result in a fast deterioration of the banana root system are severely restricted effective soil depth, extremes in soil texture (sand or clay) and the soluble salt and sodium and exchangeable sodium concentrations. Lower concentrations of soluble salts and sodium, low nutrient concentrations, poor irrigation and drainage practices, low populations of soil organisms that are beneficial to the soil, high numbers of nematodes, diseases of the root system and poor agricultural practices

(inversion of the soil profile) generally result in slow and progressive deterioration of the banana root system.

The production experience indicates that yields are limited by conditions that weaken the banana root system. Ignoring the optimum conditions for banana plant roots has lead to substantial economic losses, either in an abrupt or progressive manner, depending upon the degree of impact. Given the economic significance of the issues discussed here, it is of paramount importance to conduct more basic and applied research on the interactions among the factors that limit banana root system performance. The practical application of new concepts and technologies will be of great importance to make effective business decisions.

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Research in progress and future perspectives on the root system management

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Abstract

Plant-parasitic nematodes are the most important pests affecting the root system of bananas. Although poly-specific communities are normally found, the burrowing nematode, *Radopholus similis*, is usually the dominant species. Nematode management has mainly relied on the application of chemical granular nematicides, in addition to some cultural practices such as the propping and-or guying of fruit-bearing plants. Carbamate and organophosphate nematicides are usually rotated two to three times per year under Costa Rican conditions. However, root growth has not been improved in recent years in spite of nematicide treatments. Because root decay is not only associated with nematode damage, current research has also focused on other micro-organisms and soil conditions to evaluate their effect on root growth and its deterioration. Crop rotation, fallow, and organic amendments have been evaluated without success. Products from biological and/or organic origin were found to be available but no commercial application has been implemented yet. Environmental concerns and worker safety and health make the future of chemical nematicides uncertain; therefore, new ideas for nematode management are required to control these microorganisms in areas such as Costa Rica, where burrowing nematode is one of the main production constraints. Further research on biological control and non-chemical alternatives is required. Soil amendments to improve competition, predation and/or antibiosis may also play an important role on root growth. Genetic variation of the nematode population is also another aspect that may bring some light to understand the complex puzzle of improving banana root growth under tropical conditions.

Resumen - Investigaciones en progreso y perspectivas futuras para el manejo del sistema radical

Los nematodos fitoparásitos son las plagas más importantes que afectan el sistema radicular del banano. Aunque las poblaciones son normalmente poli-específicas, el nematodo barrenador, *Radopholus similis*, es usualmente la especie dominante. El manejo de los nematodos ha dependido principalmente de la aplicación de nematicidas químicos granulares; además de algunas prácticas culturales complementarias como el apuntalamiento de las plantas fructificadas. Nematicidas carbamatos y organofosforados son usualmente rotados dos o tres veces al año bajo las condiciones de Costa Rica. Sin embargo, el crecimiento radicular no ha mejorado en los últimos años, a pesar de los tratamientos nematicidas. Debido a que el deterioro radicular no sólo está asociado al daño causado por los nematodos, la investigación actual ha enfocado su atención a otros microorganismos y/o condiciones de suelo para evaluar su impacto en el crecimiento de las raíces y su destrucción. La rotación de cultivos, el barbecho y la incorporación de enmiendas orgánicas se ha evaluado sin éxito sostenible. Productos de origen biológico u orgánico también se han encontrado disponibles pero no se ha documentado su uso a nivel comercial. Las preocupaciones desde el punto de vista ambiental y de salud de los trabajadores hacen que el futuro de los nematicidas químicos sea incierto. Nuevas ideas en el manejo de nematodos se requieren para el control de estos organismos, en áreas como en Costa Rica, donde el daño causado por el nematodo barrenador es una importante limitación para la producción de banano de exportación. Mayor investigación en control biológico y alternativas no químicas también se necesitan. Enmiendas al suelo para mejorar la competencia, la depredación y la antibiosis también pueden tener un rol importante en el crecimiento radicular. La variación genética de las poblaciones de nematodos es también otro aspecto a considerar para el entendimiento del complicado rompecabezas que es el mejoramiento del sistema radicular de banano bajo condiciones tropicales.

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Banana yield response to nematode control in Dole farms in Costa Rica

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Abstract

There are various biotic and abiotic factors that may affect banana root development. They include soil temperature, soil texture, soil compaction, drainage, nutrition, mineral toxicity, fungi, weevils and nematodes. The objective of this presentation is to document the yield response of banana to nematode control with conventional chemical control programs. In Central America, banana yield reduction has been related to infestation of *Radopholus similis*, the effect of other nematode genera on yield has not been documented. Nematode management has been evaluated experimentally with various cultural, microbial, botanical and chemical control alternatives. Current commercial management of *R. similis* and its damage includes cultural practices such as propping, drainage, organic amendments, fallow, rotation and tillage. Additionally, the use of conventional chemical nematicides in the organophosphate and carbamate groups is required under high nematode pressure environments such as in Costa Rica. Results presented are based on 6 experiments conducted in the Rio Frio and Estrella Valley zones in Costa Rica. Yield (stems harvested, stem weight, calibration, finger length, tons per hectare and boxes per hectare) and root health data (*R. similis* numbers, percentage of functional roots and fresh weight of functional roots) has been gathered from replicated plots over several years. The information to be presented compares yields and root health with a commercial chemical control programme versus an untreated control. Reduction for all yield components was measured as a result of nematode infestation, in general differences started at 9-12 months after stopping chemical control treatments. The yield loss was measured in all experimental sites with reduction in total yield ranging from 30-50% in the absence of nematode control.

Resumen - Respuesta en producción de banano al control de nematodos en fincas de Dole en Costa Rica

Existen varios factores bióticos y abióticos que podrían afectar el desarrollo de las raíces del banano incluyendo: temperatura del suelo, textura del suelo, compactación del suelo, drenaje, nutrición, toxicidad mineral, hongos, picudos y nematodos. El objetivo de esta presentación es documentar la respuesta de la producción de banano al control de nematodos con programas de control químico convencionales. En América Central, se ha relacionado la reducción de la producción de banano con la infestación de *Radopholus similis;* el efecto de otros géneros de nematodos no ha sido documentado. El manejo de nematodos ha sido evaluado experimentalmente con varias alternativas culturales, microbiológicas, botánicas y de control químico. El manejo comercial actual de *R. similis* y su daño incluye prácticas culturales como el apuntalamiento, drenaje, enmiendas orgánicas, barbecho, rotación y labranza. Adicionalmente, el uso de nematicidas químicos convencionales es necesario en ambientes con alta presión de nematodos como en Costa Rica. Los resultados presentados se basan en 6 experimentos efectuados en las zonas de Río Frío y del Valle de la Estrella en Costa Rica. El rendimiento (tallos cosechados, peso del tallo, longitud del dedo, toneladas por hectárea y cajas por hectárea) y datos sobre la salud de la raíz (número de *R. similis*, porcentaje de raíces funcionales y gramos de raíces funcionales) se han recolectado de parcelas repetidas en diferentes años. La información a presentar compara el rendimiento y la sanidad radical entre un programa de control químico comercial y uno sin tratamiento. Se midió la reducción de todos los componentes de rendimiento como resultado de la infestación con nematodos. En general las diferencias comenzaron a partir de 9 a 12 meses después de terminar los tratamientos químicos de control. La pérdida de rendimiento se midió en todos los sitios experimentales con una reducción en el rendimiento total entre 30 y 50% en ausencia de control de nematodos.

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Relationship between functional root content and banana yield in Costa Rica

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Abstract

The study examines the relationship between functional root content and yield over the 16 years from 1987 to 2002. The counties studied were Sarapiquí, Pococí, Guácimo (production areas west of the Reventazón river), and Siquirres, Matina and Talamanca (production areas east of the Reventazón river). Banana plantations cover 38 558 ha in these counties and represent 91% of the banana crop planted in Costa Rica. Functional root fresh weights (g/plant) ranged from 38 to 87 in Sarapiquí; 43 to 102 in Pococí; 36 to 81 in Guácimo; 36 to 135 in Siquirres; 35 to 143 in Matina and 31 to 114 in Talamanca counties. The historical production, in boxes of 18.14 kg ha^{-1} $year^{-1}$, varied annually from 2019 to 2864 in Sarapiquí; 1778 to 2643 in Pococí; 1723 to 2536 in Guácimo; 2271 to 2947 in Siquirres; 2228 to 2581 in Matina and 1740 to 2984 in Talamanca counties, according to CORBANA S.A. The best yields per county were achieved in 1989: 2643 boxes ha^{-1} $year^{-1}$ in Pococí, 2947 in Siquirres and 2740 in Talamanca counties. These values coincide with functional root fresh weights (g/plant) of 102 for Pococí, 135 for Siquirres and 100 for Talamanca. A significant relationship between functional root weights and productivity was found for Sarapiquí ($y = 5.98x + 1922$; $P<0.036$); Pococí ($y = 14.05x + 1104$; $P<0.0001$); Siquirres ($y = 5.48x + 2065$; $P<0.0001$) and Talamanca ($y = 9.96x + 1922$; $P<0.0002$) counties. Results showed that for every 10 g of functional roots lost, productivity (boxes ha^{-1} $year^{-1}$) decreased by 60 in Sarapiquí, 140 in Pococí, 55 in Siquirres and 99 in Talamanca counties. Biotic and abiotic factors that can affect functional root content and productivity in Costa Rica are highlighted.

Resumen - Relación entre el contenido de raíz funcional y la producción de banano en Costa Rica

Se estudió la relación entre el contenido de raíz funcional y la productividad de 16 años (de 1987 a 2002). Dicho estudio se realizó en los cantones de Sarapiquí, Pococí y Guácimo de la zona de producción al oeste del río Reventazón y Siquirres, Matina y Talamanca de la zona de producción al este del río Reventazón. En conjunto el área suma 38.558 ha equivalente al 91% del área total sembrada en Costa Rica. Los pesos de raíz funcional (g/planta) oscilaron de 38 a 87; 43 a 102; 36 a 85; 36 a 135; 35 a 143 y 31 a 114 en los cantones de Sarapiquí, Pococí, Guácimo, Siquirres, Matina y Talamanca, respectivamente. Los datos promedio de productividad de dichos cantones, según las Estadísticas de Exportación Bananera de Costa Rica revelan rendimientos (cajas de 18,14 kg ha^{-1} $año^{-1}$) muy variables en los diferentes años y cantones, que fluctuaron de 2019 a 2864 en Sarapiquí; 1778 a 2643 en Pococí; 1723 a 2536 en Guácimo; 2271 a 2947 en Siquirres; 2228 a 2581 en Matina y 1740 a 2984 en Talamanca. La productividad por cantón muestra que 1989 fue el año con los mejores rendimientos, 2643; 2947 y 2740 cajas ha^{-1} $año^{-1}$ coincidiendo dichos valores con pesos adecuados de raíz funcional de 102, 135, y 100 g por planta para los cantones de Pococí, Siquirres y Talamanca. La relación entre raíz funcional y productividad fue significativa para los cantones de: Sarapiquí ($y = 5.98x + 1922$; $P<0.036$); Pococí ($y = 14.05x + 1104$; $P<0.0001$); Siquirres ($y = 5.48x + 2065$; $P<0.0001$) y Talamanca ($y = 9.96x + 1922$; $P<0.0002$). Las ecuaciones establecen que por cada 10 g de pérdida de raíz funcional se disminuye la productividad en 60, 140, 55 y 99 cajas ha^{-1} $año^{-1}$ en los cantones de Sarapiquí, Pococí, Siquirres y Talamanca, respectivamente. Se señalan factores bióticos y abióticos que pueden haber afectado el contenido de raíz funcional y por ende la productividad.

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Introduction

Variations in Costa Rican banana yields (boxes ha^{-1} $year^{-1}$) were studied from 1987 to 2002. A combination of factors has affected banana yield including functional root fresh weight, which, in turn, is affected by biotic factors such as nematodes and soil micro-organisms, and abiotic factors such as superficial and internal drainage, element toxicity (Al^{+3}, Fe^{+3} and Mn^{+2}), high precipitation, low and high temperatures, soil compression and cultivation, and light or heavy-textured soils.

Serrano and Marin (1998) correlated functional root weight with annual yield, calculated in boxes ha^{-1} $year^{-1}$ and boxes/processed bunch from 1987 to 1997, and found correlation coefficients of 0.85 and 0.92, respectively. When the total and functional root weights were determined in the different banana producing counties in Costa Rica from 1995 to 1999, it was found that farms with yields close to 3000 boxes/ha/yr had higher total and functional root weights than farms with lower yields (Calvo and Araya 2001). This study relates functional root fresh weight (taken by a standard sampling procedure) with yield/county from 1987 to 2002 and highlights historical biotic and abiotic factors that directly or indirectly affected functional root fresh weight.

Historical yield at national level

The data are from farms located in the Sarapiquí, Pococí, Guácimo, Siquirres, Matina and Talamanca counties, which represent 38 558 ha, or 91% of the planted area. From 1987 to 2002 there were great variations in the yield measured in boxes ha^{-1} $year^{-1}$ in Costa Rica. The total area planted with banana in 1987 was 20 987 ha with an average yield of 2476 boxes of 18.14 kg ha^{-1} $year^{-1}$ This increased to 2731 boxes ha^{-1} $year^{-1}$ in 1989, the highest yield obtained in the last 16 years (Figure 1). From 1989 to 1992, banana yields declined continuously, reaching a low of 2400 boxes ha^{-1} $year^{-1}$ Since

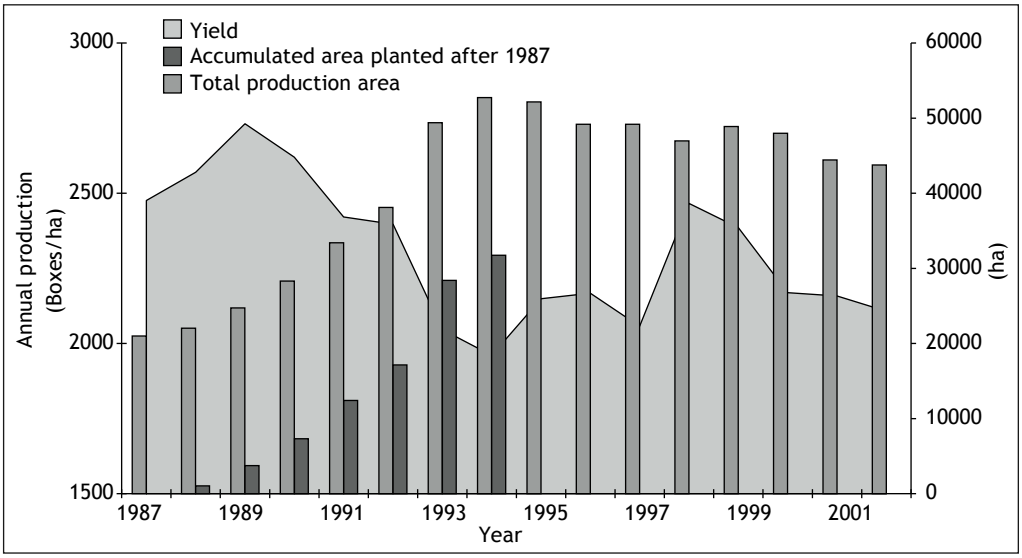


Figure 1. Changes in productivity and in the surface area of bananas planted in Costa Rica, 1987-2002.

then, some years showed limited recovery, such as 1998 where yield reached 2466 boxes/ha/yr but other years saw even lower yields, such as in 2002, which had the third lowest yield of the period with 2107 boxes ha^{-1} $year^{-1}$ for the 42 182 ha planted.

Relationship between functional root fresh weight and yield per county

Production area west of the Reventazón river

West of the river are the counties of Sarapiquí, Pococí and Guácimo. Pococí county is the largest producer in Costa Rica. It has maintained a production area of 10,169 ha and has exported more 18.14 kg boxes of bananas than any other county over the last 16 years, reaching 340 million boxes (Sanchez and Zuñiga 2003). Functional root fresh weights, taken using a standard sampling technique (Araya, these proceedings) were between 43 and 102 g/plant, and the lowest and highest weights coincided with the lowest and highest yields (Figure 2). The data from 1995 to 2002 in Sarapiquí county showed trends very close to those in Pococí (Figure 2). Functional root weights were between 38 and 87 g/plant and the yields for these years were between 2084 and 2535 boxes. The regression between functional root weight and productivity was highly significant in Pococí county ($P>0.0001$, $y = 14.06x + 1104$ $R^2 = 0.77$) as well as in Sarapiquí ($P = 0.036$, $y = 5.98x + 1922$ $R^2 = 0.55$). Thus, productivity on the Pococí farms is much more sensitive to loss of functional roots than in Sarapiquí. For every 10 g reduction of root there is a loss of 140 boxes ha^{-1} $year^{-1}$ in Pococí and and 60 in Sarapiquí. Although Guácimo county followed the same trend, the results were not significant, probably because fewer farms had historical functional root weight data.

Production area east of the Reventazón river

East of the river are Siquirres, Matina and Talamanca counties. During the period, 248 million 18.14 kg boxes were exported from Siquirres county, which maintains an average production area of 7 033 ha. Siquirres is the best producer east of the Reventazón River and second best nationally. Functional root weights (g/plant) in Siquirres were 36 to 135; in Matina, 35 to 143; and in Talamanca, 31 to 114. The corresponding annual yields (boxes/ha) were 2271 to 2947 for Siquirres; 2228 to 2581 for Matina and 1749 to 2984 for Talamanca (Figure 3). Similar to the western counties, highest and lowest yields corresponded with highest and lowest functional root fresh weights. The relationship between functional root weight and productivity was highly significant for Siquirres county ($P>0.0001$, $y = 5.48x + 2065$ $R^2 = 0.79$) and Talamanca ($P>0.0002$, $y = 9.96x + 1922$ $R^2 = 0.64$). For each 10 g of functional root weight that was lost, annual productivity decreased by 55 boxes ha^{-1} $year^{-1}$ in Siquirres and 99 in Talamanca county. Although the trend was the same in Matina county, the results were not significant.

Biotic and abiotic factors affecting banana productivity in Costa Rica from 1987 to 2002

To understand the relationship between national productivity and functional root fresh weight in Costa Rica in the study period, it is necessary to review banana industry activity. From 1987 to 1992, productivity in Costa Rica was acceptable, due to

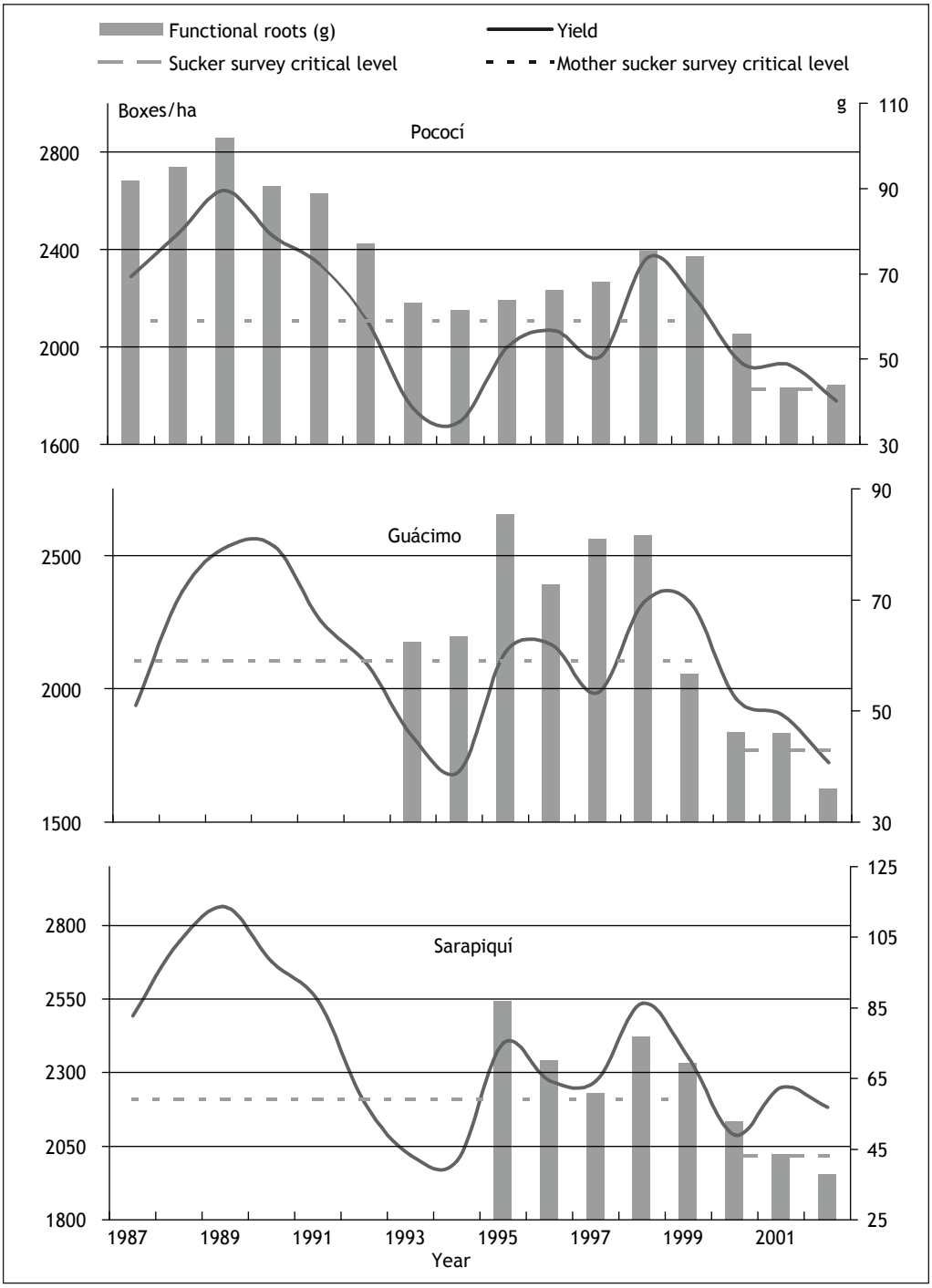


Figure 2. Functional root fresh weight (g/plant) and productivity (boxes ha^{-1} $year^{-1}$) from 1987 to 2001 for three counties west of the Reventazón River. The mother sucker survey critical weight is 60 g and the sucker survey critical weight is 42 g (Calvo and Araya 2001).

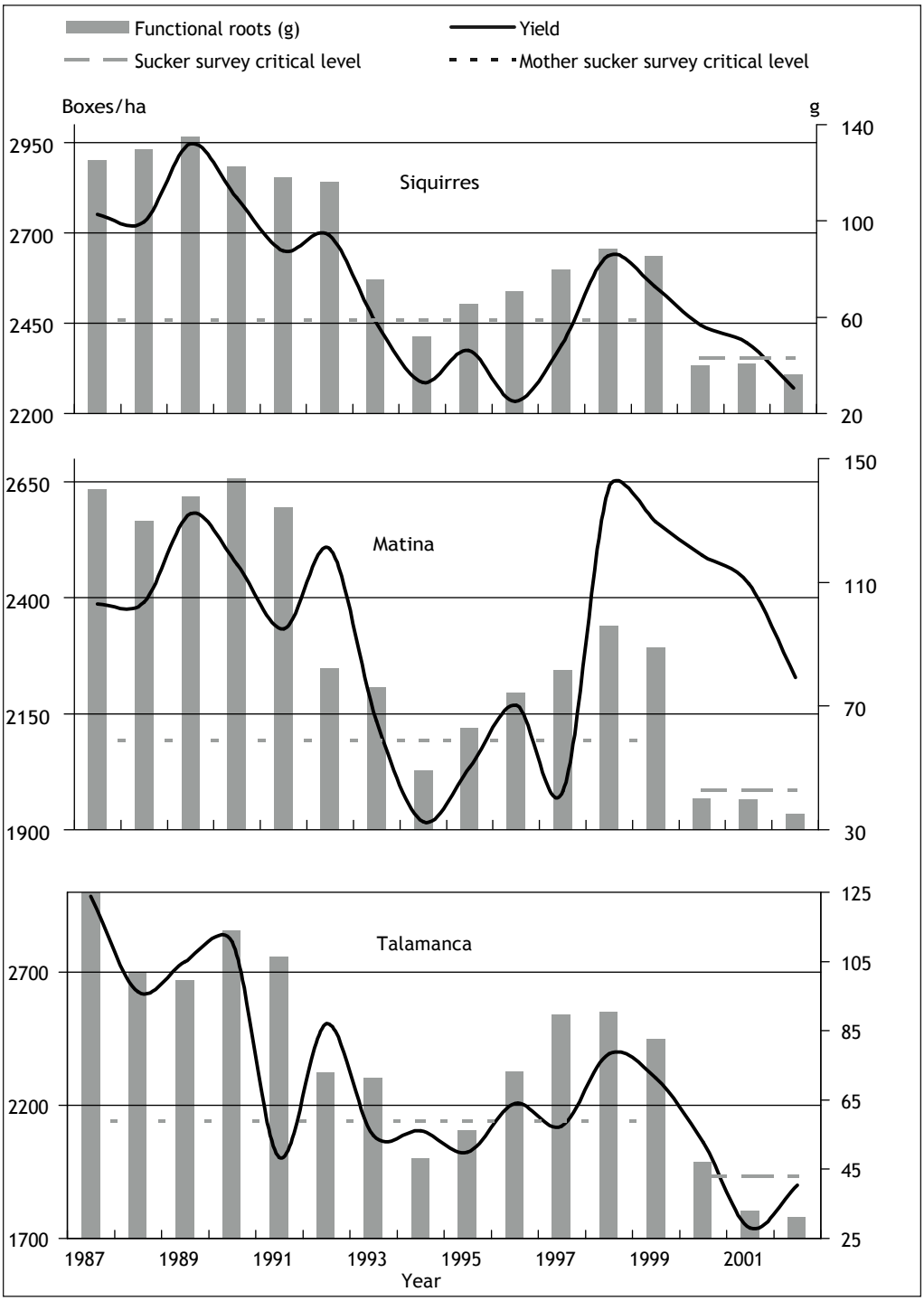


Figure 3. Functional root fresh weight (g/plant) and productivity (boxes ha^{-1} $year^{-1}$) from 1987 to 2001 for three counties east of the Reventazón River.

favourable biotic and abiotic factors. The fenamiphos nematicide was replaced in 1987 by new compounds such as terbuphos, aldicarb and ethoprop**.** The constant and indiscriminate use of fenamiphos from the beginning to the middle of the 1980s probably caused the accelerated biodegradation observed (Durán 1988). The introduction of the new compounds gave better control of nematodes, and consequently healthier root systems associated with better productivity. Propiconazole, introduced into the market in 1987, and other systemic fungicides like tridemorph and benomyl achieved better black Sigatoka control (Guzmán 2003). Finally, well-distributed precipitation with no excessive flooding or lengthy droughts, especially during 1987, 1988 and 1989, and markets with no "distortions" (no fruit export restrictions) contributed to this period of good productivity.

During 1993 and 1994, productivity dropped dramatically to 2046 and 1960 boxes ha^{-1} $year^{-1}$, respectively. Farmers did not expect this decrease in yield. During the last Banana Development Programme between 1989 and 1994 about 30 000 additional hectares of banana were planted, increasing the area from 22 022 ha in 1988 and to 52 737 ha in 1994. This expansion can be explained by the opening of new markets in the Eastern European countries. An increase in productivity was expected (Serrano and Marín 1998), but did not occur, probably because of the combination of various factors including aldicarb, which was effective, but was taken off the market in 1990, reducing the options for rotating terbuphos, ethoprop, carbofuran and oxamyl. With this, the options for controlling *Radopholus similis* decreased and the risk of inducing accelerated biodegradation of the nematicides increased (Anderson *et al*. 1998). This phenomenon could have been accelerated in banana soils west of the Reventazón River where, historically, one more dose of nematicide was applied per year compared with the eastern areas. In general, these soils have a lighter texture and a lower pH than the soils in the east. Under these favorable conditions, *R. similis* and *Meloidogyne incognita* (Davide 1980) caused more serious banana root damage. At the end of 1992, *Mycosphaerella fijiensis* showed decreased sensitivity to propiconazole, which resulted in fewer leaves at harvest and lower bunch weights (Romero and Sutton 1997, Serrano and Marin 1998, Guzmán 2003).

The globalization of the banana market is without doubt one cause of the low productivity during this period. This was manifested in two ways, 1) High global demand for fruit caused by the expectation of new markets in Eastern Europe which did not materialize and, 2) European Union protection of its ex-colonies, which negatively affected the export of Latin American bananas to Europe (Zuñiga 1994). The aforementioned factors decreased the liquidity of independent growers, which resulted in cost restructuring including a decrease in farm maintenance. This accelerated the decrease in productivity in 1994.

Low precipitation in 1995 began the slow recovery of productivity from 1995 to 1998 (Figure 4). Another factor that helped the recovery was the introduction of a cadusaphos nematicide. However, because of its high cost, it was not commonly used. Fenamiphos was reintroduced on the banana market (Navarro 1995) with manufacturer's instructions to apply only once a year to avoid accelerated biodegradation.

The "Framework Agreement" with the European Union (Zuñiga 1994) improved the banana market in Europe. New options for black Sigatoka control increased the number

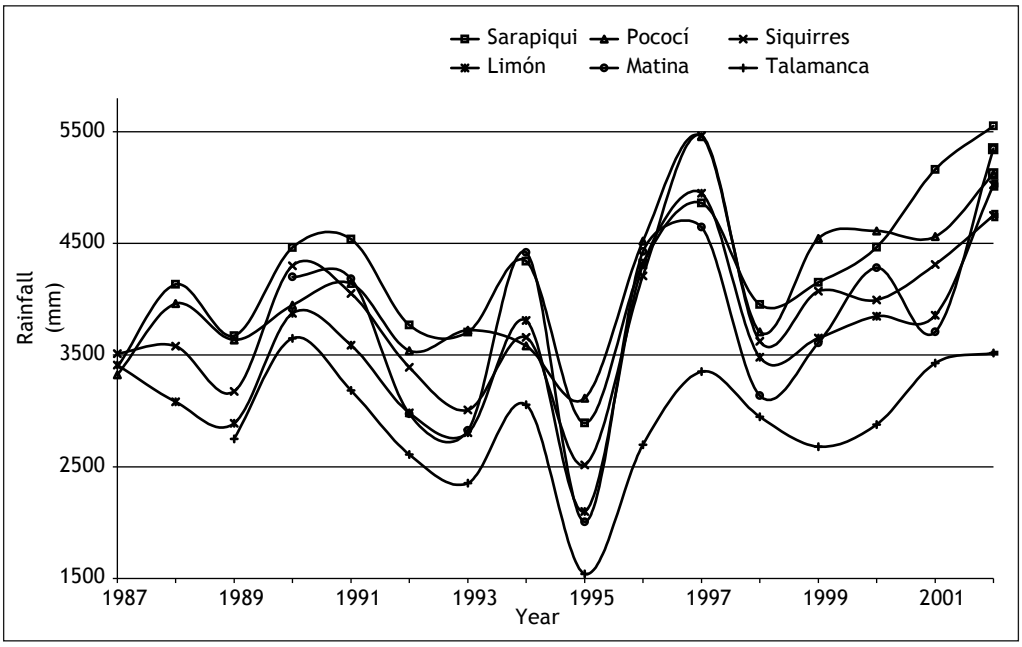


Figure 4. Annual precipitation in six banana-growing counties in the Caribbean coast of Costa Rica, 1987-2002.

of leaves at harvest and bunch weight as well. Other triazole compounds were introduced to the market in 1996 and azoxistrobin was introduced in 1997. Azoxistrobin is one of the new group of systemic fungicides called strobilurins and has effects comparable with those of propiconazole (Guzman and Romero 1997, Serrano and Marin 1998). In addition to the use of new fungicides, renewed relationships with transnational companies and with independent growers, and optimal climatic conditions during the second semester of 1997 and most of 1998, made possible the productivity increase to 2466 boxes ha^{-1} $year^{-1}$.

From 1999 to 2002 productivity in Costa Rica experienced a fast decline, and stabilized at 2107 boxes/ha/yr during 2002. This decrease was due to an inadequate distribution of rainfall: 45% of the total annual precipitation fell from November to December in 1999 and 50% from January to February in 2000. This excessive rainfall was not expected, because of the even rainfall distribution since the second semester of 1997. Plantations did not have adequate superficial drainage; therefore, as a result of soil saturation, and the concomitant anoxia and root death**,** productivity was low. In addition to inadequate rainfall distribution, the average temperature decreased during this period resulting in fewer flowering plants per hectare (Figure 5). There were fewer than 40 buds ha^{-1} $week^{-1}$ for most of the first semester of 2000, which is lower than the minimum accepted value. On average, in the Caribbean coast of Costa Rica the accumulated annual precipitation from 1999 to 2002 increased by 6.4% and 17% compared with the previous year. The 17% increase in rainfall in 2002 included two floods that took place in May and December.

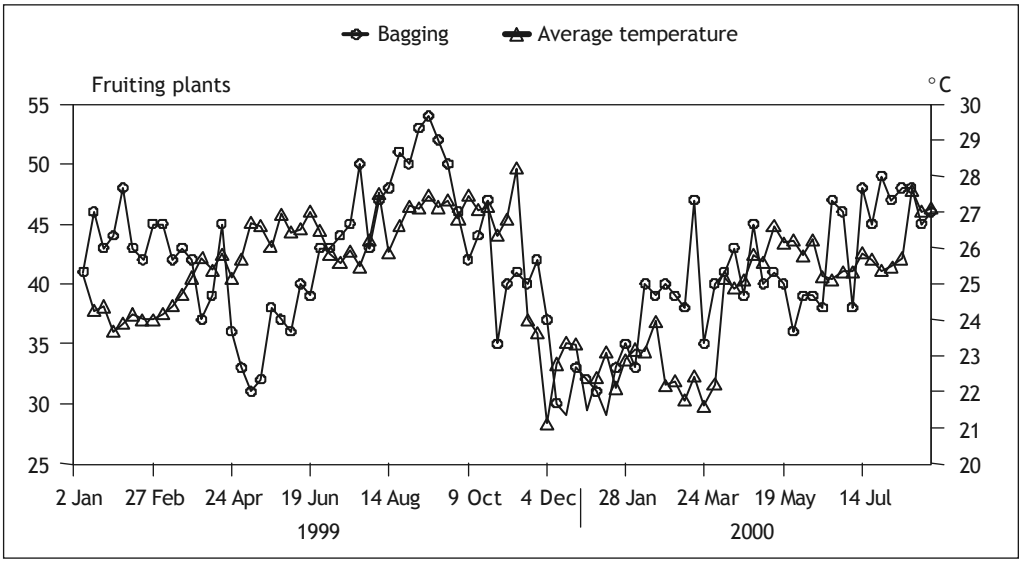


Figure 5. Effect of average weekly temperature on the number of flowering plants per hectare in Pococí county, 1999-2000.

The decrease of 216 boxes/hectare from 1999 to 2000 and the uncertainty of the global banana market (Vargas 2000) had the same effect as in 1994, with a decrease in farm maintenance. Drainage, fertilization and nematicide applications were the most affected. Lack of liquidity prevented the continued nematicide rotation that had been recommended by Anderson *et al.* (1998) and more recently by Moens *et al.* (2003). The constant use of the same nematicide compound, mainly by independent growers, caused accelerated biodegradation. This, in turn, decreased its efficacy in nematode control and consequently reduced functional root fresh weight at the national level.

The increase in precipitation from 2000 to 2002 generated an increase in the use of the azoxistrobin. At the beginning of 2001, after azoxistrobin had been applied more than 25 times, alternated with other systemic fungicides and protectants, loss of sensitivity became evident in Sarapiquí county (Guzmán 2003). The increase in disease expression at the national level, resulted in fewer leaves at harvest and lower bunch weights throughout the Caribbean coast of Costa Rica.

Finally, plant vigour and the production of the 30,000 hectares planted in the last Banana Development Programme declined slowly between 1988 and 1994. Functional root deterioration in these areas is associated with inappropriate soils and induced acidity caused by the inappropriate use of nitrogen fertilizers in the fertilization band over the years (Figure 6). In addition, it was found that acidity had penetrated deep into the profile, which is related to the plantation's age, the soil texture and the history of fertilization management practices (Serrano 2003).

It can be concluded that functional root weight was largely responsible for productivity variation. Several abiotic and biotic factors affected functional root weight. Abiotic factors included low and high precipitation, low and high temperatures, poor internal and superficial drainage, accumulated acidity (element toxicity) and the physical

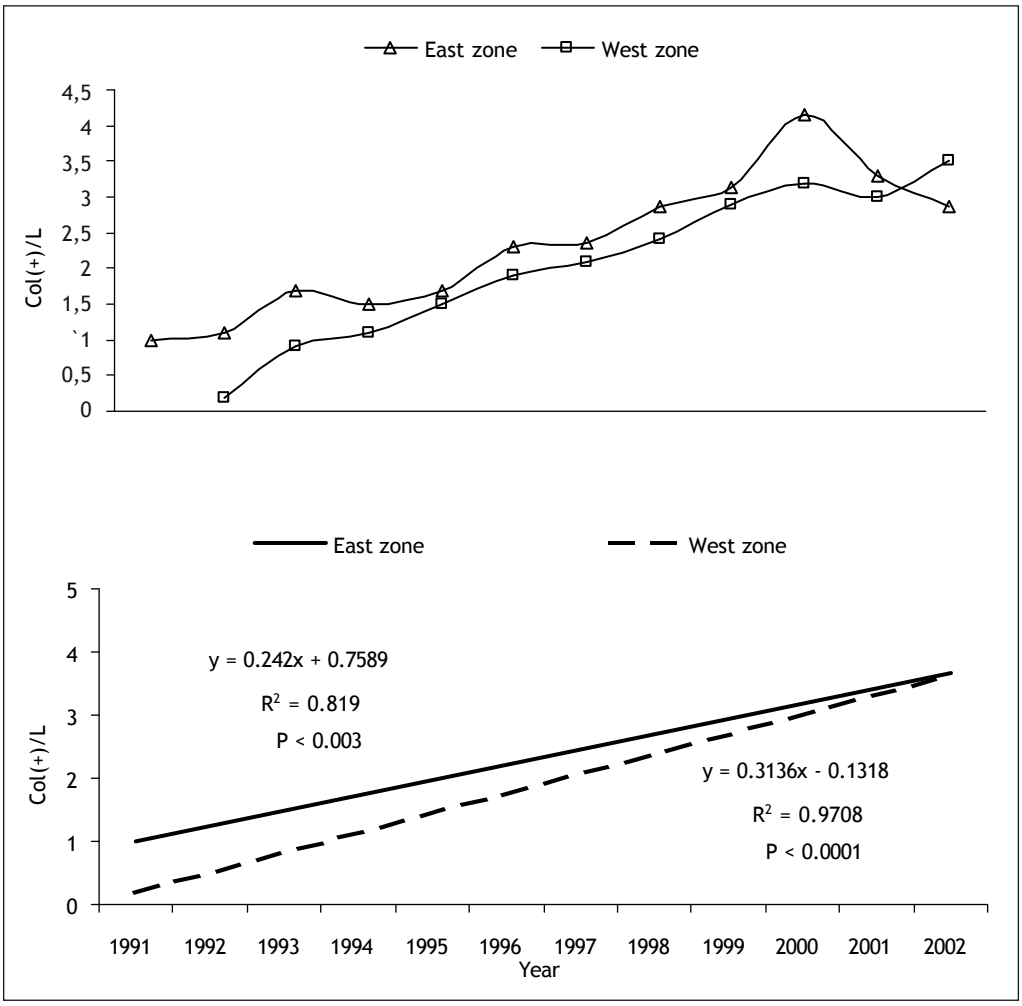


Figure 6. Induced accumulated acidity in soils of banana farms located west and east of the Reventazón River in the Caribbean coast of Costa Rica, 1991-2002.

condition of the soil. Biotic factors included nematodes and microorganisms responsible for accelerated nematicide biodegradation. In addition, continuous fluctuations in the international banana market directly influenced the restructuring of farm operation systems; reducing farm maintenance such as drainage systems, fertilization programmes and nematicide applications. This too affected functional root weights.

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2

Root anatomy and morphology

Anatomía y morfología de la raíz

Anatomy and morphology of monocotyledonous and dicotyledonous roots

Nelly Vásquez M.[1]

Abstract

In most plants, the root is the sporophyte's subterranean part carrying out activities such as anchorage, storage of food products, absorption of water and nutrients and conduction to the remaining plant parts. Roots also produce soil organic matter and provide habitat for mycorrhizae, rhizosphere and rhizoplane organisms. The first root of a plant originates in the embryo and constitutes the primary, main, or tap root. Lateral or secondary roots originate from it. In the monocots, the primary root dies early and the root system is made up of adventitious roots originating from the hypocotyl and sometimes from the stem.

At the root apex of monocots and dicots, three growth areas are recognized: an area of cell division formed by the root meristem; a cell enlargement region, and a maturation zone. The apex is protected by a layer of cells called the root cap, made of tissues with a different structure and function, among which the root cap's own formation and mucilage production and secretion, are the most important. The secretion of mucilage facilitates root growth through the soil and the root cap controls the root's gravitropic response.

In general terms, the root has a primary and a secondary structure that facilitate the study of the tissues within it. In primary growth, the following tissues are identified: epidermis (usually unicellular), cortex (storage and axial transportation of water and other materials), endodermis, pericycle and vascular tissue. In roots with primary growth, the xylem and the phloem are in alternate positions, one beside the other, showing a centripetal maturation. In many dicots, secondary growth develops later. It is important to mention that lateral roots have an endogenous origin, probably from the pericycle and endodermis. Adventitious roots, characteristic of the monocots are usually of endogenous origin, though they can sometimes be exogenous.

Finally, roots make connections and relationships with other organisms such as bacteria and mycorrhizae to work together for mutual benefit.

Resumen - Anatomía y morfología de raíces monocotiledóneas y dicotiledóneas

En la mayoría de las plantas la raíz es la parte subterránea del esporófito y realiza funciones de anclaje, almacenamiento de productos para alimentación, absorción de agua y nutrientes. Las raices también tienen funciones de: conducción de agua y nutrientes hacia el resto de partes de la planta, producción de materia orgánica al suelo y provisión de hábitats para micorrizas y organismos de la rizosfera y el rizoplano, etc. La primera raíz de la planta se origina en el embrión y constituye la raíz primaria, principal o pivotante. En monocotiledóneas, la raíz primaria muere pronto y el sistema radical queda formado por raíces adventicias que se originan en el hipocotilo y a veces en el tallo. Este tipo de raíz generalmente crece de manera superficial, lo que las hace aptas para prevenir la erosión.

A nivel del ápice de la raíz tanto de monocotiledóneas como de dicotiledóneas, se reconocen tres áreas de crecimiento: una región de división celular formada por el meristemo radical y la zona cercana de división celular; una región de alargamiento celular y una región de maduración. El crecimiento del ápice está protegido por una capa de células llamado caliptra, constituída por tejidos de diferente estructura y función, entre las que destacan la misma formación de la caliptra,

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la producción y secreción de mucílago que facilita el crecimiento de la raíz a través del suelo, y la gravipercepción de la raíces.

En términos generales, la raíz consta de una estructura primaria y una secundaria que facilitan el estudio de los tejidos que la forman. En el crecimiento primario se identifican tejidos como: epidermis usualmente unicelular, corteza (almacenamiento y transporte lateral de agua y otros materiales), endodermis, periciclo y tejido vascular. En las raíces con crecimiento primario, el xilema y el floema se encuentran en posición alterna, uno al lado del otro y presentan una maduración centrípeta. En muchas dicotiledóneas, se desarrolla posteriormente un crecimiento secundario

Es importante mencionar que las raíces laterales tienen un origen endógeno, posiblemente a partir del periciclo y la endodermis. Las raíces adventicias, típicas de las monocotiledóneas, presentan un origen usualmente endógeno, aunque a veces puede ser exógeno. Por último, las raíces forman conexiones y relaciones con otros organismos, como las bacterias y micorrizas para trabajar juntas por el beneficio mutuo.

Introduction

In most plants, the root is the part located underground which serves to anchor the plant, store food products, absorb water and nutrients, conduct water and nutrients to the rest of the plant parts. Roots also aid in: producing organic matter for the soil and providing habitats for mycorrhizal and rhizosphere organisms. In addition to these functions, the root synthesizes, accumulates and secretes a large quantity of compounds called exudates, through which it regulates the microbial community in the soil immediately surrounding it. Roots also change the physical and chemical soil properties to favour symbiotic associations and inhibit the growth of competing plants (Estabrook and Yoder 1998, Walker *et al.* 2003). Apparently 5 to 21% of all the carbon fixed photosynthetically is transferred to the rhizosphere through exudates (Marschner 1995). The first root of any plant originates in the embryo and constitutes the primary, principal or tap root, which reaches deeper into the soil than any other. Later, lateral or secondary roots grow from the primary root possibly originating from the pericycle or the endodermis.

In monocotyledons, and in some dicotyledons, the primary root dies quickly and the remaining root system is formed by adventitious roots that originate from the hypocotyl and sometimes from the stem. Thus, this adventitious system results in a fibrous root system in which no single root predominates over another. It is important to recognize the different types of roots since each has a different function. The majority of plants produce one or more orders of lateral roots. The different orders vary in thickness, branching pattern, growth rate, capacity to produce secondary growth and structural characteristics. These variations can influence their capacity to obtain water and nutrients and to survive under adverse conditions.

Three different growth regions can be identified in both monocotyledon and dicotyledonous roots: an apical cell division region formed by the root meristem; a region of cell lengthening; and a region of cell maturation. The apical zone is composed of a quiescent center and peripheral zone, with very active mitotic cells that form the larger part of the root (Figure 1). Frequently, three possible functions are mentioned for this region (Flores 1999):

- Source of cytokinin
- Model to generate and modify root histological patterns
- Regulate mitotic differentiation and properties of adjacent initial cells

The cell elongation zone measures a few mm in length and, as its name would indicate, it is the area where the cells grow in volume. The maturation zone is where the primary tissues become differentiated and root hairs develop from the trichoblasts. Nevertheless, these regions are not clearly differentiated; however, identifying them makes it easier to study this organ of the plant.

The lateral and the adventitious roots have root meristems similar to that of the primary root. Apical growth is protected by a layer of cells called the root cap (calyptra). It is covered by a layer of highly hydrated mucilage that lubricates the root as it penetrates the soil, protects it from desiccation, favours ion absorption and provides an ideal environment for the establishment and development of bacteria in the rhizophere. This cellular layer also has an important role in sensing gravity (Rougier and Chaboud 1985). In general terms, roots have a primary structure and a secondary structure that facilitate the study of the tissues that compose it.

Primary structure

Tissues that can be identified in primary growth are: a generally unicellular epidermis, the cortex (responsible for storing and axial transportation of water and other materials), the endodermis, the pericycle and the vascular tissue or stele.

The epidermis

The main function of the epidermis is water and nutrient absorption, facilitated by root hairs. These root hairs are unicellular, have a short lifespan and are limited to the region of cell maturation. Young roots with live epidermal cells and root hairs are frequently considered those responsible for the greatest nutrient uptake by increasing the surface area of the root (Marschner 1995, Peterson and Farquhar 1996) (Figure 2). The oldest epidermis may be covered by a cuticle and suberin layer. In spite of this, the epidermal cells offer little resistance to the passage of water and nutrients.

The cortex

The most space in the primary root body is occupied by the cortex. It is frequently composed of cells from the parenchyma and can have large gas spaces, store starch,

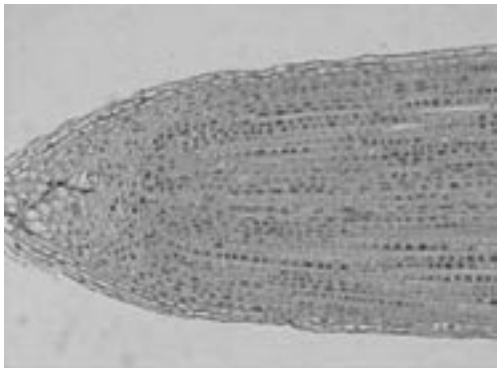


Figure 1. Root apical meristem.

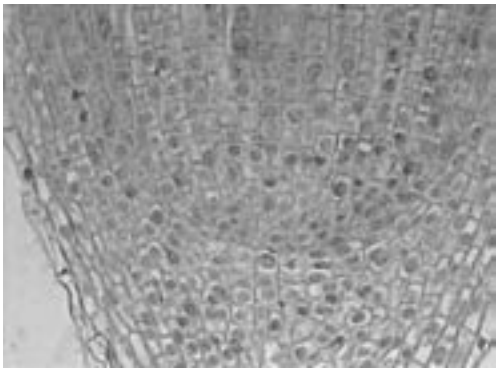


Figure 2. Root cap development.

proteins, and fat globules and lacks chloroplasts (Figure 3). It can also contain cellular inclusions such as crystals or secondary metabolites. The latter frequently provide colour and can auto-fluouresce. Many plants accumulate large quantities of dark brown tannins although they could have other coloured pigments. This natural pigmentation of the roots can help distinguish young roots from older roots, which are generally darker (Brundrett, sf.). The parenchyma tissue that forms the cortex also plays a critical role in the later transport of water and other substances via the apoplast and symplast. In monocotyledons, the cortex is maintained throughout the plant's life and the cells can develop secondary walls and lignify. In dicotyledons, the cortex is shed when secondary growth begins.

Endodermis

The endodermis tissue develops within the cortex and is characterized by a more compact, generally unicellular layer that has no gas space. It also has Casparian bands in the radial and transverse anticlinal walls (Figure 4). These cells have lignin and suberin deposits making them impermeable to water and ions. Any substances that they allow through to the stele must pass through the protoplasm of the Casparian band cells which is accomplished through the plasmalemma or the plasmodesmata. In many plants, just beyond the endodermis is a parenchymal layer called the pericycle. This layer is meristematic and is the source of lateral roots, although it can sometimes lignify. Beyond the pericycle is the vascular cylinder or stele. The roots of some monocotyledons, like corn, have a medulla as well as a vascular cylinder.

Vascular tissue

The vascular cylinder of the root is very different from that in the stem. In the primary stem, the xylem and the phloem are found in the same vascular bundle with the phloem generally toward the outside. In primary roots, the xylem and the phloem are found in alternating positions, next to one another. They also have centripetal maturation. In monocotyledons, either one single metaxylem element is in the central position or several poles of xylem and phloem surround a central medulla (Figure 5). This is the typical organization in *Musa* roots. In many dicotyledons, secondary growth develops later where the cambium and the peridermis play an important role. These roots with secondary growth shed their cortex and endodermis early.

Secondary structure

Monocotyledon roots do not have secondary growth. Nevertheless, in some monocotyledons there is a primary thickening meristem at the distal end (very near the apex and that diminishes basipetally). Secondary growth typical of the dicotyledons consists of secondary xylem and phloem production from the vascular cambium. Peridermis production is also seen from the other secondary meristem called the phellogen (Figure 6). The peridermis replaces the epidermis during the root's secondary growth. Some parts of the peridermis are differentiated like lenticels (spongy tissue that participates in gas exchange). The phellogen produces cork toward the outside and phellodermis toward the inside.

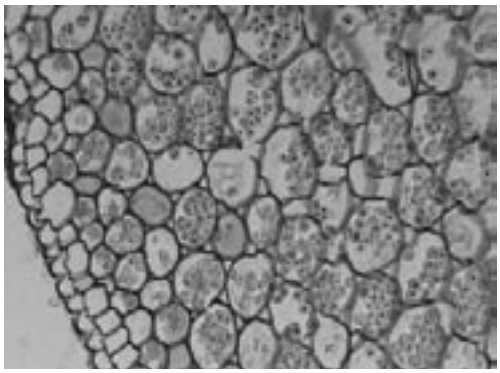


Figure 3. Epidermis and bark development.

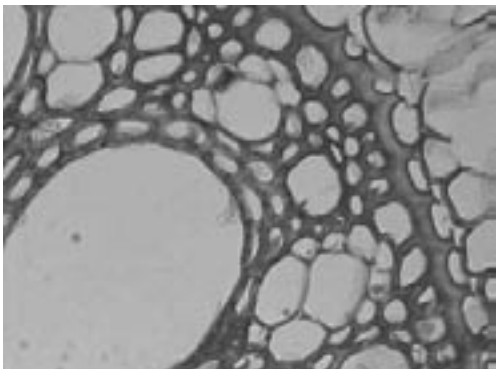


Figure 4. Development of typical endodermis with Casparian bands.

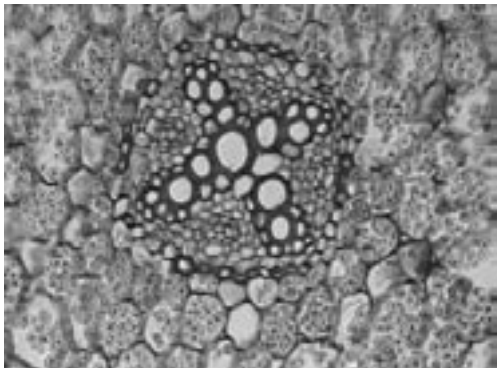


Figure 5. Development of Phleotherm endodermis with conducting cells.

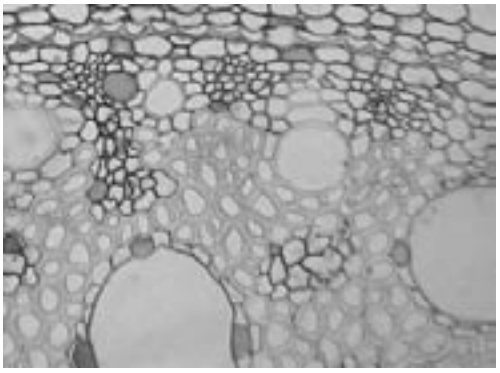


Figure 6. Xylem and phloem development in alternate positions.

Relationship with other organisms

Plants are in constant communication with a large variety of organisms, some of which are beneficial. Among these there are several notable symbiotic associations with bacteria that fix nitrogen and with mycorrhizal fungi. Other organisms, such as some fungi and bacteria, microbes, viruses and nematodes are damaging to the plant (Estabrook and Yoder 1998). Symbiotic associations between the root and organisms that fix N_2 (*Rhizobium*) are very common in the Fabaceae family (Dart 1977). Bacteria provide nitrates and plants provide carbohydrates.

Mycorrhizae

Symbiotic associations between fungi and plant roots are present in 90% of all higher plants. Only a few families lack mycorrhizal associations. Mycorrhizae extend the root absorption area significantly and make P, Cu and Zn available for the plant. Plants with few root hairs are very dependent on mycorrhizae that can provide resistance to heavy metal pollution, adverse pH, drought, high temperatures and salinity, and scarcity of soil micronutrients. The root exerts a regulatory influence on shoot growth. For example, drought, flooding, mineral nutrient deficiency, salinity or compaction, provoke

typical reactions such as reduced foliar expansion, closed stomata, epinasty (curving) of the leaves and senescence of the oldest leaves.

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Methodologies for root system assessment in bananas and plantains (*Musa* spp.)

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Abstract

The root system of field-grown plantain and banana (*Musa* spp.) plants has been little investigated because whole plant excavation is tedious and time consuming. Four methods for measuring root system size were assessed. A first approach, early screening, determines the entire root system of nursery-grown juvenile plants to forecast root growth in the field of adult plants. Few significant root trait correlations were observed between juvenile and adult plants. Hence root characteristics of adult plants cannot be adequately estimated from the root size of young plants. A second approach was based on regression of root traits on shoot traits. Regression equations attributed at least 90% of the variation in root growth to variation in shoot development, but models were not universal. Indeed shoot-root ratios vary according to the plant developmental stage and environmental conditions and thus need to be assessed at each location. A third method relied on soil core sampling. Root measurements in two soil core samples could estimate the size of the entire root system with at least 80% accuracy. This method is attractive because it only requires 5% of the time needed to excavate the whole root system. In addition, models to estimate root traits of the mat (mother with daughter plants) were significant irrespective of the suckering behaviour of the variety. The fourth approach consisted in assessing electrical capacitance to quantify root biomass as done in other plant species. *Musa* plant tissue contains a lot of water and thus secures a high electrical conductivity. Very few significant correlations between capacitance values and root system traits were found. In conclusion, root system assessment based on root core sampling is proposed as it estimates well the size of the entire root system in a fast, cheap and non-destructive way.

Resumen - Metodologías para evaluar el sistema radical en bananos y plátanos

La investigación enfocada al sistema radical de plantas de banano y plátano (*Musa* spp.) desarrolladas en el campo ha sido muy poca, debido a que excavar plantas completas es tedioso y lento. Se evaluaron cuatro métodos para medir el tamaño del sistema radical. El primer método, que es el de evaluación temprana, determina todo el sistema radical de las plantas juveniles desarrolladas en el invernadero para pronosticar el crecimiento de la raíz de plantas adultas en el campo. Se observaron únicamente unas pocas correlaciones significativas para las características de la raíz entre plantas juveniles y adultas. Por lo tanto, las características de la raíz de plantas adultas no pueden ser estimadas adecuadamente por el tamaño de la raíz de las plantas jóvenes. El segundo método se basó en la regresión de las características de la raíz sobre las características de los hijos. Las ecuaciones de regresión atribuyeron al menos un 90% de la variación en crecimiento de la raíz a la variación en el desarrollo del hijo; sin embargo, los modelos no fueron universales. En efecto, los cocientes hijo-

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raíz varían de acuerdo con la etapa de desarrollo de la planta y con las condiciones ambientales, por lo que deberán ser evaluadas en cada sitio. El tercer método se basó en el muestreo de suelo con barreno. Las mediciones de raíz en dos muestras de suelo con barreno podrían estimar el tamaño completo del sistema radical con al menos un 80% de exactitud. Este método resulta atractivo ya que se tarda únicamente un 5% del tiempo que llevaría excavar el sistema radical completo. Además, los modelos para estimar las características de la raíz de la unidad de producción (madre con plantas hijas) fueron significativos, sin importar el comportamiento de los hijos de la variedad. El cuarto método consistió en evaluar la capacitancia eléctrica para cuantificar la biomasa de la raíz, como se realiza en otras especies de plantas. El tejido de las plantas de *Musa* contiene mucha agua, lo que asegura una alta conductividad eléctrica. Se encontraron muy pocas correlaciones significativas entre los valores de capacitancia y las características del sistema radical. En conclusión, se propone utilizar el método de muestreo de raíz con barreno, ya que éste ofrece una buena estimación del tamaño total del sistema radical, de una manera rápida, barata, y sin destrucción.

Introduction

Roots constitute the link between the plant and the soil thereby providing anchorage and guaranteeing nutrient and water uptake. Roots of plantain and banana (*Musa* spp.) are also sources of plant growth regulators that contribute to lateral shoot (known as suckers) development and thus perennial growth (De Langhe *et al.* 1983, Martin Prével 1987, Stover and Simmonds 1987, Lahav and Turner 1989, Price 1995).

Research on *Musa* root systems is remarkably limited despite the paramount problems with nematodes and longevity and has largely been targeted at high value dessert bananas (Moreau and Le Bourdelles 1963, Beugnon and Champion 1966, Lassoudière 1978, Avilán *et al*. 1982). Moreover, few studies have been carried out on field-grown plants because traditional methods of root assessment under field conditions require tedious and time-consuming excavation of whole plants (Box 1996). In banana, two man-days are indeed needed to excavate one complete adult, ready-to-harvest, *Musa* spp. plant (Blomme 2000). In addition, excavation is destructive and thus complicates a dynamic assessment of root growth. Root measurement techniques that are non-destructive, quick and efficient, and provide insight into root dynamics, are critical for understanding environmental effects on root development. In addition, they constitute a good basis for investigating genetic differences among a large number of cultivars.

An alternative to field assessment of root systems of adult plants could be the evaluation of juvenile plants in the nursery, provided that there is a good correlation between the root system size at the two developmental stages. Swennen *et al*. (1986) evaluated juvenile *Musa* spp. plants grown under hydroponic conditions and were able to demonstrate large differences in root development between different genotypes. However, root growth in this artificial medium may differ from that of field-established plants. Furthermore, plants in hydroponics cannot be grown to their adult stage. The same restriction occurs in rhizotrons as described by Lavigne (1987). Hence, it is not known whether root measurements from juvenile plants adequately reflect root characteristics of adult plants.

A second alternative to the field assessment of entire root systems could be through indirect determination of root traits from shoot growth. Indeed, root and shoot growth are highly related in many plants such as in cotton (*Gossypium hirsutum* L.), pea (*Pisum sativum* L.), carrot (*Daucus carota* L.), turnip (*Brassica rapa* L.), palm species [*Roystonea regia* (HBK.) O.F. Cook, *Coco nucifera* L., *Syagrus romanzoffiana*

(Chamisso) Glassman and *Phoenix roebelenii* O'Brien] and strawberry (*Fragaria xananassa* Duch.) (Pearsall 1927, Broschat 1998, Fort and Shaw 1998). Russell (1977) mentioned that nodal root development in the cereals winter wheat (*Triticum aestivum* L.) and pearl millet (*Pennisetum glaucum* L.) could be estimated from the number of leaves. Henderson *et al.* (1983) found that the extent of root branching was very regular for Sitka spruce and could be estimated from the aboveground stem diameter. Smith (1964) reported that root size of Douglas fir, lodgepole pine and other British Columbia tree species could be estimated from aboveground measurements. In banana, Swennen (1984) and Blomme and Ortiz (1996) established positive correlations between root traits and aboveground plant characteristics, while Gousseland (1983) found that the number of cord roots of the 'Giant Cavendish' dessert banana can be estimated from the leaf area. This indicates that root growth is linked to shoot growth in banana, but environmental or developmental influences were not investigated.

Root sampling constitutes a third alternative to quickly estimate the total root size. Fort and Shaw (1998) found substantial correspondence between variability for soil core samples and whole-plant root mass of strawberry, indicating that changes in the root system growth can be effectively estimated from soil cores. Soil core samples required no more than 10% of the time to collect and process the entire plant root system. It is not clear whether this approach is applicable to plantain and bananas.

Research in carrot, maize, oats, onion, sunflower and tomato showed that root mass can be indirectly estimated from the plant's capacitance value (Chloupek 1972, Chloupek 1977, Dalton 1995, Van Beem *et al.* 1998). As the *Musa* plant tissue contains a lot of water, thus securing a high electrical conductivity, the potential of this root assessment method was investigated.

Banana and plantain agronomy and breeding stand to gain a lot from improved knowledge of root growth and development. Since excavation of entire root systems is laborious, destructive and provides non-dynamic insights, methods that are fast, easy to execute and that can be repeated over time on a same plant are needed. Therefore, the objectives of this study were to determine (i) the relationships between juvenile and adult root size, (ii) the relationships between root size and shoot traits, (iii) the optimum core sampling method for adequate estimation of the root system size and (iv) the relationship between capacitance values and root system size.

Materials and methods

Site characteristics

Experiments were carried out at the High Rainfall station of the International Institute of Tropical Agriculture at Onne (4°42' N, 7°10' E, 10 m altitude above sea level) in southeastern Nigeria. The station is located in a degraded rainforest-swamp. Annual rainfall is 2400 mm, unimodal and distributed from February until November. The soil is derived from coastal sediments. It is a deep and freely drained Typic Paleudult/ Haplic Acrisol (FAO/ISRIC 1998) of the coarse-loamy, siliceous isohyperthermic family. Nutrient status is poor, except for P, and pH is low (pH 4.3 in 1:1 H_2O in the upper 15 cm). Detailed characteristics of the station have been described elsewhere (Ortiz *et al*. 1997).

Agronomic practices

All fields had been under eight years of grass fallow before no-tillage planting of Musa spp. All fields were maintained similarly and this included the nematicide Nemacur application (a.i. fenamiphos) at a rate of 15 g/plant (3 treatments/year). In addition, fertilization was done with muriate of potash (50% K) at a rate of 600g/plant/year, and urea (46% N) at a rate of 300 g/plant/year, split over 6 equal applications during the rainy season. No mulch was applied. Furthermore, the fungicide Bayfidan (a.i. triadimenol) was applied 3 times/yearat a rate of 3.6 ml/plant to reduce black Sigatoka (Mycosphaerella fijiensis Morelet).

Early root screening

Three experiments were carried out. The first and second experiment involved, respectively, *in vitro* micro-propagated and sucker-derived plants of eight polyploid genotypes (Table 1) including the dessert bananas 'Yangambi km 5' and 'Valery' (AAA group), the plantain 'Obino l'ewai' (AAB group), the cooking bananas 'Cardaba' and 'Fougamou' (ABB group), the plantain-derived hybrids 'PITA2' and 'PITA7', and the cooking banana hybrid 'FHIA-03' (Swennen 1990b, Daniells *et al.* 2001). The third experiment involved *in vitro*-derived plants of 8 diploid accessions (Table 1), namely, 'Niyarma yik', 'Calcutta 4', 'Pahang', 'Pisang jari buaya', 'Pisang madu', 'Tjau lagada', 'Kisubi' and 'Pisang Berlin'. Micropropagated plants were produced following standard shoot-tip culture techniques (Vuylsteke 1989 and 1998). The plantlets were acclimatized for 6 weeks in a greenhouse nursery (Vuylsteke 1998, Vuylsteke and Talengera 1998), before field transplantation in May and June 1996, for the first and third experiment, respectively. In the second experiment, suckers were prepared as recommended by Swennen (1990a) and field planted in June 1996.

The experimental layout was a split plot within a randomized complete block design with two replications of two plants per genotype. Main plot treatments consisted of different times of observation. In the first and third experiment, data were collected from 6-week-old nursery plants, while field measurements were done on 12, 16 and 20-week-old plants, and at bunch emergence. In the second experiment, measurements were carried out in the field on plants aged 6, 12, 16 and 20 weeks, and at bunch emergence. Subplot treatments consisted of genotypes. Plant spacing in the field was 2 m x 2 m, except for plants evaluated at bunch emergence, which were spaced 4 m x 4 m to avoid root entanglement between neighbouring plants. The fields were irrigated during the dry season at a rate of 100 mm per month.

Data collection was carried out on the following corm and root characteristics: corm fresh weight (CW, g), corm height (CH, cm), widest width of the corm (WW, cm), number of suckers (NS) on the corm, number of adventitious or cord roots (NR), cord root length (LR, cm), the average diameter of cord roots at their base (AD, mm), and root dry weight (DR, g). The cord root length was measured using the line intersect method (Tennant 1975), while the diameter of the root was measured with Vernier calipers.

Estimating root traits from shoot traits

Twenty-seven genotypes representing the various *Musa* genome and ploidy groups were assessed in this experiment (Table 1). The planting material was obtained through meristem culture using the methods of Vuylsteke (1989 and 1998). Field transplanting

Table 1. Name, genome/parentage, ploidy level, type and suckering behavior of genotypes evaluated for rooting.

Name	Genome parentage	Ploidy level	Type	Suckering behaviour#	ES*	MR	SC	CM
'Niyarma yik'	AA	2	*Musa acuminata* ssp. *banksii*	Inhibited	3	X		
'Calcutta 4'	AA	2	*Musa acuminata* ssp. *burmannica*	Non-regulated	3	X	1	X
'Pahang'	AA	2	*Musa acuminata* ssp. *malaccensis*	Non-regulated	3	X		
'Pisang jari buaya'	AA	2	*Musa acuminata* ssp. *microcarpa*	Regulated	3	X		
'Pisang madu'	AA	2	*Musa acuminata* ssp. *microcarpa*	Regulated	3	X		
'Tjau lagada'	AA	2	*Musa acuminata* ssp. *microcarpa*	Regulated	3	X		
'Kisubi'	AB	2	Dessert banana	Regulated	3	X		
'Pisang Berlin'		2	Diploid indeterminate group	Regulated	3	X		
TMB2x 9128-3	AA x AA	2	Hybrid (Tjau lagada x Pisang lilin)	Non-regulated		X	2	
TMB2x 5265-1	AA x AA	2	Hybrid (Tjau lagada x Calcutta 4)	Non-regulated		X		
TMP2x 1297-3	AAB x AA	2	Plantain hybrid (Agbagba french reversion x Calcutta 4)	Non-regulated		X		
TMP2x 2829-62	AAB x AA	2	Plantain hybrid (Bobby tannap x Calcutta 4)	Non-regulated			2	
'Pisang M. hijau'	AAA	3	Dessert banana	Regulated		X		
'Yangambi km5'	AAA	3	Dessert banana	Non-regulated	1&2	X		X
'Valery'	AAA	3	Dessert banana	Regulated	1&2	X		X
'Rajapuri' India	AAB	3	Dessert banana	Regulated		X		
'Obino l'ewai'	AAB	3	Plantain	Inhibited	1&2	X		X
'Bobby tannap'	AAB	3	Plantain	Inhibited		X		
'Mbi egome'	AAB	3	Plantain	Regulated			1	X
'Muracho'	AAB	3	Starchy banana	Regulated		X		
'Mysore'	AAB	3	Dessert banana	Regulated		X		
'Pisang awak'	ABB	3	Cooking banana	Regulated		X		
'Foulah 4'	ABB	3	Cooking banana	Regulated		X		
'Cardaba'	ABB	3	Cooking banana	Regulated	1&2	X		X
'Fougamou'	ABB	3	Cooking banana	Regulated		X		X
IC 2	AAAA	4	Dessert banana	Regulated		X		
TMP4x 1621-1	AAB x AA	4	Plantain hybrid (Obino l'ewai x Calcutta 4)	Regulated		X		
TMP4x 548-9	AAB x AA	4	Plantain hybrid (Obino l'ewai x Calcutta 4)	Regulated	1&2	X		X
TMP4x 5511-2	AAB x AA	4	Plantain hybrid (Obino l'ewai x Calcutta 4)	Inhibited		X		
TMP4x 1658-4	AAB x AA	4	Plantain hybrid (Obino l'ewai x Pisang lilin)	Regulated	1&2			X
FHIA-03	ABB x AA	4	Cooking banana hybrid (SH-3386 x SH-3320)	Regulated	1&2			X

* CM: Capacitance Method, ES: Early Screening method, MR: Multiple Regression method, SC: Soil Core method. Within the methods, numbers show the experiment number in which the method was used. #: Suckering behaviour is inhibited when suckers do not grow fast until flowering of the parent plant; is regulated if 1-3 suckers grow very well before flowering; is non-regulated if almost all suckers grow well before flowering.

was done in June 1996 at a spacing of 2 m x 2 m. The experimental design was a randomized complete block with two replications of two plants per genotype. Shoot and root traits were assessed during mid-vegetative growth (i.e. 20-week-old plants). Shoot growth characteristics included plant height (PH, cm), circumference of the pseudostem at soil level (PC, cm), height of the tallest sucker (LS, cm), number of leaves (NL) and leaf area (LA, cm2). Leaf length and maximum leaf width were measured and LA was calculated according to Obiefuna and Ndubizu (1979). The corm and roots were completely dug out and assessed as described above. Total cord root length (TL, cm) of the mat (i.e. main plant and suckers) and total root dry weight of the mat (TD, g) were also measured. The tallest sucker was separated from the main plant and the same characteristics as above were measured.

Core sampling

In the first experiment, the small French plantain 'Mbi egome' (Swennen 1990b) and the wild diploid banana 'Calcutta 4' were assessed (Table 1). 'Calcutta 4' has a non-regulated suckering (all suckers grow simultaneously), while 'Mbi egome' has a regulated suckering behaviour (one or two suckers grow vigorously). Sucker-derived plants of 'Mbi egome' and *in vitro*-derived plants of 'Calcutta 4' were field established in August 1997. Suckers were prepared and planted according to Swennen (1990a). *In vitro*-derived plants of Calcutta 4 were grown in polybags for 6 weeks in the greenhouse before field planting. Plant spacing was 4 m x 4 m. In the second experiment, 30 progenies from a cross between two diploid hybrids, 'TMB2 x 2829-62' and 'TMB2 x 9128-3' were assessed (Table 1). Micro-propagated plants were obtained, as in experiment one, and were established in the field during August 1996 at a spacing of 3 m x 2 m. In both experiments, treatments were completely randomized.

Sixty-week-old mats were assessed in experiment one. Eight soil core samples were taken at 15 cm from the plant base. The first sample was taken near the biggest sucker and where the future axial sucker would emerge. Subsequent samples were taken clockwise at 45° intervals. Soil cores had 25 cm diameter and a 80 cm height. Soil cores were taken with a metal cylinder. Samples were washed to free roots from soil and the following characteristics were measured for each sample: number of adventitious or cord roots (NR), root dry weight (DR, g) and cord root length (LR, cm). The same characteristics were measured for the entire plant, which was excavated after core sampling. In the second experiment, root assessment was carried out as in experiment one but in July 1999 on 3-year-old mats. Three soil cores were taken per plant including the position next to the tallest sucker and at 90° and 180° clockwise from the tallest sucker.

Capacitance measurements

Measurements were carried out on *in vitro* and sucker-derived plants of different ages (Table 1). Variability in capacitance values was assessed according to the position of the electrodes (Figure 1). The soil-based positive electrode was placed at different soil depths and distances from the plant. The negative electrode was inserted in the pseudostem at variable heights and depths. Also the influence of corm size, soil temperature and water content on capacitance was investigated.

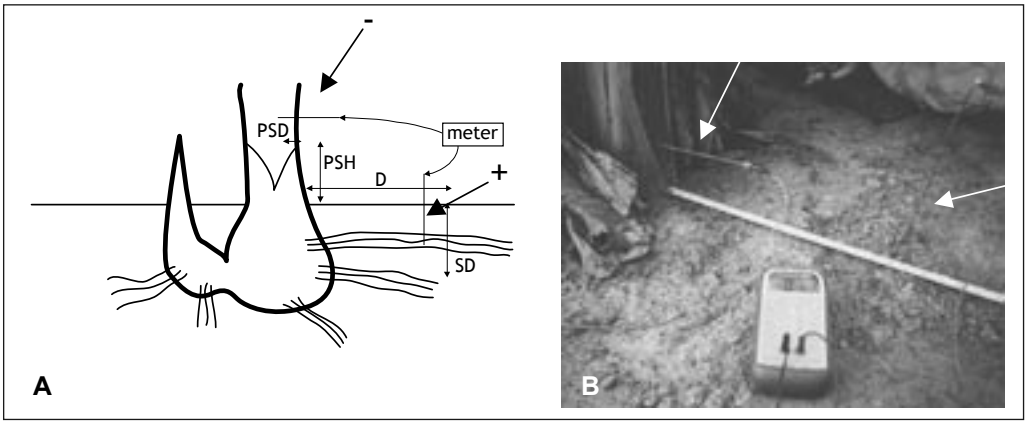


Figure 1. (A) Traits defining the position of both electrodes (PSH: Pseudostem Height, PSD: Pseudostem Depth, D: Distance from the pseudostem, SD: Soil Depth); (B) Measuring the capacitance; the arrows indicate the electrodes.

Statistical analysis

Statistical analysis was carried out using the SAS statistical package (SAS 1989). For the early screening experiments, simple Pearson correlation coefficients between identical root growth characteristics of plants at different ages across genotypes were calculated. Simple correlation and multiple regression analyses were used to estimate the relationships between aerial growth and root system characteristics. Regression was carried out using stepwise selection with root characteristics as dependent variables and shoot traits as independent variables. Ploidy level was also included as an independent variable in the regression analysis.

Data from the core sampling experiments were subjected to ANOVA to determine the effects of plant and sampling location on soil core root characteristics. Root characteristics of the core samples were regressed on whole plant root traits. Data from the capacitance experiments were subjected to ANOVA to determine the effects of the position of the electrodes on the capacitance values. To find relationships between the capacitance values and the root parameters, scatter plots and linear correlation analyses (Proc CORR in SAS) were carried out on the complete data set but also according to the type of planting material and the age of the plants.

Results and discussion

Early root screening

Few significant correlations were observed for corm and root traits between the different growth stages of diploid, triploid and tetraploid genotypes in all three experiments (Tables 2 and 3). Significant positive correlations were mostly observed for *in vitro*-derived plants. There were very few correlations for the traits considered in all three experiments between plants at 6 weeks after planting and plants in the mid-vegetative stage (*i.e.* 20 weeks old) or plants at bunch emergence. An increased difference in plant age reduced the number of significant correlations (Tables 2 and 3). Absence of significant correlations with sucker-derived plants might be attributed to differences in

Table 2. Correlation coefficients between identical growth characteristics at different ages for *in vitro* and sucker-derived triploid and tetraploid plants.

	Trait #										
in vitro	**CW**	**CH**	**WW**	**DR**	**NR**	**LR**	**AD**	**TD**	**TL**	**LS**	**NS**
6,12 (1)	na	na	na	0.34	0.22	0.38	0.39	0.34	0.37	na	na
6,16	na	na	na	0.22	0.61	0.12	0.4	0.08	-0.02	na	na
6,20	na	na	na	0.41	0.13	0.20	0.05	0.22	0.1	na	na
6,Fl (2)	na	na	na	0.75*	0.57	0.30	0.03	0.18	-0.3	na	na
12,16	0.17	0.15	0.49	0.71*	0.26	0.47	0.56	0.66	0.5	0.58	0.47
12,20	0.27	0.52	0.34	0.87**	-0.03	0.60	0.46	0.91**	0.81*	0.64	0.1
12,Fl	-0.32	-0.33	-0.18	0.07	-0.18	-0.45	0.24	0.12	-0.22	-0.03	0.27
16,20	-0.18	-0.03	-0.01	0.62	0.35	0.58	0.73*	0.70	0.6	0.98***	0.89**
16,Fl	0.22	0.34	0.03	-0.05	0.29	0.18	0.06	0.33	0.42	0.45	0.87**
20,Fl	0.07	-0.07	-0.22	0.37	0.39	-0.16	0.26	0.41	-0.07	0.42	0.87*
Sucker-derived	**CW**	**CH**	**WW**	**DR**	**NR**	**LR**	**AD**	**TD**	**TL**		
6,12	-0.10	-0.30	0.03	-0.18	-0.06	0.07	0.14	-0.18	0.07		
6,16	0.44	0.60	0.11	0.46	0.55	0.40	-0.23	0.46	0.40		
6,20	-0.22	-0.52	-0.69	0.32	-0.10	0.20	0.39	0.32	0.20		
6,Fl	0.07	0.39	-0.20	-0.40	-0.09	-0.60	0.15	-0.12	-0.37		
12,16	-0.30	-0.69	-0.10	0.22	0.17	0.41	-0.22	0.22	0.41		
12,20	0.40	0.48	-0.53	-0.47	-0.20	-0.20	-0.31	-0.47	-0.20		
12,Fl	0.36	0.13	0.29	0.29	-0.65	-0.18	-0.50	0.42	0.08		
16,20	0.03	-0.19	-0.10	0.64	0.10	0.68	0.15	0.64	0.68		
16,Fl	-0.35	-0.21	-0.67	0.35	0.13	-0.78*	0.01	0.79*	0.21		
20,Fl	0.33	-0.06	0.09	0.33	0.04	-0.32	0.67	0.52	0.32		

#: AD: average basal cord root diameter (mm), CH: corm height (cm), CW: corm fresh weight (g), DR: root dry weight (g), LR: cord root length (cm), LS: height of the tallest sucker (cm), NR: number of cord roots, NS: number of suckers, TD: total root dry weight of the mat (g), TL: total length of the cord roots of the mat (cm), WW: corm widest width (cm)

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

(1): 6,12: correlation between plants aged 6 and 12 weeks, (2) Fl: at flower emergence

na: not applicable.

physiological age of the suckers at planting, which influenced subsequent growth. In addition, large genotypic variation exists for vegetative growth cycle and plant size at bunch emergence (Swennen and Vuylsteke 1987), which may explain the absence of correlations between root growth during the early vegetative stage and early reproductive stage in both propagule types. We conclude that the root characteristics of adult plants cannot be estimated from the root size of juvenile plants irrespective of the type of planting material.

Estimating root traits from shoot traits

Significant correlation coefficients between aerial and root system characteristics were found during vegetative development (Table 4) confirming earlier reports (Beugnon and Champion 1966, Gousseland 1983, Swennen 1984, Lavigne 1987, Blomme and

Table 3. Correlation coefficients between identical growth characteristics at different ages for *in vitro*-derived diploid plants.

	Trait #										
in vitro	CW	CH	WW	DR	NR	LR	AD	TD	TL	LS	NS
6,12 (1)	na	na	na	-0.48	-0.37	-0.25	0.79*	-0.48	-0.25	na	na
6,16	na	na	na	-0.09	-0.27	-0.18	0.33	-0.22	-0.25	na	na
6,20	na	na	na	0.38	0.56	0.52	0.11	0.36	0.46	na	na
6,Fl (2)	na	na	na	-0.03	-0.76*	-0.42	0.05	-0.26	-0.40	na	na
12,16	0.61	0.53	0.65	0.46	0.64	0.80*	0.68	0.62	0.85*	-0.24	0.11
12,20	0.25	0.66	-0.01	0.13	0.22	0.36	-0.42	0.31	0.45	-0.67	0.48
12,Fl	0.01	-0.09	0.17	0.17	-0.20	-0.35	0.40	0.37	-0.16	-0.06	0.91**
16,20	0.05	0.76*	-0.22	0.41	0.36	0.73*	-0.13	0.47	0.80*	0.77*	0.13
16,Fl	-0.12	-0.03	0.01	0.37	0.03	0.09	0.06	0.15	0.14	0.43	0.02
20,Fl	0.40	-0.43	0.47	0.19	0.04	0.10	-0.15	0.44	0.27	0.48	0.44

AD: average basal cord root diameter (mm), CH: corm height (cm), CW: corm fresh weight (g), DR: root dry weight (g), LR: cord root length (cm), LS: height of the tallest sucker (cm), NR: number of cord roots, NS: number of suckers, TD: total root dry weight of the mat (g), TL: total length of the cord roots of the mat (cm), WW: corm widest width (cm)

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

(1): 6,12: correlation between plants aged 6 and 12 weeks, (2) Fl: at flower emergence

na: not applicable.

Table 4. Correlation coefficients (P<0.05) between aerial growth and root system characteristics at 20 weeks after planting.

Trait #	**LA**	**PH**	**PC**	**LS**
DR	0.72***	0.65***	0.65***	-0.09
NR	0.46*	0.41*	0.29	0.16
LR	0.64***	0.54**	0.46*	0.08
AD	0.47*	0.51**	0.70***	-0.38*
TD	0.65***	0.53**	0.38	0.2
TL	0.41*	0.25	0.01	0.49*

#: AD: average basal cord root diameter (mm), DR: root dry weight (g), LA: leaf area (cm2), LR: cord root length (cm), LS: height of the tallest sucker (cm), NR: number of cord roots, PC: plant circumference (cm), PH: plant height (cm), TD: total root dry weight of the mat (g), TL: total length of the cord roots of the mat (cm)

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

Ortiz 1996). Similar relationships between root and shoot traits were also found for the East African highland bananas (AAA-EA group) (Sebuwufu *et al*. 2004). Furthermore, regression analysis produced several equations (Table 5) that attributed at least 90% of the variation in root growth to variation in shoot development. The best shoot indicators of root growth were leaf area, pseudostem circumference and height of the tallest sucker. Swennen (1984) already demonstrated that ratooning can be improved by increasing rooting of the parent plant.

These regression models suggest that a reduced leaf area, as caused by black Sigatoka, will adversely affect root development. Hence increased (photosynthetically active) leaf area (from optimal plant spacing, thereby reduced shading) and improved nutrient

Table 5. Regression models to predict root system characteristics at 20 weeks after planting using aerial growth characteristics and ploidy level as independent variables.

	Trait # (Independent variables)				
Trait #	**LA**	**PC**	**LS**	**PL**	**R2**
DR	0.00163***	0.596**			0.93
NR	0.00146***	1.255***			0.93
LR	0.0667***	23.47**	0.94		
AD		0.0938***		0.681***	0.97
TD	0.00207***	0.426	0.171*		0.93
TL	0.0995***		14.69***		0.92

#: AD: average basal cord root diameter (mm), DR: root dry weight (g), LA: leaf area (cm^2), LR: cord root length (cm), LS: height of the tallest sucker (cm), NR: number of cord roots, PC: plant circumference (cm), PL: ploidy level, TD: total root dry weight of the mat (g), TL: total length of the cord roots of the mat (cm)

^: independent variables

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

status of the plant would stimulate root development. Indeed roots are sinks for assimilates that need to come from functional leaves. The pseudostem is made up of leaf sheaths and hence reflects the number of leaves and plant vigour. Plant pseudostem circumference thus reflects shoot growth and is an important determinant of root vigour in the regression models.

The size of the tallest sucker reflected positively the extent of the mat root system. Most suckers observed on 20-week-old plants were peepers (*i.e.* small sucker with scale leaves) or sword suckers (*i.e.* larger sucker with lanceolate leaves). The latter suckers have their own root system, confirming observations by Robin and Champion (1962) and Beugnon and Champion (1966). The observed positive effect of ploidy on cord root diameter confirms earlier observations by Monnet and Charpentier (1965).

Shoot-to-root ratios depend on the developmental stage of a plant (Brouwer 1966). In banana, Gousseland (1983) estimated cord root number from leaf area and reported an effect of plant developmental phase on the accuracy of the regression model. He reported that the number of cord roots is underestimated during the early vegetative phase. Shoot-to-root ratios also vary across environments (Brouwer and De Wit 1969, Squire 1993, Martinez Garnica 1997, McMichael and Burke 1998, Blomme 2000). Refinement of the regression equations is needed by taking account of the plant developmental stage and environmental conditions. In conclusion *Musa* root system development can be estimated from easily measurable above ground characteristics. This provides a fast and non-destructive assessment of root development.

Core sampling

Most roots of the assessed mats were observed within a 60 cm radius from the plant and up to 70 cm depth. For the first experiment, data on root characteristics obtained through soil core sampling involved about 1.1 to 2.6% of the total root system, depending on the root trait under consideration (Table 6). For 'Calcutta 4', a significant inter-plant effect was observed for the dry weight, number and length of the roots present in soil cores (Table 7). This can be explained by the high variability in mat root system size (Table 6). However, no significant differences were observed for sampling

Table 6. Mean and coefficient of variation for different root (whole mat and soil core) characteristics for 60 weeks old 'Calcutta 4' and 'Mbi egome' mats.

		Genotype			
		Calcutta 4		Mbi egome	
Trait #		Mean	CV (%)	Mean	CV (%)
DR	Whole mat	262.9	37	336.0	43
	Soil core	2.9	71	4.4	56
	Soil core/Whole mat (%)	1.1	66	1.4	52
NR	Whole mat	491.0	22	465.5	22
	Soil core	13.0	49	11.5	44
	Soil core/Whole mat (%)	2.7	44	2.5	44
LR	Whole mat	10809.2	31	10200.0	26
	Soil core	238.1	47	259.5	40
	Soil core/Whole mat (%)	2.2	36	2.6	37

#: DR: root dry weight (g), NR: number of cord roots, LR: cord root length (cm).

Table 7. Mean squares and significance for different soil core root characteristics for 60 weeks old 'Calcutta 4' and 'Mbi Egome' mats.

			Trait #		
Genotype	Source of variation	df	DR	NR	LR
Calcutta 4	Plant	10	16.0***	141.0***	55,998***
	Sampling location	7	2.17	25.92	7661
	Residual	70	2.70	28.30	6981
Mbi egome	Plant	11	15.31***	34.33	25,642***
	Sampling location	7	19.65***	52.78*	23,683**
	Residual	77	3.61	20.89	7,244

#: DR: root dry weight (g), NR: number of cord roots, LR: cord root length (cm)
*, **, *** Significant at P<0.05, 0.01 and 0.001, respectively.

location within a plant (Table 7). This could be due to the high number of well-developed suckers uniformly spaced around the main plant. Significant inter-plant differences in root characteristics were also observed for 'Mbi Egome', but the effects of sampling location were even more important (Table 7), which may be explained by the regulated suckering behavior (*i.e.* development of 1-3 large suckers on the plant) of this cultivar causing sucker root systems to be less uniformly distributed around the main plant.

Root dry weight, number and length of the cord roots in the core samples were regressed on the corresponding characteristics from the mat. All models were significant at $p<0.01$, with $R^2 \geq 0.58$, 0.73 and 0.81 for regressions based on 1 or 2 (Table 8), or 3 core samples (data not shown), respectively. Sampling locations nearest to the tallest sucker did not increase R^2 values (Table 8). Data from the second experiment also revealed large differences attributable to variation in suckering behavior among the 30 genotypes assessed. However, this did not appear to affect the regression of core samples on whole plants for root size estimation. The lowest R^2 values were obtained with single core samples and were respectively 0.71, 0.81 and 0.78 for root dry weight,

Table 8. R^2 values for root dry weight, cord root number and cord root length, of regressions between one (A)/two (B) soil core sample(s) and whole mat samples for 60 weeks old 'Calcutta 4' and 'Mbi egome' mats.

A											
Genotype	Trait #	Sample No. (1)									
		1	2	3	4	5	6	7	8		
Calcutta 4	DR	0.73	0.79	0.81	0.80	0.88	0.58	0.78	0.92		
	NR	0.90	0.91	0.86	0.78	0.93	0.83	0.80	0.86		
	LR	0.94	0.90	0.92	0.83	0.95	0.88	0.90	0.95		
Mbi egome	DR	0.73	0.75	0.88	0.68	0.79	0.79	0.94	0.87		
	NR	0.79	0.86	0.93	0.73	0.84	0.95	0.98	0.83		
	LR	0.89	0.90	0.90	0.84	0.91	0.96	0.98	0.91		
B		Sample No.									
		1,2	1,3	1,4	1,5	1,6	1,7	1,8	2,3	2,4	2,5
Calcutta 4	DR	0.82	0.85	0.80	0.85	0.82	0.85	0.88	0.86	0.87	0.90
	NR	0.95	0.94	0.88	0.94	0.95	0.91	0.94	0.89	0.92	0.96
	LR	0.96	0.97	0.93	0.97	0.97	0.96	0.97	0.92	0.93	0.97
Mbi egome	DR	0.82	0.90	0.79	0.86	0.80	0.95	0.91	0.87	0.80	0.79
	NR	0.90	0.94	0.85	0.89	0.90	0.97	0.92	0.96	0.89	0.87
	LR	0.95	0.96	0.92	0.95	0.94	0.99	0.97	0.94	0.92	0.93
		2,6	2,7	2,8	3,4	3,5	3,6	3,7	3,8	4,5	
Calcutta 4	DR	0.81	0.83	0.89	0.84	0.91	0.89	0.88	0.94	0.91	
	NR	0.94	0.90	0.92	0.87	0.94	0.92	0.88	0.90	0.90	
	LR	0.95	0.93	0.96	0.92	0.96	0.96	0.95	0.97	0.94	
Mbi egome	DR	0.83	0.93	0.90	0.88	0.88	0.89	0.94	0.90	0.80	
	NR	0.95	0.98	0.93	0.92	0.96	0.98	0.97	0.91	0.88	
	LR	0.96	0.97	0.98	0.94	0.95	0.97	0.96	0.94	0.94	
		4,6	4,7	4,8	5,6	5,7	5,8	6,7	6,8	7,8	
Calcutta 4	DR	0.87	0.89	0.96	0.79	0.87	0.93	0.73	0.84	0.92	
	NR	0.91	0.88	0.93	0.92	0.92	0.94	0.87	0.92	0.87	
	LR	0.96	0.96	0.97	0.94	0.95	0.98	0.91	0.96	0.95	
Mbi egome	DR	0.79	0.93	0.84	0.84	0.92	0.88	0.93	0.88	0.93	
	NR	0.90	0.94	0.85	0.94	0.97	0.92	0.99	0.95	0.94	
	LR	0.94	0.97	0.92	0.96	0.97	0.98	0.98	0.97	0.97	

number of cord roots and cord root length (Table 9). At least 80% of the variation in mat root traits could be explained by taking two core samples, while 85% could be explained with three core samples.

Table 9. R^2 values for root dry weight (DR), cord root number (NR) and cord root length (LR), of regressions between single, double and triple soil core samples and the whole mat samples for 30 progenies from a cross between 'TMPx 2829-62' and 'TMPx 9128-3'.

	Sample No. (1)						
Trait #	1	2	3	1,2	1,3	2,3	1,2,3
DR	0.78	0.80	0.71	0.86	0.81	0.80	0.85
NR	0.86	0.86	0.81	0.91	0.87	0.89	0.90
LR	0.85	0.86	0.78	0.91	0.85	0.88	0.89

#: DR: root dry weight (g), NR: number of cord roots, LR: cord root length (cm)

(1) Sample 1 corresponds to site of the future axial sucker; the following samples are taken clockwise around the parent plant at 45 degree intervals.

The results from both experiments indicate that mat root system characteristics can be adequately estimated from two soil core samples. Moreover, root samples collected from two soil cores requires only 5% of the time needed to excavate and measure the entire root system of an adult *Musa* plant.

Capacitance measurements

Distance of the soil-based electrode from the plant had no significant effect on capacitance readings (Table 10). In contrast, soil depth, pseudostem height and insertion depth, soil temperature and water content had a significant effect on capacitance. Very few significant correlations between capacitance values and root system traits were found. The specific morphology of the banana plant might be the cause. For example, the enclasping leaf sheaths with their numerous air spaces that make up the pseudostem and the underground corm (*i.e.* the real stem) with many suckers, might influence the capacitance readings. Therefore root system traits of juvenile and adult field-grown *Musa* spp. plants cannot yet be estimated through capacitance measurements.

In conclusion, root systems can best be assessed from shoot measurement and root core sampling as both methods are fast, easy to execute and can be repeated over time on the same plant. Hence a dynamic picture on root development can be developed. Both methods however are location specific.

Table 10. Mean square and significance tests for the capacitance value.

Source of variation #	df	Mean square for capacitance
PSH	1	0.325***
PSD	2	0.784***
D	2	0.0057
SD	3	0.590***

#: PSH: pseudostem height, PSD: pseudostem depth, D: distance from the pseudostem, SD: soil depth. *, **, *** Significant at P<0.05, 0.01 and 0.001, respectively.

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Distribution of banana roots in time and space: new tools for an old science

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Abstract

The distribution of plant roots is the ultimate manifestation of a series of biological processes that operate throughout the plant's life, in an integrated way, to establish new roots, to regulate the rate of root extension, to influence the direction of root growth and to contribute to root survival. This, combined with the practical difficulties of its estimation, makes root distribution a fairly complex character of plants. Still, root distribution is of paramount significance. It determines the exchange surface between the plant and the soil, the volume of soil influenced by root activity, the depth of soil exploration, the amount of carbohydrates devoted by the plant to root growth and development, the likelihood of infection by soil microorganisms and many other quantitative aspects of the soil/plant system.

Since one of the first reports on the roots of bananas by Fawcett (1921), we have collected more than a hundred contributions in connection with the banana root system. These include descriptions of banana roots and root system, quantitative studies on root growth and its response to environmental factors, anatomical details on root initiation and branching, reports of root distribution and root function (especially water and nutrient uptake), analyses of the interactions between roots and soil pathogens or mycorrhizal fungi and, more recently, germplasm evaluations for some root traits. Fifteen reports are really informative with respect to the spatial distribution of banana roots. They provide a rather unified qualitative picture of how many and where banana root axes ('cord roots') are most likely to be found.

Little is known of the lateral roots and root hairs, which contribute significantly to water and nutrient uptake. Compared with the long-lived root axes, they are clearly transient structures. Anatomical data show that they are initiated from root axes following an acropetal sequence. Therefore, the maintenance of a sufficient pool of lateral roots and root hairs depends on the continued production and growth of root axes. As a result, the volume of soil where uptake of water and nutrients occurs is continuously changing as a function of root growth and production. Unfortunately, these time-related components of root distribution remain poorly addressed.

An important question to be raised with regards to root distribution studies is whether a realistic improvement of root traits, be it for performance or sustainability, can be achieved in the future. Available options are the identification, selection or development of improved germplasm, as well as the development/adoption of appropriate cultivation practices. The existence of a significant genetic polymorphism for a number of root traits and the reported tremendous effects of soil conditions on root growth and development support both options. However, there is an urgent need for a list of desirable root properties to achieve better crop performance. This is probably where data are critically lacking. Nonetheless, with existing information we can simulate root architecture in a dynamic way and begin to evaluate current practices. We present an example of the evaluation of sampling practices using a dynamic simulation of a banana root system.

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Resumen - Distribución de las raíces de banano en tiempo y espacio: nuevas herramientas para una ciencia antigua

La distribución de las raíces en la planta es la manifestación última de una serie de procesos biológicos que ocurren de manera integrada durante la vida de la planta, para establecer nuevas raíces, regular su índice de extensión, influenciar la dirección de su crecimiento y contribuir a su supervivencia. Lo anterior, combinado con las dificultades prácticas para su estimación, hacen que la distribución de la raíz sea una característica bastante compleja de las plantas. Aún así, la distribución de la raíz es de extrema importancia, pues ella es la superficie de intercambio entre la planta y el suelo y de allí depende el volumen de suelo influenciado por la actividad de la raíz, la profundidad de exploración del suelo, la cantidad de carbohidratos utilizados por la planta para el crecimiento y desarrollo de la raíz, la probabilidad de infecciones por micro organismos del suelo y muchos otros aspectos cuantitativos del sistema suelo-planta.

Desde los primeros informes sobre raíces por Fawcett (1921), hemos recolectado más de cien contribuciones relacionadas con el sistema radical del banano. Entre éstas tenemos descripciones de las raíces de banano y de su sistema radical; estudios cuantitativos sobre el crecimiento de la raíz y su respuesta a factores ambientales; detalles anatómicos sobre la iniciación de la raíz y sus ramificaciones; informes sobre distribución y función de las raíces (especialmente absorción de agua y nutrientes); análisis de las interacciones entre raíces y patógenos del suelo u hongos micorrícicos; y más recientemente, evaluaciones de germoplasma para algunas características de las raíces. Quince de éstas contribuciones ofrecen bastante información sobre la distribución espacial de las raíces de banano y presentan un panorama cualitativo bastante unificado de cuántos y donde es más probable encontrar los ejes ("raíces primarias") del sistema radical del banano.

Se conoce poco sobre las raíces laterales y pelos absorbentes, los cuales contribuyen significativamente a la absorción de agua y nutrientes. Comparados con los ejes de raíz de larga vida, éstas son estructuras transitorias. La información anatómica muestra que se inician en los ejes radiculares, siguiendo una secuencia acropétalo. Por lo tanto, el mantenimiento de reservas suficientes de raíces laterales y pelos absorbentes depende de la producción continua y del crecimiento de los ejes radiculares. En consecuencia, el volumen de suelo utilizado por la raíz para absorber agua y nutrientes se mantiene en constante cambio, como una función del crecimiento y producción de raíces. Desafortunadamente, el tipo de componentes relacionados con el tiempo de distribución de las raíces a recibido poca atención.

Una pregunta importante que se debe plantear con respecto a los estudios de distribución de raíces, sean éstos para propósitos de rendimiento o sostenibilidad, es si será posible lograr en el futuro un mejoramiento realista de las características de la raíz. Algunas opciones disponibles son la identificación, selección y desarrollo de germoplasma mejorado, así como el desarrollo/adopción de prácticas apropiadas de cultivo. La existencia de un polimorfismo genético significativo en varias características de la raíz y el tremendo efecto reportado de las condiciones del suelo sobre el crecimiento y desarrollo de las raíces apoyan ambas opciones. Sin embargo, existe una urgente necesidad de una lista de propiedades deseables en las raíces para obtener mejores rendimientos de cultivo. Este es probablemente el aspecto en el cual se necesita mayor información. Sin embargo, con la información existente podemos simular la arquitectura del sistema radicular en una forma dinámica y empezar a evaluar las practicas actuales. Presentamos aquí un ejemplo de la evaluación de las practicas de muestreo, usando una simulación dinámica del sistema radical del banano.

Introduction

There is a fairly general agreement about the typical horizontal and vertical distributions of the banana root system: 90% of the roots extend within one meter from the plant, with about 70% of the total root mass of banana plants being confined in the upper 20 to 40 cm of the soil (Fawcett 1921, Champion and Sioussaram 1970, Lassoudière 1978,

Gousseland 1983, Robinson 1985, Araya *et al.* 1998). One may therefore ask: why a new report on the distribution of banana roots?

A root system is a population of roots of different types and ages that evolve continuously as a result of root formation, growth and senescence. This means that the overall capacity of the root system to keep pace with the various demands placed on it depends on the ability of the plant to maintain an appropriate root population. In this context, what really matters is to understand how the root system responds to environmental constraints and how root form interacts with root function and plant health. The fact that this meeting has been organized is a clear indication that current management practices based on an average picture of banana root distribution remain unsatisfactory.

There is therefore an urgent need for studies of root system architecture that would account for root distribution in space and in time. Only such studies will provide the unifying framework to co-analyse e.g., the processes of soil exploration and resource acquisition, the dynamics of root activity in the rhizosphere and the space-time dynamics of plant-interacting soil organisms.

Much has been accomplished since the first report on *Musa* root architecture at the beginning of the last century (Hartman *et al.* 1928) and reviews of this work have been recently published (Price 1995, Draye 2002a). The purpose of this paper is to highlight the dynamics of soil exploration by the banana root system and to illustrate ways to use this information to address root distribution in time and space.

Production, growth, directions and survival of the various banana root types

The functional root system of *Musa* is based entirely on adventitious root axes, also known as cord roots, arising from a subterranean rhizome (also called the corm) and producing primary and higher-order laterals.

Root axes

The adventitious roots – hereafter referred to as root axes – are the major coarse determinants of root distribution. They are relatively straight and cylindrical, up to 5.2 m long (Fawcett 1921) and about 4 to 10 mm in diameter (Acquarone 1930, Riopel and Steeves 1964, Monnet and Charpentier 1965). New axes tend to have increasingly larger diameters (Blomme 2000, Lecompte *et al.* 2002).

Production

Position

Adventitious root formation is restricted to a 3-cm long arc near the growing point at the top of the rhizome (Skutch 1932). New roots are therefore produced higher up as the rhizome grows (Summerville 1939, Kwa 1993) and this leads ultimately to the production of roots above the soil surface (Moreau and Le Bourdellès 1963). This phenomenon is especially detrimental in soils of low fertility, in windy areas, and under conditions of high parasite load (Braide and Wilson 1980), and may be exaggerated by

a condition referred to as “high mat”, viz. the tendency of corms of successive ratoon cycles to rise above the soil surface (Stover 1972).

A sucker attached to the parent plant may produce 200 to 300 roots before the emission of the first active, non-lanceolate leaf (Champion and Olivier 1961, Robin and Champion 1962). At flowering of the parent plant, 172 to 203 roots may be visible on the tallest sucker (Moreau *et al.* 1963) and counts exceeding 400 roots have been recorded on the subsistent corm of pruned suckers (Turner 1972). It is likely that an interplay of growth substances co-regulate the development of the root system of the parent plant and its suckers and that the suckers contribute to the nutrition of the parent plant and vice-versa as long as they remain attached. It is thus highly recommended that the roots originating from different corms be distinguished from one another when considering root architecture or root function.

Timing

The production of root axes by young *Musa* plants depends on the type of planting material. On suckers, 10 to 34 roots emerge between 4 and 15 days following planting (Beugnon and Champion 1966, Gousseland 1983, Lavigne 1987). These first axes (preformed roots) are most probably growing in the cortex of the corm when the sucker is uprooted and prepared for planting. Suckers that are dug for planting material during periods of reduced root formation may have low numbers of preformed roots (Beugnon *et al.* 1966). The formation of new roots appears to be interrupted from about 15 days until 75 to 90 days after planting (Champion *et al.* 1961, Moreau *et al.* 1963, Beugnon *et al.* 1966, Gousseland 1983, Lavigne 1987). When the planting material is a section of corm that contains a lateral bud (bits), one to 10 small fibrous roots are initially produced, which do not extend further than the planting hole. Root formation on the new plant starts 3 to 5 weeks after planting and continues thereafter (Turner 1972). Finally, in the case of *in vitro* plants, the roots produced in the regeneration medium do not grow further in soil or hydroponics and new root formation starts 4 to 5 weeks after planting, at the end of the acclimation phase (Blomme 2000, Stoffelen 2000).

Leaving aside a single study reporting the existence of a second period of root emission at five months in aeroponics (Lavigne 1987), root formation is steady until flowering (Beugnon *et al.* 1966, Gousseland 1983). It is however highly variable with age and date (Beugnon *et al.* 1966), promoted by high planting densities (Mohan and Madhava Rao 1984) and can be arrested during periods of low temperatures (Turner 1972, Robinson 1987). About 130 visible roots were counted at 6 months (Summerville 1939), 296 at 7 months (Moreau *et al.* 1963), 262 to 490 at 8 to 9 months (Beugnon *et al.* 1966) and 80 and 638 at flowering (Moreau *et al.* 1963, Turner 1972, Mohan *et al.* 1984, Lavigne 1987). The plant loses its capacity to form new roots at the end of the vegetative phase and subsequent emission is confined to the suckers (Lavigne 1987).

The scars left by the roots traversing the cortex of the corm can be used to estimate the total number of roots produced, including those that have died (Gousseland 1983). At flowering, the main plant may have produced 400 to 800 cord roots, against 344 to 378 for the tallest sucker (Champion *et al.* 1961, Robin *et al.* 1962, Moreau *et al.* 1963).

The number of roots of the parent plant evolves as leaf area evolves (Gousseland 1983, Lavigne 1987), suggesting a balance between the root and stomatal hydraulic

conductance. The root number is also correlated with size of the plant such as leaf size, bunch size (both number of hands and fingers) and pseudostem diameter (Champion *et al.* 1961, Beugnon *et al.* 1966, Lassoudière 1980). In addition, the fruit weight of the parent plant is correlated with the number of roots of the tallest sucker, itself correlated with size of the sucker, mainly the pseudostem circumference. Many of these correlations are dependent on place and date.

Growth

The elongation rate of root axes ranges between 1.2 and 4.0 cm/day (Riopel *et al.* 1964, Beugnon *et al.* 1966, Lassoudière 1978, Robinson and Alberts 1989). It is independent of root length (Lavigne 1987, Lecompte *et al.* 2003). There appears to be a maximum growth rate closely related to the apical root diameter. The degree to which individual roots reach that maximum value depends on carbon allocation to the root apical meristem and impedance of root growth (Lecompte *et al.* 2003). The root growth rate also follows the diurnal (Lassoudière 1978) and seasonal (Robinson 1987) variations of the leaf emergence rate and is adversely affected by mechanical impedance (Gousseland 1983), low pH (Rufyikiri 2000), elevated water tables (Hartman *et al.* 1928) suboptimal soil temperatures (Robinson *et al.* 1989) and oxygen deficiency (Aguilar *et al.* 1998). Based on plausible estimates of root elongation (1.2 to 4.0 cm/day) and lifespan (5-month), a single axis may thus reach a length of 2.6 to 7.5 m, a range that encompasses most observations of maximum root length in good conditions.

Direction

The first reports on banana root axes suggested that there are horizontal and vertical axes (Fawcett 1921, Hartman *et al.* 1928). It was later argued that the difference between horizontal and vertical roots is one of age and length, and intermediate oblique roots are also present (Acquarone 1930, Summerville 1939). It was further suggested that the earliest -oldest- roots produced at the base of the young rhizome tend to grow downwards, so that roots with lower diameters may be preferentially observed in the subsoil (Lassoudière 1978), although a few vertical roots are regularly found on mature flowering plants (Blomme 2000).

These views were recently challenged by detailed studies of the initial growth direction of roots emerging from the rhizome and of the directional growth of these roots thereafter (Lecompte *et al.* 2002, Lecompte *et al.* 2003). On one hand, these studies showed that a high proportion of root axes emerge with a low angle to the horizontal and that this proportion is similar for early and late roots. On the other hand, they indicated that roots tend to curve towards the horizontal plane with age. Ultimately, one should account for the large impact of variations in bulk density and mechanical impedance on the soil profile as well as on the localized prevalence of suboptimal soil conditions (Godefroy 1969, Hahn *et al.* 1996).

Survival

Root lifespan can be inferred from a temporal series of counts of the total number of roots produced by a rhizome, including those that have died (see above) and of the number of living roots. Among 110 roots produced during the first 3 months on the parent plant, 50 had disappeared at 3 months and 102 at 7 months (Moreau *et al.* 1963), indicating that the lifespan of root axes was from about 2 months to more than

4 months. By comparison, glass rhizotron experiments gave estimates of 4 to 6 months (Robinson 1987) and Lassoudière (1980) found live roots on the plant crop at the harvest of the first ratoon, that is 10 months after their presumed date of emergence. The level of activity of the latter roots is unknown. Interestingly, they were less affected by nematodes than the roots of the follower.

The root axes present at flowering remain alive during the reproductive period (Turner 1970), with a moderate decrease of about 8% (Blomme 2000); and about half of them may still be present at harvest of the follower (Lassoudière 1980). Because root production vanishes at flowering, the proportion of healthy roots is lower during the reproductive phase (6 to 17%) than at the end of the vegetative phase (16 to 50%; Champion *et al.* 1961, Robin *et al.* 1962, Blomme 2000). Furthermore, root length decreased by 40% during the reproductive period, while root number decreased by only 8% (Valsamma *et al.* 1987, Blomme 2000) indicating that long roots would be more prone to root decay than short ones. This may be related to their being older and to the fact that they explore larger volumes of soil and have higher chances of encountering new hazards. Therefore the maintenance of a high root survival rate after flowering is critical to maintain an adequate root population.

The overall load of factors impeding a root system can be estimated using the distribution of root length (number of roots in successive length classes $[x_i,x_{i+1}[$, where $w=x_{i+1}-x_i$ is the width of each class). In 10 week-old *vitro*-plants growing in nutrient solution, that distribution appears to be constant, which would be expected if both new root formation and elongation were constant and roots had not been exposed to hazards. In such conditions, the average root length of young plants in hydroponics sometimes exceeds 75 cm (Swennen *et al.* 1986, Stoffelen 2000). Conversely, in a study by Moreau and Le Bourdellès (1963) with mature field-grown plants, the distribution closely resembled an exponential model: the number of roots in any length class (w=10 cm) was about 65% of that in the preceding class, with 32 to 42% of the roots in the [0,10[cm length class (i.e. the class includes 0 but excludes 10) and 1% in the [90,100[cm class (see also Laville 1964, Beugnon *et al.* 1966). Accordingly, the average root length of field-grown plants during the vegetative phase is thus usually very short, about 30 cm or less (Beugnon *et al.* 1966, Blomme 2000), and cannot be indicative of the volume of soil explored. In theory, the exponential distribution corresponds to a situation where new roots are produced continuously, grow at a constant rate and die only of hazards, which must occur at a constant rate, independent of root age. In conditions of constant root production and growth, the rate of hazards would thus provide a measure of the total biotic and abiotic pressure impeding the root system. The higher the rate, the lower the proportion of roots growing to the next length class. In the study by Moreau and Le Bourdellès, the proportion of roots growing to the next length class were 64, 65 and 66% in three different soils, suggesting that under the conditions stated above the biotic and abiotic pressures in these soils were rather similar.

In an assessment of root density in the top 50 cm layer (weight of roots per weight of soil) using the core sampling technique, Gousseland (1983) reported a 67% decrease in root densities from 30 to 130 cm from the corm. However, after we adjusted this number to the circumference explored by roots at 30 and 130 cm, the total weight of roots present at 130 cm was 42% higher than that of roots present at 30 cm. In a sepa-

rate experiment, the proportion of root weight was not affected by the distance from the pseudostem (Araya *et al.* 1998). Such problems emphasize the inability of crude estimates of root weight data to address issues of root length and root dynamics in soil.

Lateral roots

Having a usually determinate growth type and a short lifespan, lateral roots do not generally extend far from their parent root. Therefore, while root axes determine the overall exploration around the plant, laterals determine the intensity of local soil exploration in the vicinity of these root axes. In this respect, they represent such high numbers and densities in the soil that they comprise most of the length and area of the root system. In addition, lateral root formation appears to be much more responsive to local soil conditions than is the growth of root axes, making lateral roots the key players in root architectural plasticity and adaptation.

Production

Lateral roots in *Musa* arise in an acropetal sequence, i.e. new laterals appear closer to the tip than do the previous laterals (Riopel 1966). The general topology of a banana root axis and its laterals resembles that of a herringbone pattern repeated at each order of branching, any root producing lateral roots in a herringbone pattern. However, root branching is affected by rhizosphere conditions as well as by the plant status that may either locally promote or repress the production of lateral roots.

The process of lateral root formation involves the initiation of a primordium in the close vicinity of the parent root apex, followed by a so-called "maturation" phase at the end of which the lateral protrudes from the parent root. The duration of the maturation phase is constant and similar for all root orders of a given genotype, a feature that can be used to estimate the root growth rate of field roots (Lecompte *et al.* 2001). It was estimated at 3.6 days for 'Grande naine' in an andosol in Guadeloupe and at 3.8 days in hydroponics. Lateral roots were consistently found to protrude closer to the tip on roots whose apices are less active (Lassoudière 1978).

First-order laterals usually emerge 10 to 30 cm behind the tip of the root axis (Laville 1964, Riopel *et al.* 1964, Lassoudière 1978, Blomme 2000). They are 0.5 to 4.0 mm in diameter and reach a density of up to 8 to 10 per cm of root axis in hydroponics (Stoffelen 2000) and in the field (Blomme 2000). The density and length of lateral roots may be slightly depressed in the proximal 10 cm of root axes, probably under the influence and proximity of the corm. Secondary laterals, 1 mm or less in diameter, are often produced on primary laterals (Acquarone 1930, Laville 1964, Blomme 2000) and reach densities of up to 8.7 per cm of primary lateral (Blomme 2000). In nutrient solution, 95% of primary laterals are covered with secondaries (Stoffelen 2000), with a density of 3.0 per cm. Tertiary laterals are rare and less than 200 µm in diameter (Acquarone 1930, Riopel *et al.* 1964). The pattern of lateral root formation comprises two elements: the restriction to protoxylem-based ranks, and a rather regular spacing within ranks (Charlton 1982), with the logical consequence that the number of lateral roots per unit length of root axis should be proportional to the root diameter (Draye 2002b).

Swennen and colleagues distinguished feeder and pioneer axes, with respectively high and low densities of primary laterals (Winderickx 1985, Swennen *et al.* 1986).

Compared with the large conical pioneers, feeder axes are cylindrical in shape and have a diameter similar to that of large primary lateral roots (Acquarone 1930). Feeder roots, however, were only observed on suckers (or *in vitro* plantlets) undergoing a transfer to hydroponics and could not be seen on the suckers produced by plants already grown in hydroponics. Further attempts to distinguish feeders and pioneer root types in the field were also difficult (Blomme 2000). A few observations suggest that they might be replacement roots arising from portions of root axes situated in the cortex of the corm, as a response to a rapid transfer to water medium.

The root tips of the root axes often die when they encounter hard obstacles at right angles. In this case, several lateral roots, almost as large as the parent root, develop behind the dead tip (Acquarone 1930). These laterals have an indeterminate growth (Riopel 1960) and the same internal organzation as primary roots (Acquarone 1930, Riopel 1960, Laville 1964). Because they arise from a region where lateral root primordia are normally present and since their density (number of roots per cm of axis) is similar to that of lateral roots, it is likely that they develop from young primordia of the normal acropetal sequence of lateral root formation. This view is supported by the fact that replacement roots are only produced if the root is damaged within about 2 cm from its apical meristem. Root axes experiencing local mechanical constraints also produce large lateral roots with an apparent indeterminate growth. Typically, where root axes abruptly change direction, large laterals protrude from the external side of the bend. This reaction appears to be proportional to the intensity of the constraint (Lassoudière 1971).

Growth

Information on the root growth rate of lateral roots remains scanty. First-order lateral roots extend at a rate of 0.7 to 1.5 cm/day (Lassoudière 1978) to reach a final length of 3 to 15 cm (Acquarone 1930, Laville 1964), while secondary laterals can be 0.3 to 4 cm long (Acquarone 1930, Laville 1964, Blomme 2000). It would be interesting to verify whether the relationship between root apical diameter and potential elongation rate, which was found for root axes (see above), also holds for laterals.

The length to which lateral roots grow is probably determined early in their development. Swennen and colleagues (1986) observed a succession, along water-grown root axes, of segments covered with, alternatively, shorter and longer primary laterals. Given cyclical variations of pH and nutrients which were adjusted weekly, it seems reasonable to propose that the primary laterals have a determinate growth and that their maximum length is determined by rhizosphere conditions prevailing near the tip of the axis at the time the lateral root primordia are initiated (Hackett 1968), as reported with other species for the response to localized nutrient supply. The production of replacement roots (see above) might be a special case of such a mechanism if one considers not only the influence of rhizosphere conditions but also that of internal conditions.

Direction

As far as we know, there is no indication of a gravitropic growth for lateral roots. Lateral roots emerge from their parent root at a given azimuth and insertion angle and will adjust their direction of growth in response to soil mechanical anisotropy. Insertion angles would appear to be around 75°, while azimuth angles are determined by the

radial location of the lateral root relative to the protoxylem poles. Since the number of poles is linearly correlated with root diameter, the set of azimuth angles for the laterals of a given root will be proportional to that root diameter.

Survival

Life spans as short as 6 to 10 days (Lassoudière 1978) to as long as 8 weeks (Robinson 1987) have been reported for first-order lateral roots and are greatly affected by biotic and abiotic constraints. Second-order laterals remain alive for up to 5 weeks (Robinson 1987). Roots of any order, therefore, tend to have a shorter lifespan than their parents. As there is no indication of adventitious lateral root formation in banana, the acropetal pattern of lateral root formation along the parent root implies a parallel acropetal sequence of lateral root decay. A root is therefore comprised of 3 zones: a distal unbranched zone where lateral roots mature, an intermediate branched zone between the regions of lateral root emergence and lateral root decay, and a proximal unbranched zone where lateral roots have died.

The length of the branched zone is a function of the lifespan of laterals and of the growth rate of the parent root. In conditions of continuous root growth, that distance is expected to be constant. However, if the root growth slows, the length of the branched zone will gradually reduce. Ultimately, if root growth stops, the branched zone will gradually vanish. This means that the maintenance of a sufficient amount of active lateral roots to achieve efficient resource acquisition depends on a sustained root axis growth. Our inability to reduce conditions that interfere with the growth of root axes (see above) is likely to be a significant component of many soil-related issues of intensive cropping systems. The higher the biotic and abiotic load reducing fine root survival, the more critical the need for conditions that favour the growth of the adventitious roots.

Moving back to root distribution: root architecture models

As shown in the preceding section, there exists a significant amount of information on the various processes that determine the architecture of the banana root system. On the whole, this information seems consistent with the various reports of banana root distribution, viz. that 90 % of the roots extend within one meter from the plant, and about 70% of the total root mass of banana plants is confined to the upper 20 to 40 cm of the soil. Still, one would expect process-related information to allow a better understanding of the response of root distribution to the various biotic and abiotic factors than is possible with mere one-shot descriptions of root distribution in specific conditions.

During the last decade, a number of models of root architecture have been developed to facilitate the integration of process-related information into the context of a whole root system in time and space (Pagès *et al.* 2000). These models use mathematical formulae of the process to simulate the activity of every root meristem in time and space, taking account of root production, growth, directional growth and senescence. The coordinates, size, age and topological position of every root segment and meristem are stored and can be analyzed and presented visually at every time step of the simulation. Depending on the deterministic or stochastic formulation of the processes, some degree of variability can be introduced in the simulated root system. Further, the simultaneous consideration of several processes during the simulation makes it possible to connect

different processes, such as growth and branching, or growth of different roots. In this respect, it is interesting to note that whole plant models were recently proposed (Drouet and Pagès 2003).

A prototype model for *Musa* is currently under development, initially written in the computer language C, and recently ported to object-oriented Java code. It can be presented as a UML (Unified Modelling Language) diagram (Figure 1). The model allows the simulation of a banana field comprising a number of plants. Each plant is initiated as a propagule (e.g. sucker or *in vitro* plant) that initialises a root and a shoot system. The implementation of the shoot system is limited to a carbon production function taking into account plant age and daily temperature. The implementation of the root system, however, is fairly comprehensive and includes all of the above processes. The code is designed to make it easy to test different implementations of the various proces-

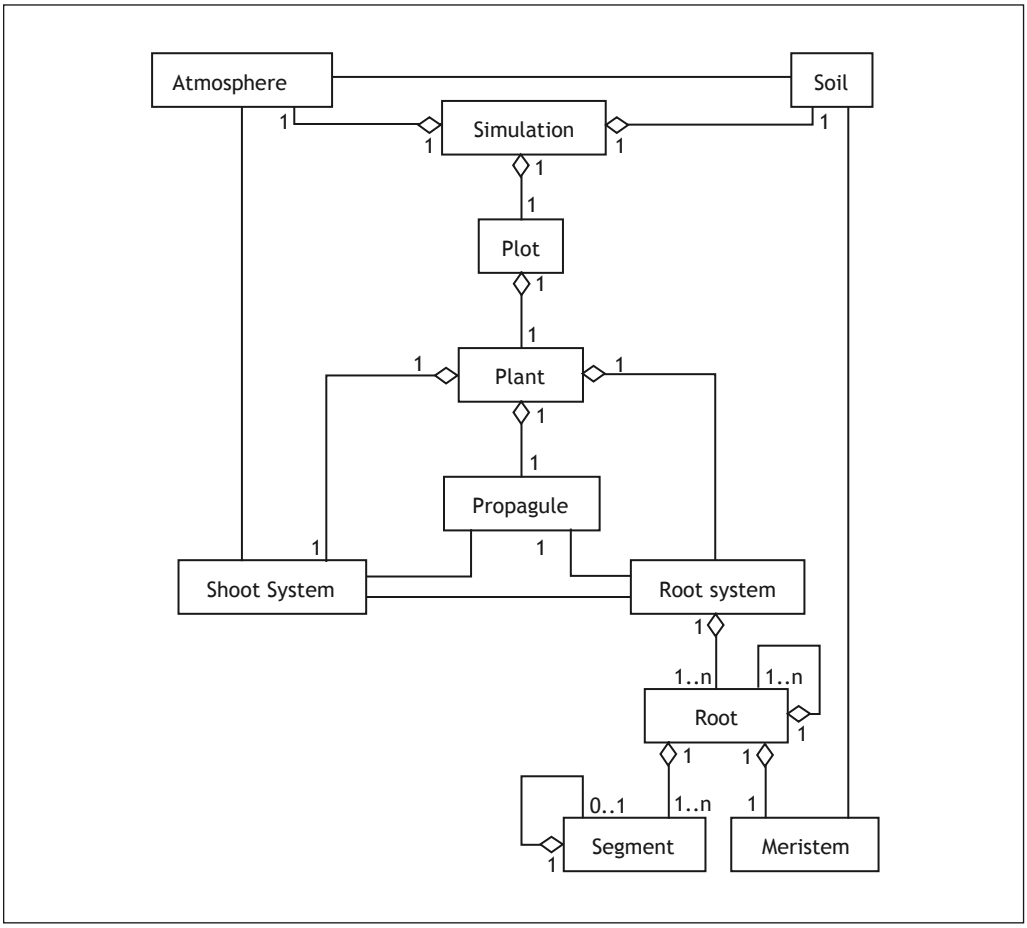


Figure 1. Object-oriented UML representation of the *Musa* root architecture model. Lines connecting different components (or objects) indicate associations. Diamonds indicate composition relationships. For example: a root system is comprised of 1..n roots, every of which has a unique meristem, 1..n laterals and 1..n root segments that succeed each other. The meristem is linked to the soil because root growth calculation uses soil information (temperature, porosity, mechanical anisotropy).

ses. The current model lacks the ability to simulate sucker development, which would require a clear understanding of allocation rules within the banana stool.

It would be premature to make any statement regarding the precision and relevance of the simulated root systems without intensive testing and further development of the *Musa* model. For this reason, the present report is limited to a few visual illustrations of model output (Figure 2). However, we are confident that a validated root architecture model of bananas will lead to a better understanding of the root system of bananas in the future.

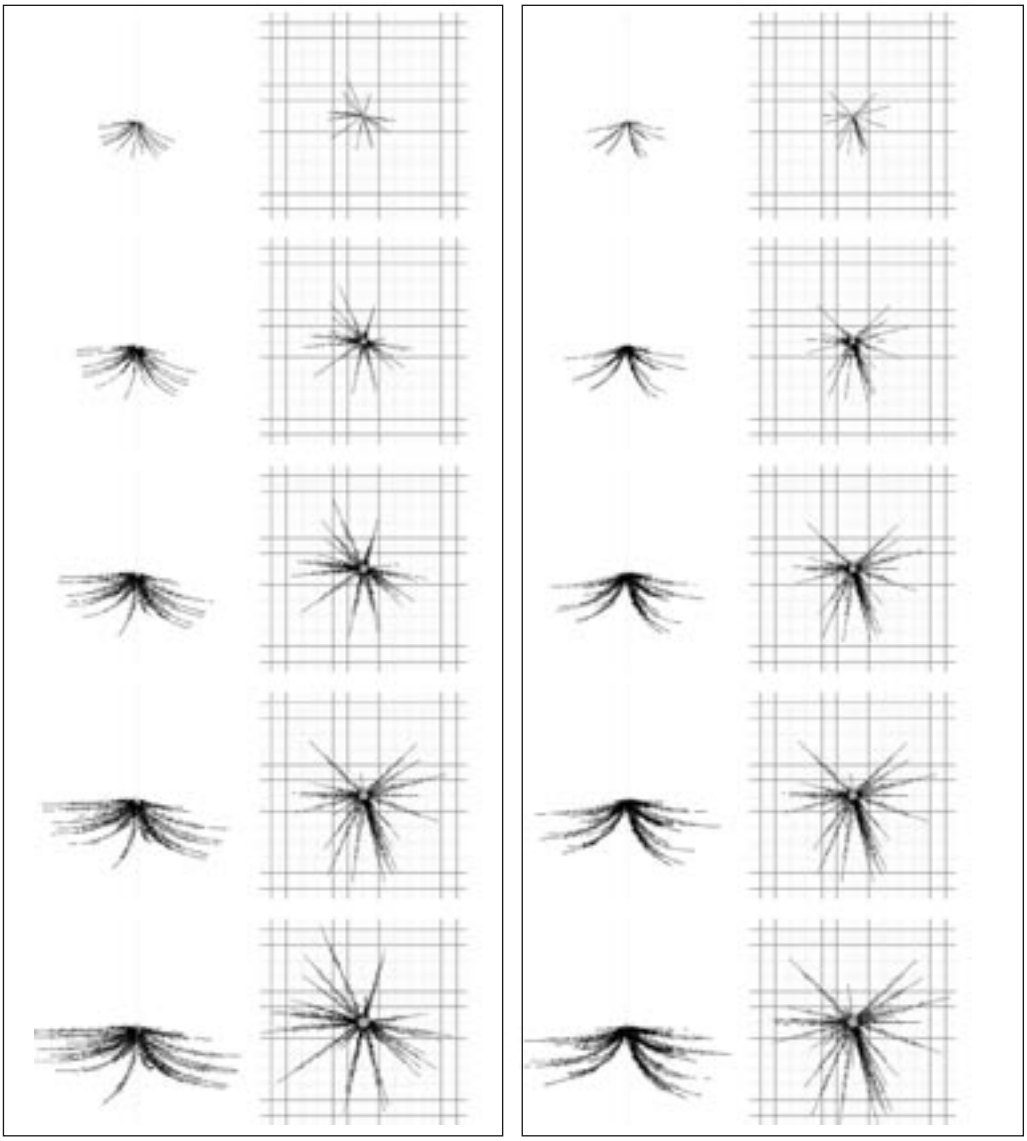


Figure 2. Illustration of the output of the *Musa* root model. Vertical (left) and horizontal (right) projections of two simulated root systems at 10, 20, 30, 40 and 50 days (from top to bottom). Grid size = 10 cm x 10 cm.

New methodologies to evaluate root observation methods

The inherent difficulties in observing and quantifying plant root systems have been a major incentive for the development of a series of root observation methods (Smit *et al.* 2000). Beyond the complete root system excavation, four methods have been used in bananas: core sampling (Blomme 2000), sector sampling (Araya and Blanco 2001), trench profiles (Delvaux and Guyot 1989) and rhizotrons (Lassoudière 1978). Each of these has its own benefits and drawbacks and makes it possible to estimate a limited number of factors from the plant and/or the root environment. Except for complete root system excavation, the methods involve a sampling strategy that is likely to influence the precision of the estimates and may introduce additional bias. Root architecture models provide a way to estimate the precision and bias with limited input, as well as to identify the conditions under which a method is likely to be robust or error prone.

We present here a fictitious example illustrating how root architecture models can be used to evaluate the precision of root length and root number estimates obtained with the core sampling strategy. The results should not be taken as recommendations for core sampling, although they highlight the importance of some factors affecting the precision of the estimates.

Using the *Musa* root model, 90 root systems with the same total root length and root numbers have been simulated. These root systems differ only in the spatial arrangement of the roots so that the resulting data set would seem appropriate for testing the sensitivity of the core sampling procedure to the major source of variability between plants and around a plant. A virtual sampling was performed for each of the root systems by calculating every 10 days the number and length of root axes and lateral roots in a number of core configurations (number of cores sampled per plant, diameter of the core, distance of the core from the base of the plant). This allowed the computation of average root length and numbers in each sample as well as their confidence limits. These estimates were plotted (Figures 3 to 5) against the true root length and number, and separately for root axes and first order laterals.

This simulation study highlighted the critical effect of the distance between the core and the plant base. At large distances, the length / number of roots in the core are very weak predictors of the total root length / number, which seems consistent with the usual observation that most of the roots are close to the plant. Based on these simulations, a distance of 30 cm or less would be acceptable, yet it is likely that the maximum distance would have been higher had the simulations been run for longer periods. The effect of the core diameter was predictable. At a given distance d from the plant base, large cores intercept a higher proportion of the roots (longer than d) than small cores, and this proportion is directly proportional to the length of the arc intercepted by the core, which normally approximates the core diameter.

Finally, increasing the number of cores may significantly reduce the confidence interval of the estimates (by about 2/3 in these simulations). This example used 25 cm diameter cores sampled at 40 cm from the plant, so that the maximum number of cores was 8. Therefore, confidence limits estimated with n = 8 are the best results that could be achieved with core sampling.

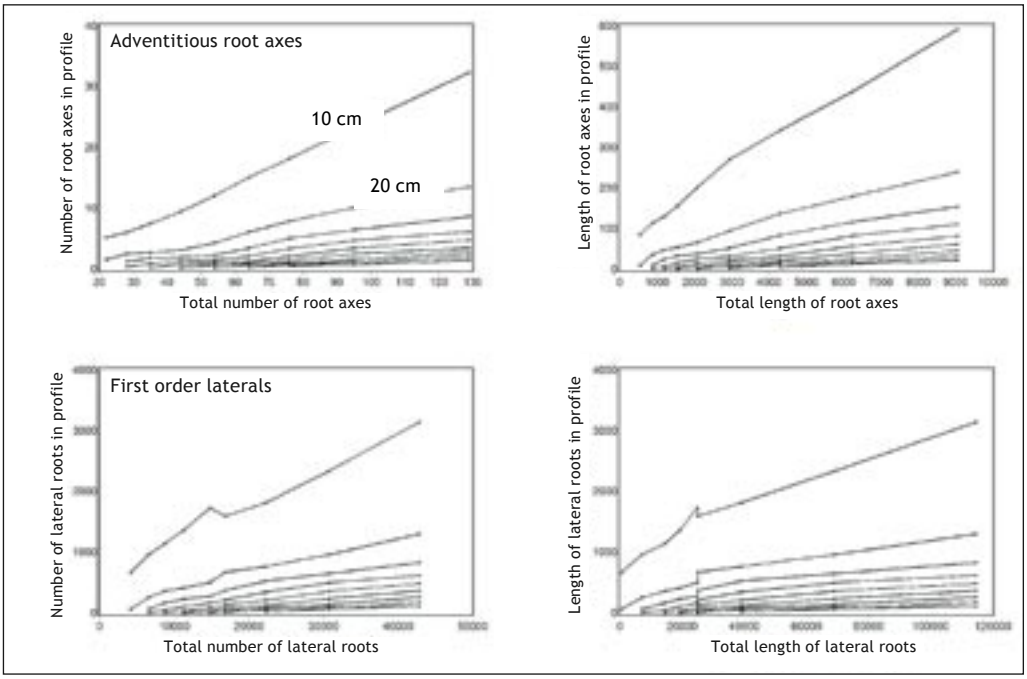


Figure 3. Fictitious core sampling experiment. Effect of the distance of the core from the plant base (from 10 cm to 90 cm by 10 cm intervals). The core diameter was 25 cm.

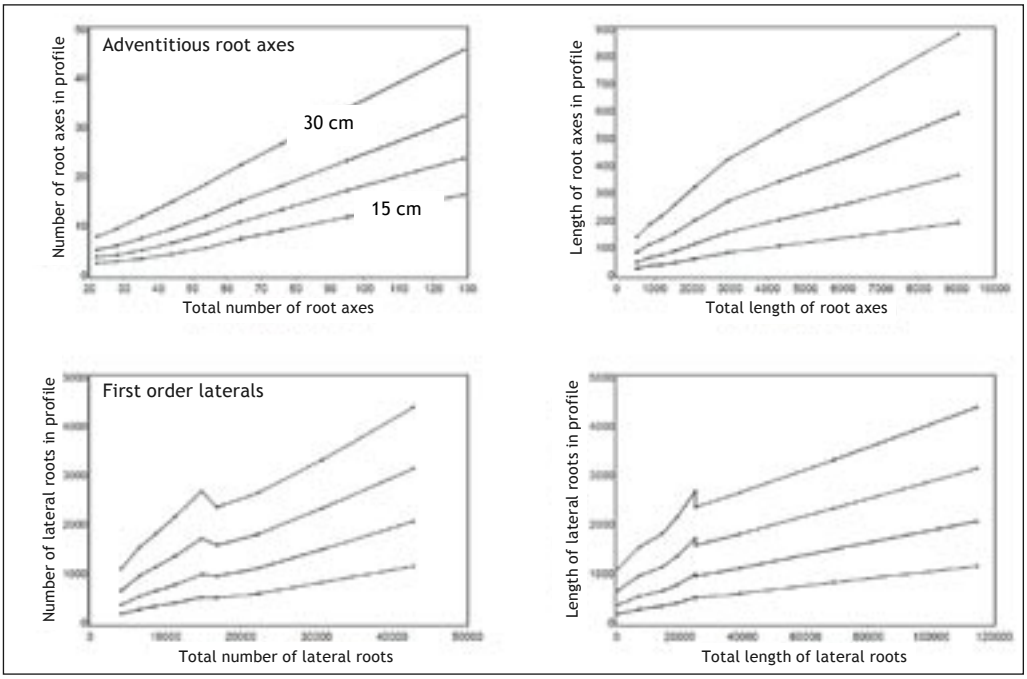


Figure 4. Fictitious core sampling experiment. Effect of the core diameter (from 15 cm to 30 cm by 5 cm intervals). Samples were taken at 20 cm from the plant base.

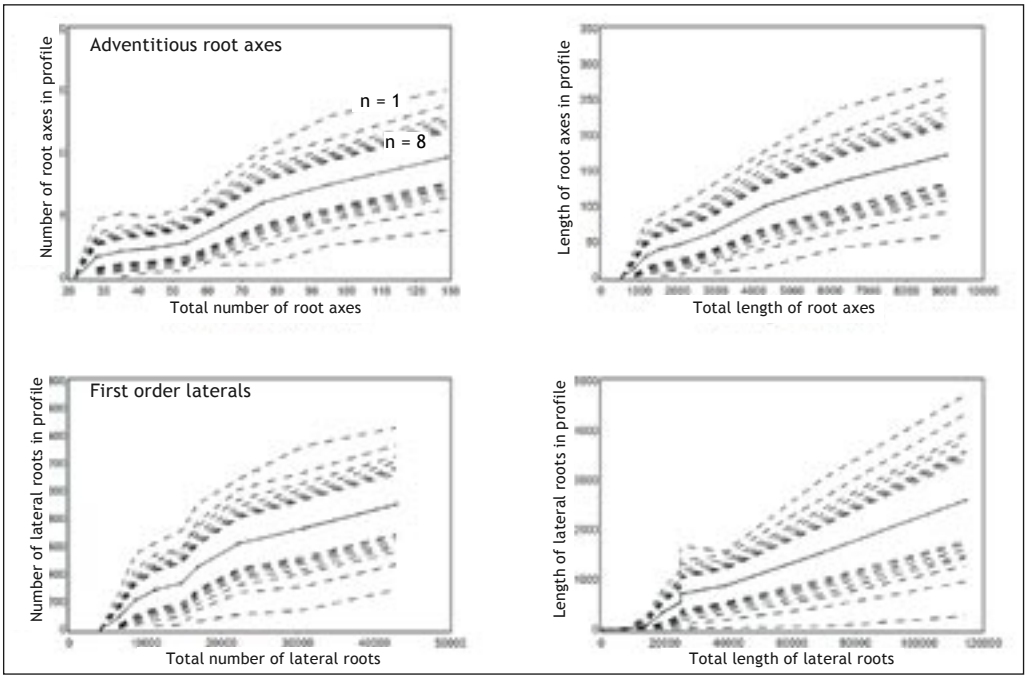


Figure 5. Fictitious core sampling experiment. Effect of the number of cores (n = 1 to 8). The core diameter was 25 cm and cores were sampled at 40 cm from the plant. Continuous line: average values; dotted lines: 95% confidence limits for each number of cores.

The calibration of root architecture models is indeed a prerequisite for using them for recommendations. This calibration should, in principle, be performed repeatedly for every genotype and environmental condition. However, if such calibration data were obtained for a expanding set of genotypes / conditions and if they were adequately documented, they could be used to produce more generic models integrating the effect of genotype and conditions. It is therefore hoped that the quantification of banana root systems in the future will yield new estimates of the dynamic parameters underlying root distribution and will provide good descriptions of the plant and environmental conditions.

Perspectives

Bananas and plantains lend themselves to a dynamic modelling of their root architecture, a promising step towards an integrated and rational understanding of crop growth and performance. The experience accumulated through more than a century of research has provided a framework to initiate the formulation of a developmental model of *Musa* root architecture, comprising root formation, branching, elongation and senescence, each expressed as a function of genotype, plant status, root age and localized rhizosphere conditions. In principle, this model could be further extended to include as input soil heterogeneity in time and space, genetic correlations between the various root parameters, or also to combine its output with root function data.

While observing architectural differences among genotypes or treatments, one should always attempt to connect these differences to root function. In particular, nutrient and water uptake are not necessarily proportional to root length or surface. In several instances, there even appears to be an excess of roots, the significance of which remains unexplored. In addition, root construction costs have been considered to be proportional to root weight, however it is likely that the amount of photosynthetic energy required to form a unit of root length increases in adverse conditions, as shown with mechanical impedance (Whalley *et al.* 2000).

With regard to crop performance, the guarantee of optimum root behaviour depends on our ability to take account of root plasticity. The most significant causes of reduced performance in roots in *Musa* have been identified and the nature of their architectural consequences is being clarified, although the effects of these factors on the late development of lateral roots remain unknown. It may be wise to establish standard root system descriptors accounting for root plasticity and to be evaluated in defined and rigorously controlled conditions. Given the huge variability of root development under field conditions, this may be the only way to bring together the outcome of different research projects. However, before such descriptors can be established, quantitative data on soil heterogeneity (in time and space) prevailing in banana cropping regions are needed.

A root system is a population of roots of different types and ages that evolve dynamically according to root formation and root senescence. The overall capacity of the root system to keep pace with the various demands placed on it depends on the ability of the plant to maintain an appropriate root population. In this respect, the importance of appropriate cultivation practices should not be underestimated (Delvaux *et al.* 1989). Yield decline in plantain, for example, does not occur in backyard or compound gardens (Braide *et al.* 1980). The genetic improvement of the root system remains another possibility. However, in addition to the inherent difficulties of *Musa* breeding, most questions concerning the characteristics that should be targeted remain unanswered.

Acknowledgements

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Development and formation of plantain roots (*Musa* AAB Simmonds)

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Abstract

All organs that constitute the plantain plant are important and serve a specific function. However, roots and leaves can be considered the two most important organs, because on their physiological behavior and disease status depends the plant's supply of water and nutrient elements as well as its photosynthetic activity, processes that are closely related to production and yield. A more detailed analysis will probably lead us to consider the root as the most important organ, which unfortunately has not received the attention it deserves by researchers. The plantain root system is spreading and fibrous made up of primary, secondary and tertiary roots, and root hairs. Color is related to age, and may vary from creamy white to yellowish brown. Roots are very fragile early in their life, becoming less so in time, but remaining flexible. The thickness and length of roots are closely related to soil structure and texture. In general, in light soils roots are thin and can reach about 3 m in length, while in heavy soils they are thicker and can reach about 2 m. Roots initiate at the central cylinder or cambium of the corm from which they move to the outer surface through the corm cortex, and emerge either through the nodes or between them, in groups of one, two, three, or up to four roots, without any particular pattern. The root contains the following tissues: epidermis, exodermis, mesodermis, central cylinder or stele, and root-cap. In the vegetative phase, root differentiation is continuous, only interrupted when the lateral bud or follower is separated from the mother plant, to be used as planting material. The follower's roots continue their growth and development once planted. In this new production unit, root differentiation begins when a second or new corm is formed. The spatial distribution of the root system is a radial horizontal type, where the greatest number of roots is found in the upper 20 cm of soil. The growth and development of the root system is oriented to the soil's most fertile areas, mostly toward those sites showing high concentrations of organic matter.

Resumen - Desarrollo y formación de las raíces de plátano (*Musa* AAB Simmonds)

Todos los órganos que conforman la planta de plátano son importantes y cumplen con una función determinada. Sin embargo, las raíces y las hojas podrían ser considerados como los órganos más importantes, porque de su comportamiento fisiológico y de su estado fitosanitario, dependen la absorción de agua y elementos nutritivos y la actividad fotosintética, procesos estrechamente relacionados con la producción y el rendimiento. Un análisis más detenido, posiblemente nos lleve a considerar que la raíz sea el órgano más importante de una planta de plátano, la cual infortunadamente no ha recibido la atención que se merece por parte de los investigadores. La morfología radicular del plátano corresponde a un sistema fasciculado y fibroso, conformado por raíces primarias, secundarias, terciarias y los pelos absorbentes. El color guarda relación con su edad y puede variar de blanco cremoso a pardo amarillento. Su consistencia es sumamente frágiles a edad temprana, pero luego con el tiempo se vuelven más resistentes y continúan siendo flexibles. Su grosor y longitud guarda estrecha relación con la estructura y textura del suelo. Generalmente, en suelos livianos son delgadas y pueden alcanzar alrededor de los tres metros de longitud, mientras que en suelos pesados son más gruesas y alcanzan longitudes de aproximadamente dos metros. En cuanto a su anatomía, las raíces se originan en el cilindro central o cambium, desde donde avanzan hacia la superficie externa o corteza del cormo y emergen por lo nudos o bien por los entrenudos, en grupos conformados por una, dos, tres y hasta cuatro raíces, sin ajustarse a ninguna clase de patrón. La raíz está formada por las siguientes

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estructuras: epidermis, exodermis, mesodermis, endodermis, cambium y la cofia. En la fase vegetativa la diferenciación de raíces es un proceso continuo y sólo se interrumpe cuando la yema vegetativa o hijo es separado de la planta madre, para ser utilizada como semilla, en la que las raíces diferenciadas continúan con sus procesos de crecimiento y desarrollo, una vez que se siembran. En esta nueva unidad productiva, el proceso de diferenciación de raíces se inicia tan pronto se forma el segundo cormo. Su distribución espacial puede considerarse como del tipo radial horizontal, encontrándose el mayor número de raíces en la capa de suelo correspondiente a los primeros 20 cm de profundidad. Su crecimiento y desarrollo está orientado hacia las áreas más fértiles del suelo, especialmente hacia aquellos sitios que poseen alto contenido de materia orgánica.

Introduction

The constant growth of the human population leads to a greater demand for food production, which for different reasons has not been achieved in several countries, with fatal consequences for people. Public and private institutions, through research centres, continuously seek appropriate economical ways to solve these problems. This leads to the direct and indirect improvement of production factors that can be controlled, such as the development of new cultivars and the establishment and use of new and innovative agronomic practices.

Unfortunately, in the attempt to obtain new, more productive, higher-yielding cultivars, researchers have only considered these factors, forgetting the plant as a whole, such that the organs of the plant that are responsible for its physiological function, have not received the attention and importance they deserve in research. Therefore, when surveys have been conducted, the bunch or perhaps the leaves have been the focus as the most important organ; few agriculturalists have considered the roots as important, reflecting the little attention and interest given to the plant root system.

Among the group of organs that make a plant, the complementary nature and interdependent function of roots and leaves should be considered as two of the most important since the plant's photosynthetic activity, and absorption of water and nutrients, depend on them. The latter functions are closely related to production, and to yield. Among the plant's organs the root is, without doubt, one of the most important, as it serves not only to anchor the plant to the ground, but also has the primary function of absorbing and extracting water from the soil, along with essential nutrients necessary for growth, development and plant production. Everything related to growth and production depends directly on the stage of development, as well as on the cationic exchange capacity of the root system. It also bears mentioning that of the 16 nutrient elements listed as essential for plant growth, 13 are extracted from the soil by the root system.

Morphological description

The roots arise from the corm in bundles, they are fibrous and their components have a predetermined growth pattern, as happens with other cultivated species. The roots emerge from the corm either adjacent to, or between, the nodes and either individually or in groups of up to four elements (Belalcázar 1991). According to Cardeñosa (1954), the root system consists of the main roots, the secondary and tertiary roots, and absorbent hairs. The secondary roots branch off the main roots that are more or less consistently thick along their length and do not exceed one cm in diameter. The tertiary roots branch off the secondary roots. The main, secondary and tertiary roots are subsequently

smaller in length and thickness and branch off at right angles. Root hairs grow at the ends of the main, secondary and tertiary roots. The main function of the root hairs, which only grow to a few mm in length, is to absorb water and nutrients. Their capacity to function is directly related to their range.

Root colour, which depends on the age and stage of development, may vary from creamy white to yellowish brown, becoming darker as the root ages. Young roots are fragile, particularly at the tip, which is protected by the root-cap. Roots become more rigid with age, but maintain their flexibility. Root length is influenced by soil texture and structure; the longest roots grow in light sandy loams, and the shortest are found in heavy clay loam soils. Roots in light soils may reach and exceed 3.0 m, while those in heavy soils may barely reach 2.0 m. The converse is true for diameter. At the junction of the rhizome or corm, the diameter varies from 0.4 to 1.0 cm in light soils, while in heavy soils it can be 0.6 to 1.3 cm. Thickness is not constant along the root's length, but decreases gradually, in both types of soils, from the base to the tip.

The functional or active life of the root is related to different factors, such as the cultivar, presence of insect pests, nematodes and diseases, climate, and chemical and physical properties of the soil. Observations have shown that the functional life of main roots may vary from 5 to 8 months, but apparently functional roots have still been recorded at the time of bunch harvest, at 18 months after planting, and about 11 months after the root differentiation process has finished.

Anatomical description

Roots originate at the surface of the central cylinder or cambium, generally in groups of four. Where they originate and develop, the cambium becomes very active, dividing repeatedly at all levels, until forming a primary, cone-shaped meristem with a wide base, from which the buds of 4 adventitious roots develop in acropetal succession. These roots always grow together at the same level. This way there is continuity between the corm's vegetative buds, and the root.

As the roots grow they have to emerge through the thick cortex of the corm. Unlike other plants, they do not damage the tissues through which they grow, because of the enzymes exuded by the root bud and whose function it is to soften the cortex. However, mechanical damage has been observed in some cases at 1 mm from the end of the emerging root tip. However, at 2 mm from the rhizome surface, the root tip breaks the exodermis (Figure 1).

In general terms, the root is made up of the following structures: epidermis, mesodermis, endodermis, and central cylinder or stele (Figures 2 and 3), which have the following anatomical construction (Cardeñosa 1954).

Epidermis and exodermis

The epidermis is a layer of cells with slightly thickened lignified walls. Their shape is rounded in a transverse section, and rectangular in a longitudinal one. Extensions to the external part are evidenced at fixed points where the conically shaped root 'hairs', or absorbent hairs, originate. The exodermis is composed of 2 to 4 cell layers, quite similar in shape to those of the epidermis, but different in that the cells are a little larger. Also, as the root ages the endodermis walls become thicker and suberize.



Figure 1. Longitudinal section of a primary root of a 'Maqueño' plantain, showing its anatomical structure: A. epidermis and exodermis, B. mesodermis, C. endodermis, D. peripheral areas of the stele (central cylinder), E. secondary lateral root (Photo: R. Cardeñosa).

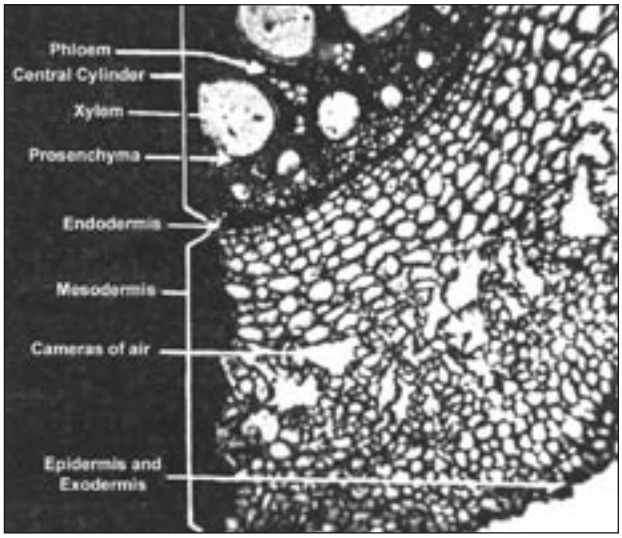


Figure 2. Cross-section of a 'Maqueño' plantain root, showing its anatomical constitution (Photo: R. Cardeñosa).



Figure 3. Longitudinal section of a 'Maqueño' plantain root, showing its anatomical structures: A. epidermis and exodermis, B. mesodermis, C. endodermis, D. stele (central cylinder) (Photo: R.Cardeñosa).

Mesodermis and endodermis

The mesodermis has a variable number of layers of parenchymatous cells, which vary in shape from the external layers to the inner ones. Cells similar to those in the exodermis are found in the first layer, while the cells of the subsequent layers are larger, spherical, and generally partially disappear producing 'watery' or gas filled cavities. In the inner layers, the cells gradually return to a shape similar to that of the cells in the external layers of the mesodermis. Intercellular spaces and laticifer vessels are found between the cell layers.

The endodermis is composed of a single layer of thin cells, which in a transverse section are rectangular. The wall adjacent to the stele is very thickened and lignified, while the external portion is thinner. In longitudinal sections, the cells are elongated, and some protuberances can be seen on the surface, as well as small orifices running through the cell wall (Figure 4).

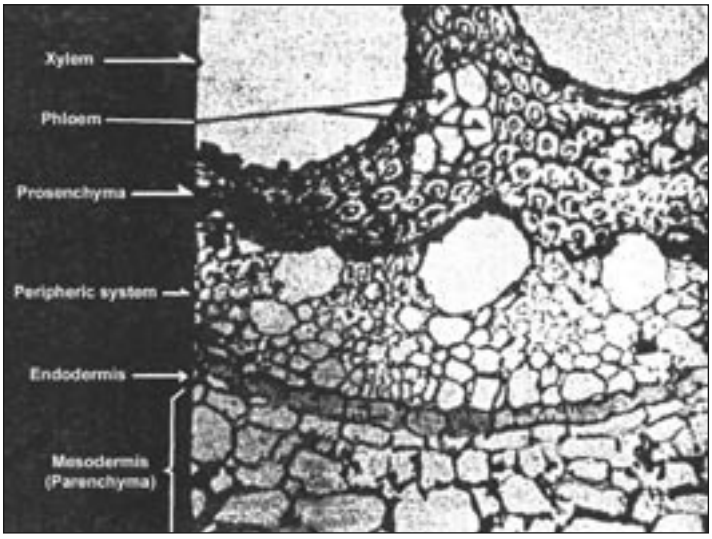


Figure 4. Cross-section of a 'Maqueño' plantain root, showing the endodermis and other anatomical structures of the stele (Photo: R. Cardeñosa).

Central cylinder or stele

Groups of thin-walled cells, with variable diameters in transverse sections, surrounded concentrically by cells with larger diameters can be found at the periphery of the stele of developing roots but not in mature roots. This is apparently due to meristematic tissue that gives rise to vessels and prosenchyma on its inner layers and to secondary roots at certain external points. The tracheids, which increase in size toward the centre, are distributed across the stele. Several cell layers of the prosenchyma with thick, apparently lignified walls exist between the xylem and the phloem.

The root tip

The root tip does not differ essentially from that common to other monocotyledons. It is composed of several layers of small cells, the quiescent centre (calyptrogen), the epidermal stem cells, and the root-cap, which originates before the bud of the root initial has merged from the main root (Figure 5).

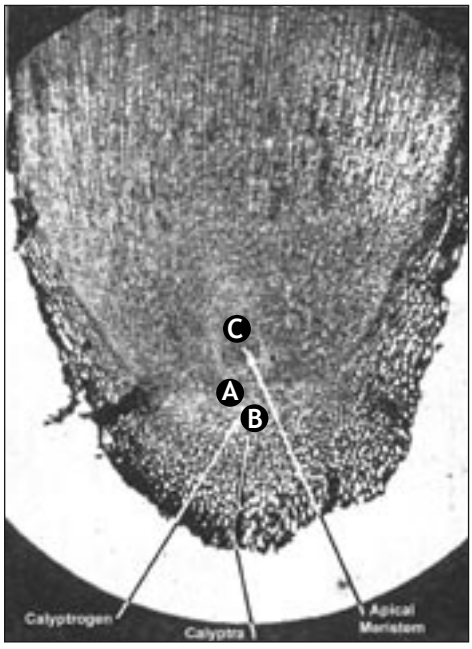


Figure 5. Longitudinal section of a 'Maqueño' plantain root tip, showing: A.- quiescent centre, B.- root-cap, C.- apical meristem (Photo: R. Cardeñosa).

Root differentiation and emission

Taking into account that asexual reproduction is the most common method of propagating plantain, its root system is made up of adventitious, fibrous roots arranged in bundles and with a dynamic differentiation and emission process (Schumann 1900). If the climate and soil conditions (particularly water supply) are favourable, new root growth and development begin in the planting material immediately after planting. However, root formation ceases in the corm itself because of the damage caused as it is separated from the parent plant (Belalcázar 1991). More than one hundred roots can be differentiated in corms before they are separated from the parent plant (Table 1). These roots emerged, grew, and developed over a period of 6 months. After that time, the number of roots decreased, due mostly to insect pests and nematode attack.

A second corm is formed as a result of the plant growth pattern in the first production cycle, at which point leaf differentiation, vegetative bud and root processes also occur (Figure 6, Table 1). The root system is notably dynamic. Two months after seeding, it had produced 23 roots, and after 9 months, the total number of differentiated roots amounted to 267. Taking account of the number of roots produced by the second corm, these results show that this process begins as soon as the corm is planted and ceases when floral differentiation ends, which occurs when the plant has produced about 50% of its leaves (19±1 leaves) (Belalcázar 1991).

Root spatial distribution

Root system growth and distribution may be conditioned or limited by physical or chemical factors inherent in the soil, such as porosity, effective depth, degree of aeration, and natural fertility. Therefore, any type of physical or chemical barrier can limit root growth and development (Cardeñosa 1954, Belalcázar 1991). According to the literature, root length may be influenced by soil texture and structure -- reaching greater lengths in light sandy loams than in heavy clay loams.

It has been noticed that most root growth and development occurs in the top 20 cm of soil and that the spatial distribution is horizontal and radial (Table 2).

Table 1. Emission of leaves and the number of roots emerging from the planting material (planted corm) and the new corms arising from it (new corms) of the plantain 'Dominico hartón' in the first production cycle.

Time (months)	Number leaves emitted	Number of roots emerging from:	
		Planted corm	New corms
1	2.0*	28	
2	4.5	33	23
4	14.0	60	64
6	22.5	102	173
8	28.5	80	237
10	34.5	75	267
12**	38.5	37	241

*25 plants average, ** Flowering. Source: Belalcázar *et al*. (1990).

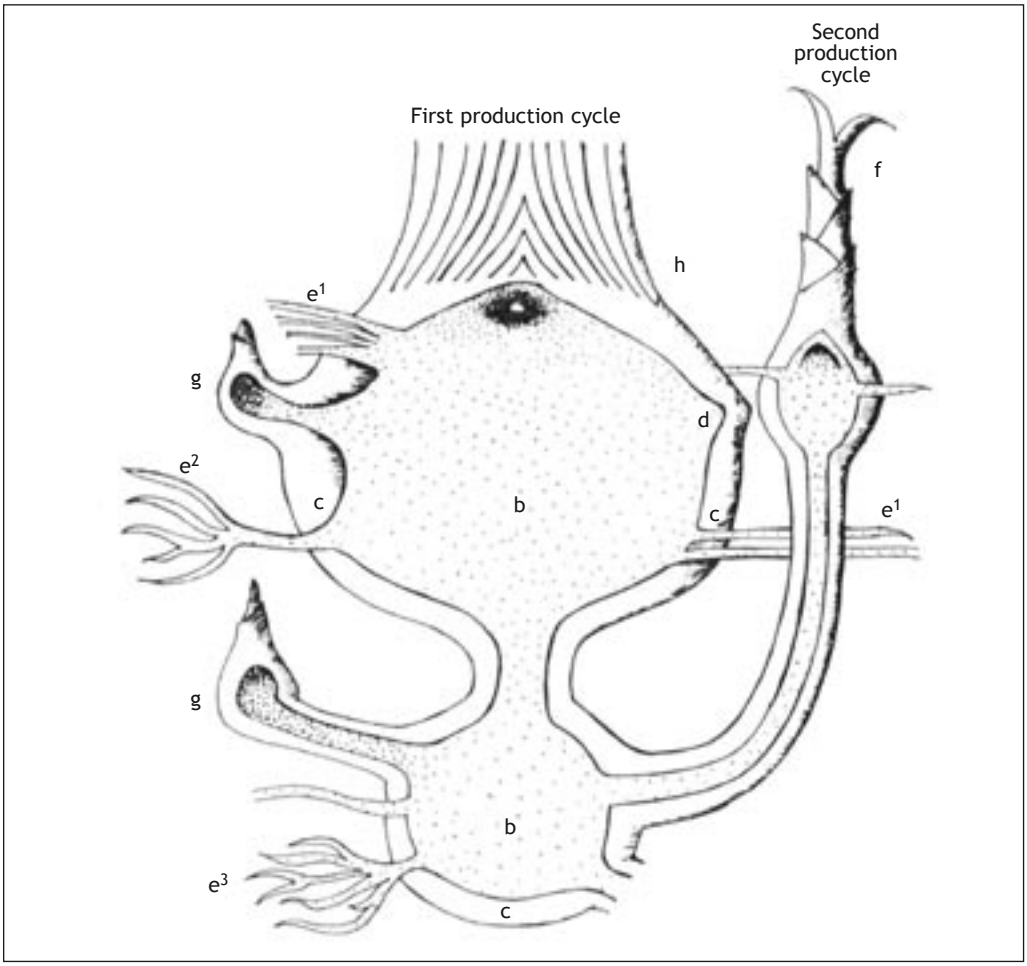


Figure 6. Diagramatic longitudinal section of the underground corm of the 'Dominico hartón' ('False horn') plantain, showing the second corm formation (Diagram from A. Belalcázar, 1991). a - growing-point or apical meristem, b - mesodermis (endodermis and cambium), c- cortex (epidermis and exodermis), d - bud, e - groups of emerged roots, f - g - suckers, h - sheaths.

Table 2. Spatial distribution of the number of roots, with depth and horizontal distance from the corm, of the plantain cv. 'Dominico hartón' in the first production cycle. Source: Belalcázar (1991).

	Horizontal distance from the corm (cm)					
Depth (cm)	**0-20**	**20-40**	**40-60**	**60-80**	**80-100**	**Proportion (%)**
0-20	105	74	63	33	22	64
20-40	27	24	21	19	8	17
40-60	18	13	8	6	6	11
60-80	11	10	7	5	0	7
80-100	2	0	0	0	0	1
Proportion (%)	35	25	21	11	7	

Almost two thirds of the roots are concentrated in the topmost soil layer closest to the corm, and the number and percentage of roots gradually decreases as the depth increases, such that at a depth of 1 m, only 1.2% of the emerged roots are present (Table 2). However, because this experiment was conducted in sandy loam soil, with an effective depth over 1.50 m, with good aeration and water and nutrient availability, one may conclude that the root system of the 'Dominico hartón' clone plantain is shallow, and additionally, is not influenced by factors related to physical or chemical qualities of the soil, or by water availability.

The exploratory activity of the root system, measured by the number of roots, was very marked horizontally: 82% of the developed roots were recorded in the 0-20 cm depth within a 60 cm radius from the corm (Table 2). The highest percentage of roots (64%) was found in the first 20 cm depth of soil. The difference between this layer, and that from 20-40 cm deep, was very great (47%). Only 17% of the roots were found in this layer.

The above results make it possible to conclude that root system activity is higher in the uppermost soil layers, and that among the tropisms that influence root growth, chemitropism has the most influence. The root system is guided to the most fertile zones of the soil that usually correspond to the layers closest to the surface where the greatest amounts of organic matter are found. This organic matter is a source of the majority of essential elements required by the plant, such as phosphorus, which favours root differentiation and growth and plantain development.

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Stratification and spatial distribution of the banana (*Musa* AAA, Cavendish subgroup, cvs 'Valery' and 'Grande naine') root system

M. Araya[1]

Abstract

The stratification and spatial distribution of the root system of 'Valery' and 'Grande naine' bananas was examined at different plant heights, vigour and under different weed control systems in commercial banana plantations in Costa Rica. Changes in the proportion (%) of root fresh weight as horizontal distance from the plant increased, were of similar magnitude in 'Valery' plants of different heights. This was also true for soil depth. Root proportions decreased as horizontal distance from the plant increased, partly because the volume of the soil blocks were different at 30, 60 and 90 cm from the plant pseudostem. For the three distances from the pseudostem, the percentage of root fresh weight decreased sharply with increased soil depth. Independent of the distance from the stem, all plants showed the highest root weight (40%) in the top 15 cm of soil. More than 65% of the total root fresh weight was found in the upper 30 cm of the soil, and the first 45 and 60 cm of the soil profile contained more than 79 and 88% of the roots at any plant height. When working with non-flowering 'Grande naine' plants reaching 180-190 cm height in sites with plants showing poor, regular or good vigour, no difference was found in total root fresh weight, or in the fresh weight of thick (> 5 mm), thin (1 - 5 mm) or fine (< 1 mm) roots. A difference in the proportion of the fresh weights of the root thickness classes was observed. The distribution was as follows for thick, thin, and fine roots, respectively: 49, 47 and 4% in sites with poor vigour; 63, 33, and 4% in sites with regular vigour and 56, 38, and 6% in sites with plants of good vigour. The total weight of fresh roots and percentage of thick roots decreased as horizontal distance increased at any level of plant vigour. The proportion of fine roots in sites with poor and good vigour was higher at 30-60 cm from the plant base than at the other distances. In sites with poor vigour the total root system did not penetrate more than 75 cm deep while in sites with regular or good vigour it reached 120 cm deep. About 95% of the total root fresh weight was detected in the upper 45 cm in the sites with poor vigour (47% thick, 44% thin, and 4% fine roots). The same layer contained 80% (53% thick, 23% thin, and 4% fine roots) of the root fresh weight in sites with regular and 81% (47% thick, 28% thin, and 6% fine roots) in sites with good plant vigour. No difference in the total root fresh weight was detected in 'Grande naine' plants when weeds were controlled for more than 5 years by hand chopping or herbicides. The proportion of thick, thin and fine roots was 66, 30 and 4% respectively. Again, the proportion of root fresh weight of every root type decreased as the horizontal distance from the plant base and soil depth increased. For both weed management systems, the total root system was found in the upper 60 cm, with 85% in the first 30 cm layer. Even though no statistical difference was found in bunch weight, the manual weed control plot yielded bunches 1.4 kg heavier than those where chemical weed control was used.

Resumen - Estratificación y distribución espacial del sistema radical del banano (*Musa* AAA, subgrupo Cavendish, cvs 'Valery' y 'Grande naine')

La estratificación y la distribución espacial de sistema radical de los cvs 'Valery' y 'Grande naine' fueron examinadas a diferentes alturas de planta, vigor y bajo dos sistemas diferentes de control de malezas en plantaciones comerciales de banano en Costa Rica. Los cambios en los porcentajes del peso fresco de las raíces fueron de similar magnitud en 'Valery' conforme se aumentó la distancia horizontal desde la base de la planta, en plantas de diferentes alturas. Los cambios entre los

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porcentajes con las profundidades de suelo también fueron de similar magnitud. El porcentaje de raíces decreció conforme aumentó la distancia horizontal desde la base de la planta, debido en parte a que el volumen de los bloques de suelo fue diferente a 30, 60 y 90 cm. Para las tres distancias horizontales, el porcentaje de raíces decreció con la profundidad del suelo. Independientemente de la distancia al tallo, todas las plantas mostraron el mayor peso (40%) de raíces en los primeros 15-cm de suelo. Más del 65% del total de raíces se encontró en los primeros 30 cm de suelo y en los primeros 45 y 60 cm del perfil del suelo se encontró más del 79 y 88% de las raíces, en cualquiera de las alturas de planta evaluadas. Cuando se trabajó con plantas no florecidas de 'Grande naine' de 180-190 cm de altura en áreas con pobre, regular y buen desarrollo, no se encontraron diferencias en el contenido fresco del total de raíces ni en el peso fresco de las raíces gruesas (> 5 mm-d), delgadas (1 - 5 mm-d) o finas (< 1 mm-d). Se observó diferencia en la proporción del peso fresco de los diferentes grosores de raíces. La distribución fue la siguiente para raíces gruesas, delgadas y finas, respectivamente: 49, 47 y 4% en áreas con plantas de pobre desarrollo; 63, 33 y 4% en sitios con plantas de regular desarrollo y 56, 38 y 6% en sitios con plantas de buen desarrollo. El porcentaje del total de raíces y raíces gruesas decreció conforme se incrementó la distancia horizontal en cualquier desarrollo de planta. La proporción de raíces finas en sitios con plantas de pobre y buen desarrollo fue mayor a 30-60 cm de la base de la planta que a las otras distancias. En los sitios con plantas de pobre desarrollo el total del sistema radical se encontró sobre los 75-cm de profundidad, mientras en sitios con plantas de regular y buen desarrollo el sistema radical alcanzó los 120-cm de profundidad. Cerca del 95% del peso fresco del total de raíces se detectó en los primero 45 cm del suelo en los sitios con plantas de pobre desarrollo (47% de gruesas, 44% de delgadas y 4% de finas). En esa misma capa se encontró un 80% (53% de gruesas, 23% de delgadas y un 4% de finas) en el sitio con planas regulares y un 81% (47% de gruesas, 28% de delgadas y 6% de finas) en el área con plantas de buen desarrollo. No se encontraron diferencias en el peso fresco del total de raíces de 'Grande naine' cuando el control de malezas se realizó por más de 5 años con chapeas o herbicida. La proporción de raíces gruesas, finas y muy finas fue de 66, 30 y 4%, respectivamente. Nuevamente el porcentaje del peso fresco de cada tipo de raíz decreció conforme aumentó la distancia horizontal de la base de la planta o aumentó la profundidad del suelo. Para ambos sistemas de manejo de malezas, el total del sistema radical se encontró en los primeros 60 cm de suelo, con 85% en los primeros 30 cm. Aún cuando no se detectaron diferencias estadísticas en el peso de los racimos, las parcelas con control manual de malezas produjeron racimos con 1.4 kg más de peso.

Introduction

As stated by Stover and Simmonds (1987) and Price (1995), descriptive studies and scientific research on the banana (*Musa* AAA) root system are quite limited, especially research on root physiology, metabolism and interactions between the soil and soil microorganisms. This lack of research is probably related to the complexity of the chemical, physical and biological interactions that occur between roots and the surrounding soil environment (McCully 1999). Some work has been undertaken to understand the development (Skutch 1932, Beugnon and Champion 1966, Lavigne 1987, Blomme and Ortiz 1996, Keshava and Iyengar 1997, Draye *et al*. 1999), function (Mohan and Rao 1984), and distribution (Riopel 1966, Sioussaram 1968, Champion and Sioussaram 1970, Avilán *et al*. 1982, Gousseland 1983, Mathew *et al*. 1987, Price 1995, Araya *et al*. 1998) of the banana root system. In an effort to estimate the root system based on measurements of aerial parts, Blomme *et al*. (2001) found that leaf area, pseudostem circumference and height of the tallest sucker were the best indicators.

In the present study, the stratification and spatial distribution of the root system of 'Valery' and 'Grande naine' bananas was examined at different plant heights, vigour and under different weed control systems in commercial banana plantations in Costa Rica.

Formation and functions of the root system

The banana root system follows the same overall arrangement of many other monocotyledons (Esau 1965). It consists of adventitious roots (Skutch 1932, Price 1995) that usually arise in groups of three or four from a common primordium within the corm, and emerge from the corm individually or in groups of two, three or four roots (Figure 1). Roots are produced continuously until flowering (Beugnon and Champion 1966, Mohan and Rao 1984, Lavigne 1987). On each first order adventitious root, sometimes called a primary root, root axis or cord root, a system of secondary roots may be formed, and on this, tertiary roots develop (Riopel 1966, Swennen *et al*. 1986, Sandoval and Müller 1999), each order being progressively thinner and shorter than the former (Figure 1). Roots of the second and third orders originate in the protoxylem near the root tips of the first and second order roots, and continue to be produced as the first and second order root extends through the soil (Stover and Simmonds 1987, Robinson 1996). When the tip of a first order root is damaged by biotic or abiotic factors, two or three second order laterals may develop from behind it into long cord roots (Lassoudière 1978, Kobenan *et al.* 1997).

Banana roots are responsible for anchorage, water and nutrient supply, and exchange of various growth substances with the shoots, including plant growth hormones such as: cytokinins, abscisic acid, ethylene, gibberellins, auxins and jasmonic acid (Barber 1992, Itai and Birnbaum 1996).

Different types of roots have distinctly different ion uptake patterns, both spatially and temporally, and uptake changes with age and distance from the root tip (Waisel and

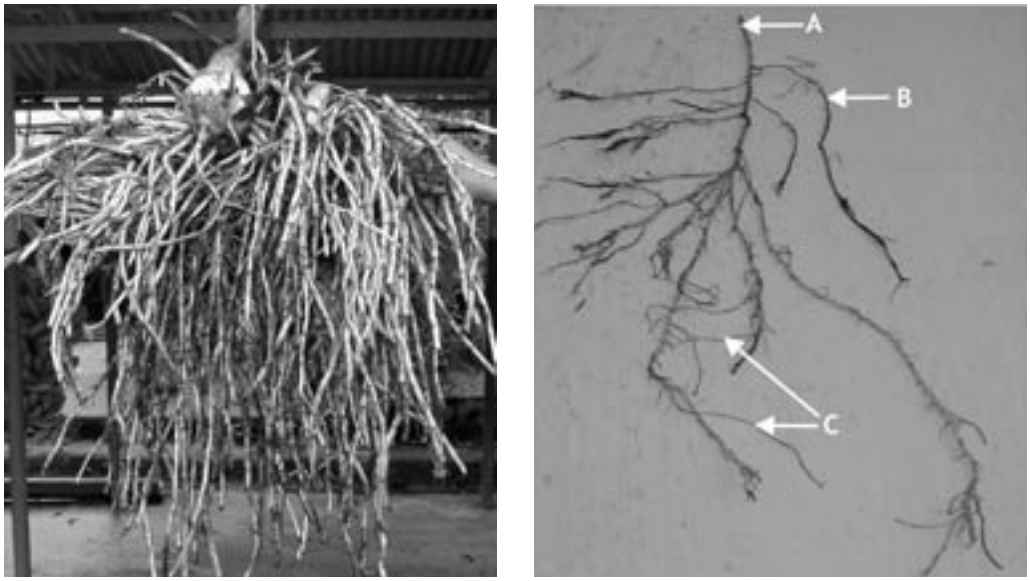


Figure 1. Left: root system of *Musa* AAA cv. 'Grande naine' originated from *in vitro* propagation material showing the first order adventitious root (root axis, cord root or primary roots) that emerged from the corm of a plant excavated and extracted from the field. Right: First order adventitious root (root axis, cord root or primary root) (A) where second (B) and third order (C) roots develop.

Eshel 1992, Zobel 1992, Gao *et al*. 1998). Uptake depends on the root surface area, the kinetics of nutrient uptake by the root and the rate of nutrient supply to the roots by mass flow or diffusion (Barber 1992). Nutrients move to the root surface radially, which means that the nutrient supply to the root per unit of root surface area is greater for fine roots than for coarse roots. Moreover, young roots are generally considered to have a higher activity of nutrient uptake than old roots (Gao *et al*. 1998). This causes finer roots to have on average a higher nutrient concentration in solution at the root surface and a greater uptake rate. Atkinson (1989) proposed that increased root system size would be advantageous for soil resource use.

Robinson (1987), working with the Cavendish subgroup banana cv. 'Williams', found that cord roots were functional for 4-6 months, whereas secondary and tertiary roots for 8 and 5 weeks, respectively, and root hairs for about 3 weeks, before rotting away.

Effect of abiotic factors on the root system

Functional and healthy roots are essential for good production. Therefore, most agricultural investment (soil preparation, fertilization, irrigation scheduling, pest control) is aimed at providing optimal conditions for root growth. Bananas have been regarded as an adaptable crop within certain, well-defined climates and soil types. The recommended soils for banana are slightly acidic, deep, rich and well drained, such as clay loam or loam soils (Lahav and Turner 1992, Delvaux 1995, Borges *et al*. 1999). Soil type, compaction, drainage, and variations in climate have a strong influence on the development of the root system (Avilán *et al*. 1982, Stover and Simmonds 1987, Barber 1992, Klepper 1992, Robinson 1996, Blomme *et al*. 2002, Dorel 2002). Great variation exists in the spatial and temporal distribution of resources in the soil, and since resources vary in mobility, rooting patterns may also vary. Heavy, compact, poorly-drained soils and water tables at depths of less than 1 m severely limit root extension, and yields are depressed accordingly (Stover 1972, Lassoudière 1978, Stover and Simmonds 1987, Robinson 1996).

Godefroy (1969) found a deeper rooting pattern for plantain (*Musa* AAB) cultivated on a sandy clay soils. Araya and Blanco (2001) observed that in soils where plants had poor development, the root system only reached 75 cm, with 99% of their roots in the first 60 cm. This was related to soil compaction beyond 60 cm depth, which is usually associated with less pore space and poor drainage, thus impeding root growth (Bennie 1996). Soil structure alters root distribution (Irizarry *et al*. 1981, Bennie 1996, Blomme *et al*. 2002). In bananas, Weert (1974) found that in soil with less than 5% macropores root penetration was drastically reduced. Similar results were reported by Avilan *et al.* (1982), where soil with 3 and 5% of macropores in the first 30 cm depth showed root deformation and reduced root weight. Blomme *et al*. (2002) found that ploughing the soil to depths of up to 30 cm improved the root system of 6 genotypes belonging to four *Musa* spp. groups. In other crops, it is well documented (Wiersum 1957, Bennie 1996, Charlton 1996, Fitter 1996, Goodman and Ennos 1999, Pezeshki *et al*. 1999) that soil density, moisture, pore structure, soil aeration, soil nutrient content and nutrient supply restrict root growth and elemental uptake.

Soils with poor drainage affect *Musa* root development and yield, because depth to the watertable limits root penetration (Godefroy 1969, Lassoudière 1971 and 1978, Irizarry *et al.* 1980, Avilan *et al*. 1979 and 1982). Aguilar *et al*. (2003) demonstrated that even

short-term O_2 deficiency in the banana root zone could, within minutes, adversely affect root aeration and consequently, within minutes to hours, root functions such as net solute transport and root elongation. Furthermore, the reduced products of the chemical and microbiological transformation due to the depletion of oxygen may behave as toxins depending on their concentrations (Drew and Stolzy 1996). Differences in the development of aerenchyma in banana roots has been reported by Aguilar *et al*. (1999), who mentioned that this could be useful in selecting cultivars for flood tolerance. Irizarry *et al*. (1980) found the best plantain yield when the water table was lowered to 36 cm depth. Also they recorded an increase in roots per volume of soil with a free water table at 48 cm depth. Ghavami (1976) found that bunch weight increased and the root system was deeper as depth to the water table increased to 120 cm. Under soil water deficit, a reduction in fresh and dry weight of banana fruits was found by Hegde and Srinivas (1989). Bhattacharyya and Madhava (1988a, b, 1989, 1990, 1992) and Robinson *et al*. (1991) found that manipulation of the soil water regime through the use of soil covers, such as banana trash and sugarcane leaf trash increased root cation exchange capacity, enhanced banana leaf production, leaf relative water content, and the C/N ratio in the leaves, and reduced the shooting-harvest interval.

In some conditions, the application of mulch stimulated better root development, which resulted in better anchorage, and improved water and nutrient absorption (Swennen and Wilson 1985). Bhattacharyya and Madhava (1986) found that banana plants, grown with a soil cover of banana trash and sugarcane leaf trash, had shallow root systems, but enhanced yield. One benefit of the use of banana trash and sugarcane leaf trash as a soil cover was the reduction and stabilization of the soil temperature down to 15 cm deep (Bhattacharyya and Madhava 1986, Robinson *et al.* 1989). It is known that soil temperature affects root growth, and an optimum exists for each crop (McMichael and Burke 1996). The dampening effect on soil temperature may be reproduced with manual weed control in banana plantations. Talwana *et al*. (2003) hypothesized that lower soil temperatures in mulched areas may slow the feeding activity and reproduction of *R. similis* and thereby reduce root damage. Manual weed cutting in banana plantations supplies sufficient ground cover and when done periodically provides good mulch, which is also a source of nutrients and organic matter (De La Cruz *et al*. 2001). Ruhigwa *et al*. (1995a) observed that mulch and weeds on the soil surface stimulated ramification of plantain roots. Refuse from harvested banana plants and from deleafing for black Sigatoka (*Mycosphaerella fijiensis*) control is another source of mulch, and also of nutrients and organic matter, and thus acts as fertilizer (Ruhigwa *et al*. 1995a, Vargas and Flores 1995). Ruhigwa *et al*. (1995a, b) found that plantain with *Pennisetum purpureum* mulch had a shortened fruiting cycle and gave the highest yield. Also, Salau *et al*. (1992) found that mulching stimulated vegetative growth and increased yield.

The beneficial effects of mulching are attributed in general to the improvement of physical, chemical and biological soil properties. However, the use of mulch provides other benefits such as reduced soil erosion, reduced temperature fluctuation, reduced evaporation rate, reduced nutrient leaching and increased water infiltration (Obiefuna 1991, Salau *et al*. 1992, De La Cruz *et al*. 2001). Additionally, decreases in pesticide application might reduce soil, air and human pollution.

Effect of biotic factors on the root system

Genomic group, ploidy level and the health of the plant affect the root system (Swennen *et al*. 1986, Stover and Simmonds 1987, Blomme 2000, Blomme *et al*. 2000, 2003). Moreover, the age of the plant and cropping patterns can modify the root distribution of any crop (Mohan and Rao 1984, Barber 1992, Klepper 1992). Also, the extension of the feeding zone varies widely among species and clones (Swennen *et al*. 1986 and 1988, Mathew *et al*. 1987, Klepper 1992). In local conditions, when comparing six genotypes and working with excavated plants (Figure 2), 'Yangambi Km5' presented the highest

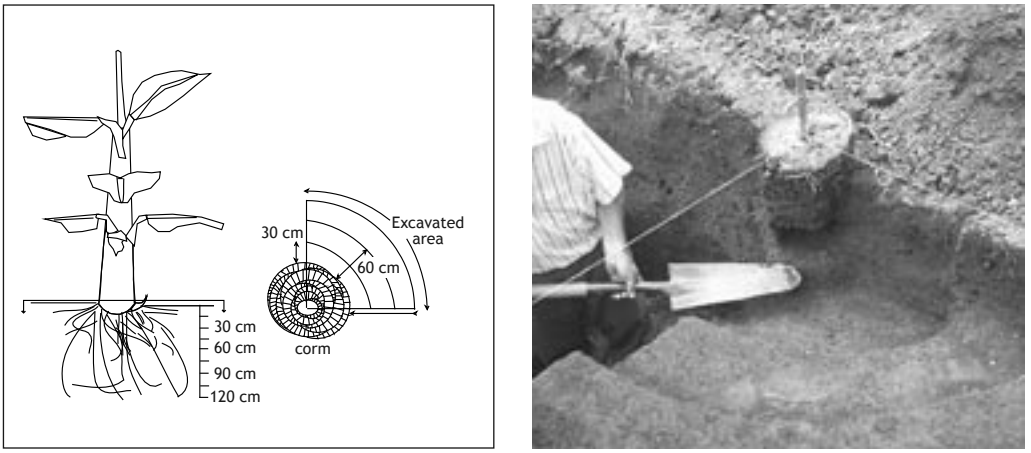


Figure 2. Left: schematic representation of the excavated area. Transverse section A-A. Right: Evaluation of a plant in the field.

(3584 g/plant) and 'Valery' the lowest (892 g/plant) amount of roots (Figure 3). The distribution of thick (> 5 mm), thin (1-5 mm) and fine (> 1 mm) roots varied within genotypes and only thick roots varied among genotypes. In any genotype, the highest proportion was of thin roots (61-77%) followed, with the exception of 'Valery', by thick and fine roots (Figure 4). The horizontal and vertical root distribution follows the same pattern in all genotypes, decreasing as distance from the plant base or soil depth increased (Figure 5). Blomme *et al*. (1999) also reported that 'Valery' has a small root system.

Vesicular-arbuscular mycorrhizae (VAM) are a type of symbiosis between plant roots and fungi. Most cultivated plants, including bananas, are hosts of mycorrhizae (Girija and Nair 1988, Iyer *et al*. 1988, Villalobos *et al*. 2001, Azcón *et al*. 2002). Mycorrhizae improve transplant recovery and survival, enhance growth rate, and increase drought resistance, effects that are thought to be directly or indirectly due to the ability of the fungus to aid in uptake of phosphorus (John 1988, Blal *et al*. 1990, Jaizme *et al*. 2002). One approach is attempting to develop VAM as a nematode control tool in bananas (Umesh *et al*. 1988, Parvatha *et al.* 2000, Elsen *et al*. 2002) that could be included in a strategy for the integrated management of banana nematodes.

Nematodes are important pathogens in bananas and in many countries rank second after black Sigatoka. However, they will not be included here, because interesting

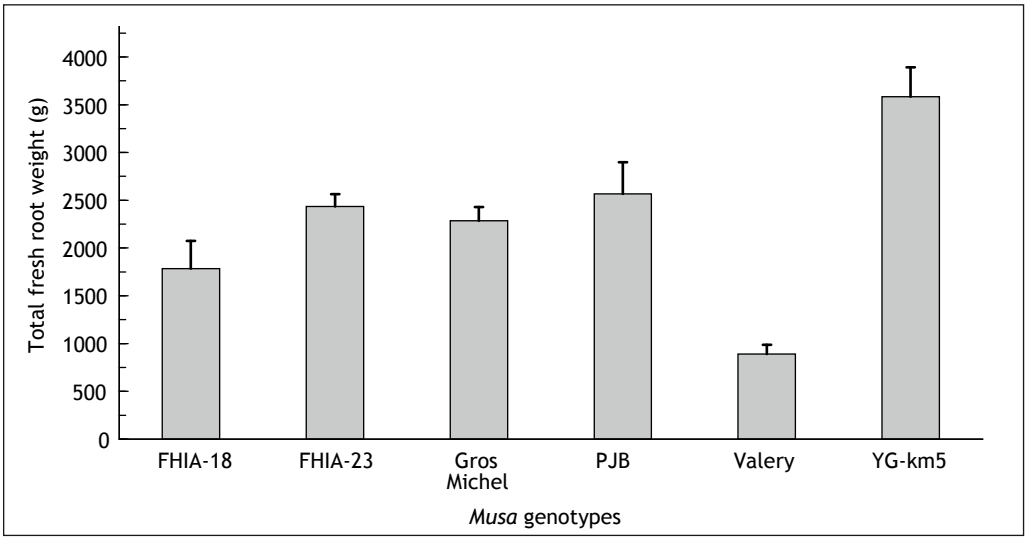


Figure 3. Total root fresh weight in the excavated area of banana (*Musa* spp.) genotypes. Data are mean ± standard error of 10 plants.

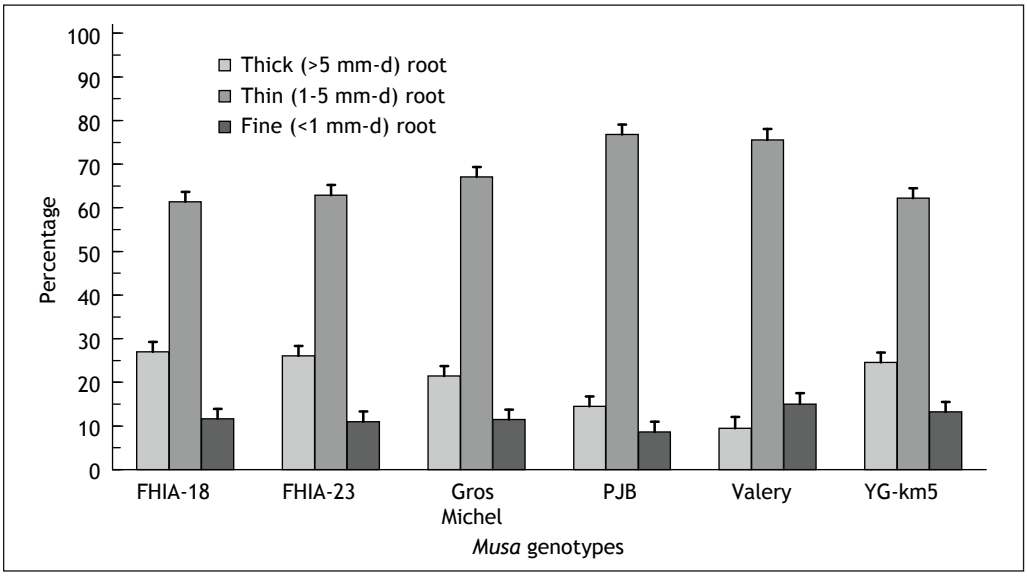


Figure 4. Distribution of root types by genotype. Data are mean ± standard error of 10 plants.

book chapters have already been written on this subject (Gowen and Quénéhervé 1990, Gowen 1995, De Waele 2000, De Waele *et al*. 2000, Gowen 2000a, b, Sarah 2000). Moreover, there are two presentations about nematodes in these proceedings. Associations between nematodes and other organisms have been noted in bananas (Pinochet and Stover 1980, Aguilar 2002, Batlle and Pérez 2002). In local conditions, *Trichoderma* spp., *Fusarium* spp., *Penicillium* spp., and *Cylindrocladium* spp. were

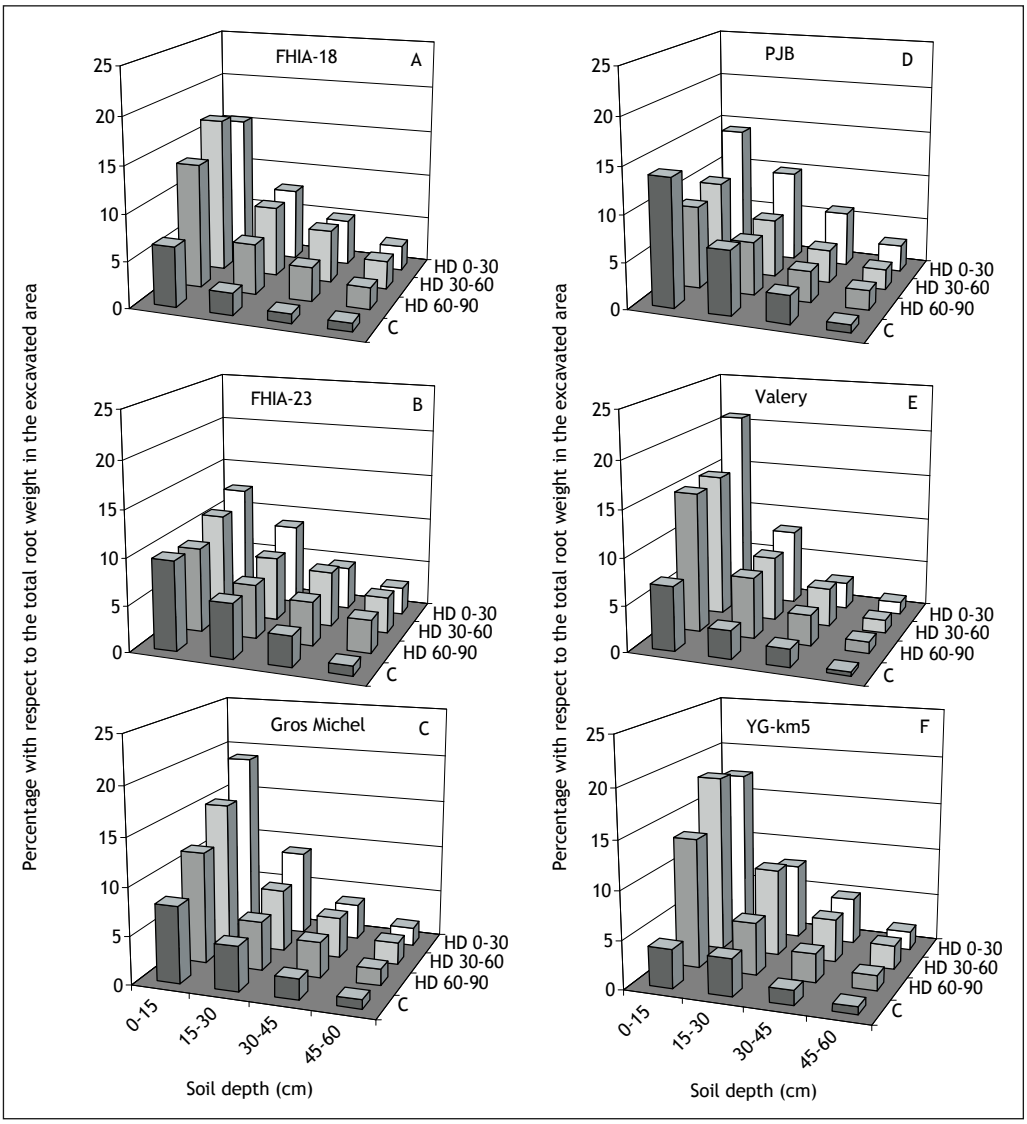


Figure 5. Vertical and horizontal distribution (%) of banana (*Musa* spp. genotypes) roots. HD=horizontal distance from the plant pseudostem. Data are means of 10 plants.

associated with banana roots showing damage mainly by *R. similis* (Aguilar 2002). *Cylindrocladium* spp. has also been associated with *R. similis* root damage in banana plantations in Martinique and Guadeloupe (Loridat and Ganry 1991). Stover (1966) and Pinochet and Stover (1980), monitoring banana root nematode lesions from plantations in Central and South America, Somalia and the Philippines, reported evidence of *Fusarium solani*, *F. moniliforme*, *Cylindrocarpon musae* and *Acremonium stromalicum*. In Lebanon, *F. oxysporum* and *Rhizoctonia solani* were associated with banana root damage caused by *Helicotylenchus multicinctus* or *Meloidogyne incognita* (Sikora

and Schlösser 1973). However, there are some endophytic fungi that colonize the roots and protect them against biotic or abiotic factors (Pocasangre *et al*. 2000). These authors found five non-pathogenic strains of *Fusarium* that were able to reduce *R. similis* in banana cultivars. More information about this approach is presented in these proceedings.

Spatial root distribution in 'valery' plants differing in height

Roots generally spread over 2-3 m and up to 5 m from the plant (Riopel 1966, Avilán *et al*. 1982, Gousseland 1983) and over 1 m in depth (Price 1995). However, most of the root system occurs within a 60 cm radius of the stem and within 30 cm of the soil surface (Sioussaram 1968, Champion and Sioussaram 1970, Avilán *et al.* 1982).

Araya *et al*. (1998), working with excavated plants (Figure 2) of *Musa* AAA cv. 'Valery', did not find an effect of plant height on the spatial distribution of the roots, expressed as the proportional distribution of fresh weight. This means that changes in the proportion of root fresh weight, as horizontal distance from the plant increased, were of similar magnitude in vegetative plants of 120 (2 leaves), 150 (4 leaves), 180 (6 leaves) or 210 (8 leaves) cm high or 390 cm high in plants within 1 to 3 days from bunch (inflorescence) emergence. This was also true for soil depth. They found in the upper 30 cm of the soil profile a higher proportion of root fresh weight at 0-30 cm horizontal distance from the pseudostem than further away (Figure 6). The proportion

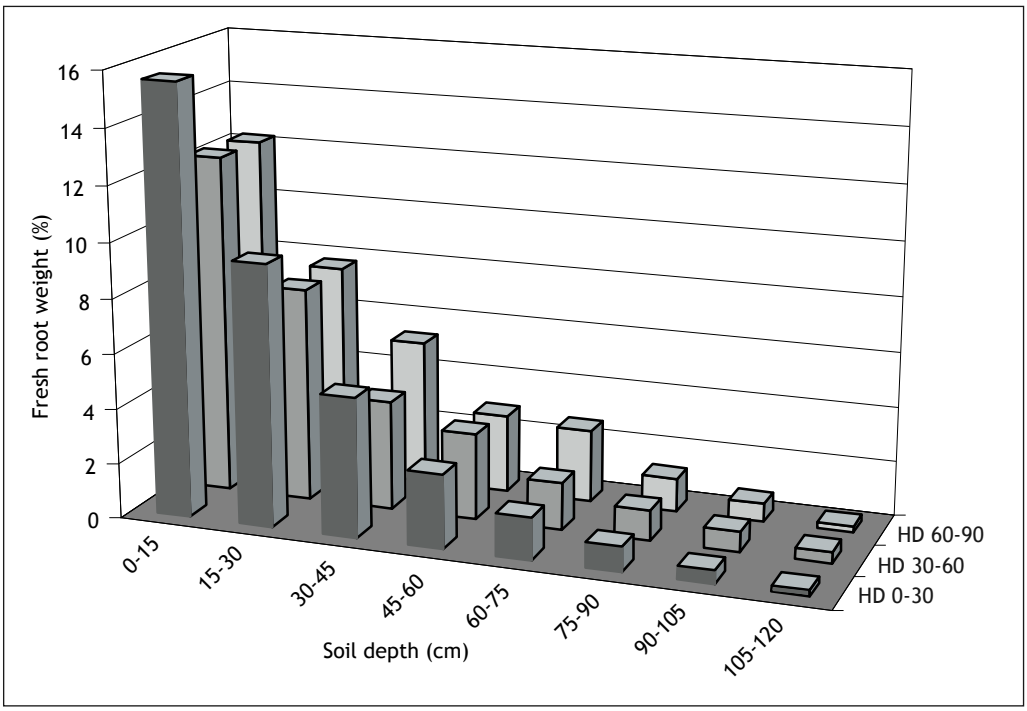


Figure 6. Spatial distribution of *Musa* AAA (cv 'Valery') roots. HD = horizontal distance from the plant pseudostem. Data are mean of 20 plants.

of the roots decreased as horizontal distance from the plant increased, partly because soil block volume was different at 30, 60 and 90 cm from the pseudostem. In the smallest plant (120 cm high) the volume of the soil blocks at 60 and 90 cm from the plant base was 2.3 and 3.6 times the volume at 30 cm, while in the plants close to bunch emergence, it was 2.0 and 3.1, respectively. For the three distances from the stem, the proportion of root weight decreased sharply with soil depth (Figure 6). Independent of the distance from the stem, all plants showed the highest root weight in the top 15 cm of the soil (40%). More than 65% of the total root fresh weight was found in the upper 30 cm of soil and more than 79% and 88% of the roots were found in the first 45 and 60 cm of the soil profile, respectively, at any plant height. The total root fresh weight in the excavated area (0-90 cm from the stem and 0-120 cm depth) was 1.2 kg for plants 120 cm high, 1.0 kg for 150 cm, 1.1 kg for 180 cm, 1.5 kg for 210 cm high and 1.2 kg in plants just before bunch emergence.

Stratification and spatial root distribution in 'Grande naine' plants differing in vigour

Araya and Blanco (2001) did not find differences in total root fresh weight or in the root fresh weight of thick (> 5 mm), thin (1 - 5 mm), or fine (< 1 mm) roots per plant among sites with plants of different vigour and bunch weight (Figure 7). Changes were observed in the proportion of root types with plant development. In sites with good plant vigour there was 56% of the root fresh weight in thick roots, 38% in thin roots and 4% in fine roots. For the sites of moderate vigour, the distribution was 63% for thick roots,

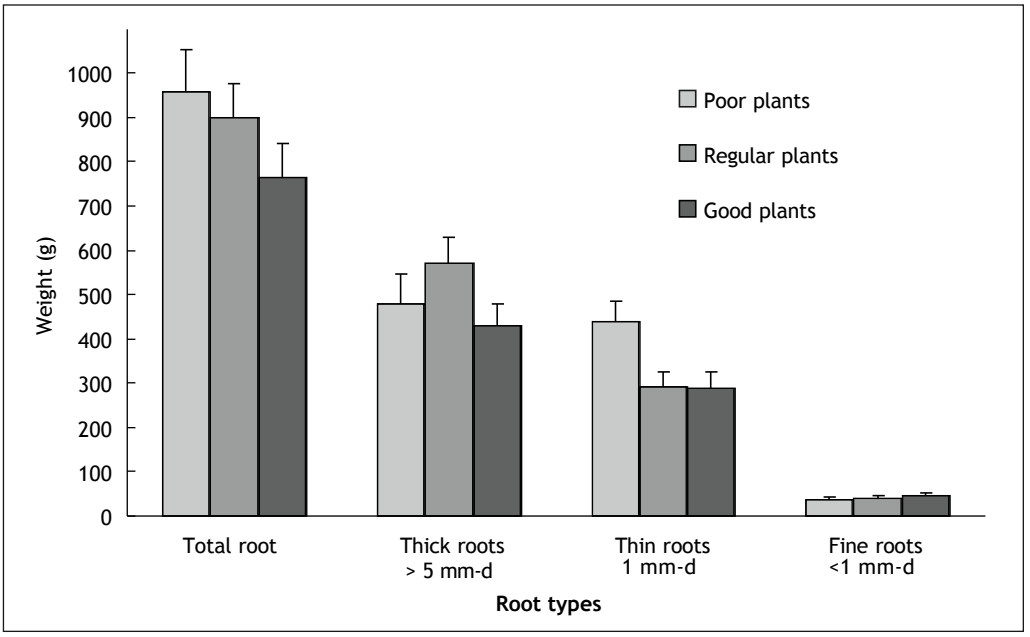


Figure 7. Root fresh weight by root type in the excavated area of bananas (*Musa* AAA cv. 'Grande naine') with poor, regular and good plant vigour. Data are mean ± standard error of 10 plants.

33% for thin roots and 4% for fine roots. These values changed to 49% thick roots, 47% thin roots and 4% fine roots in sites with poor vigour. The proportion of total root fresh weight, per volume of soil, (Figure 8A) decreased as horizontal distance from the plant increased at any plant development site. When roots were partitioned in classes, the same pattern was observed for thick roots (Figure 8B). However, the proportion of thin roots (Figure 8C) in poor and good plants was larger at 30-60 cm from the plant base than at the other distances. This was also true for fine roots (Figure 8D) in the plants with good development.

In plants with poor vigour, no roots penetrated deeper than 75 cm while in plants with regular and good vigour they reached 120 cm depth (Figure 9A). About 95% of the total root fresh weight was detected in the upper 45 cm of soil in plants of low vigour (47% thick, Figure 9B; 44% thin, Figure 9C; and 4% fine, Figure 9D). In the same layer there was 80% (53% thick, 23% thin, and 4% fine) in sites with plants of regular vigour and 81% (47% thick, 28% thin, and 6% fine) in sites with vigorous plants. The total root fresh weight in the excavated area (0-90 cm from the pseudostem and 0-120 cm depth) was 0.95 kg for the plants of poor vigour, 0.9 kg for the moderate and 0.76 kg for plants with good vigour.

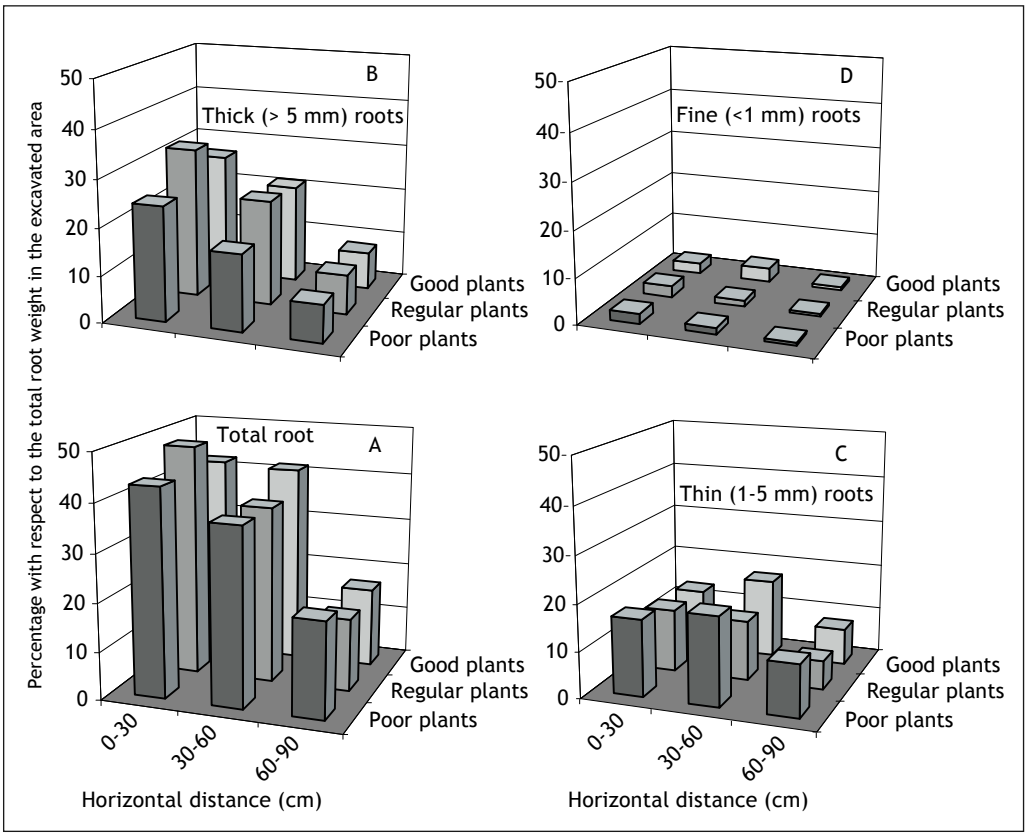


Figure 8. Horizontal distribution (%) of roots from bananas (*Musa* AAA cv. 'Grande naine') of poor, regular and good plant vigour. Data are means of 10 plants.

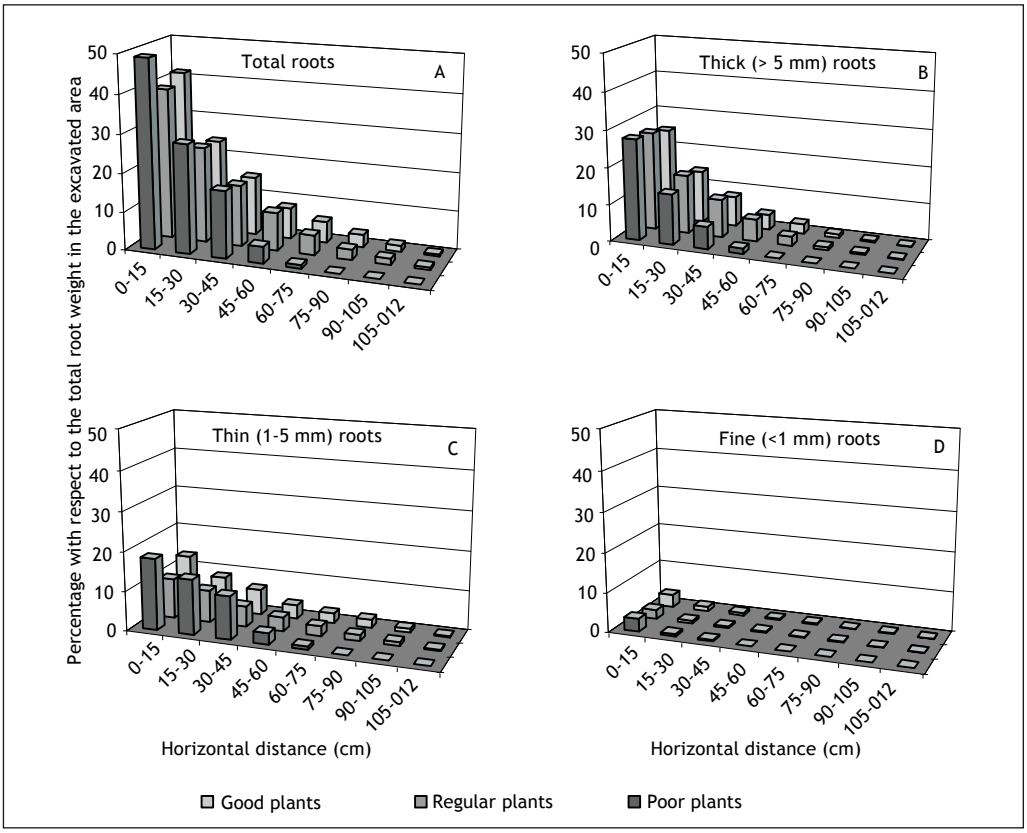


Figure 9. Vertical distribution (%) of roots from bananas (*Musa* AAA cv. 'Grande naine') of poor, regular and good vigour. Data are means of 10 plants.

Stratification and spatial root distribution in 'Grande naine' under two weed management systems

No difference was found in total root fresh weight between sites with chemical (767 g/plant) or manual weed control (781 g/plant). Also, there was no difference between management systems in any root thickness class, but root types differed between them (Figure 10). The average root fresh weight for both weed management systems was 516 g of thick roots per plant, 222 g of thin roots and 33 g of fine roots per plant. No differences were observed between weed management systems in the horizontal or vertical proportional distribution of fresh thick, thin or fine roots per plant. The proportion was 66% for thick, 30% for thin and 4% for fine roots. The proportion of root fresh weight of every root type decreased as horizontal distance from the plant and soil depth increased (Figure 11A-C). In both weed management systems, the total root system was found within the first 60 cm of soil depth. About 85% of the total root fresh weight was detected in the upper 30 cm, and 44% of the root system was located in a 30 cm radius around the pseudostem.

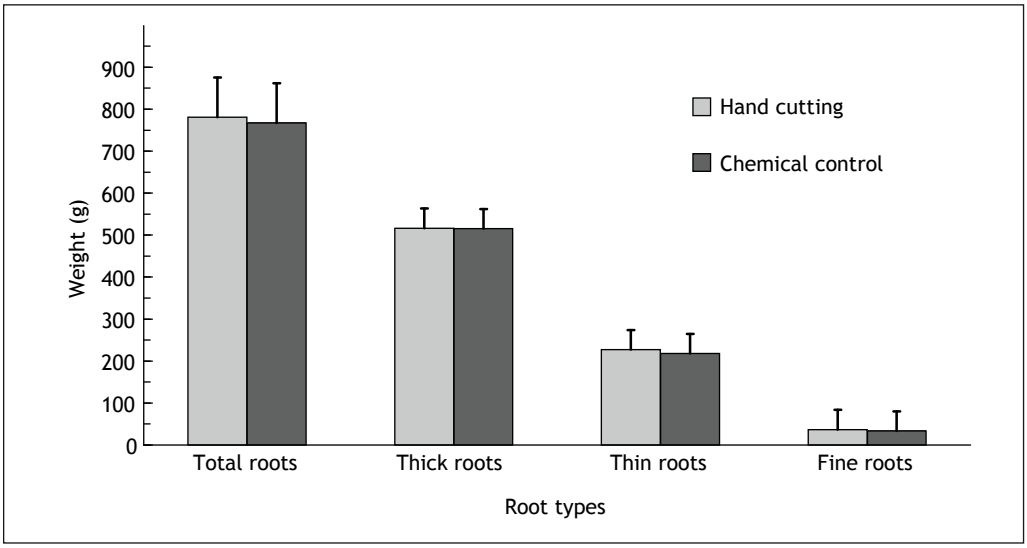


Figure 10. Fresh root weight by root type in the excavated area of bananas (*Musa* AAA cv. 'Grande naine') with chemical or manual weed-control. Data are mean ± standard error of 10 plants.

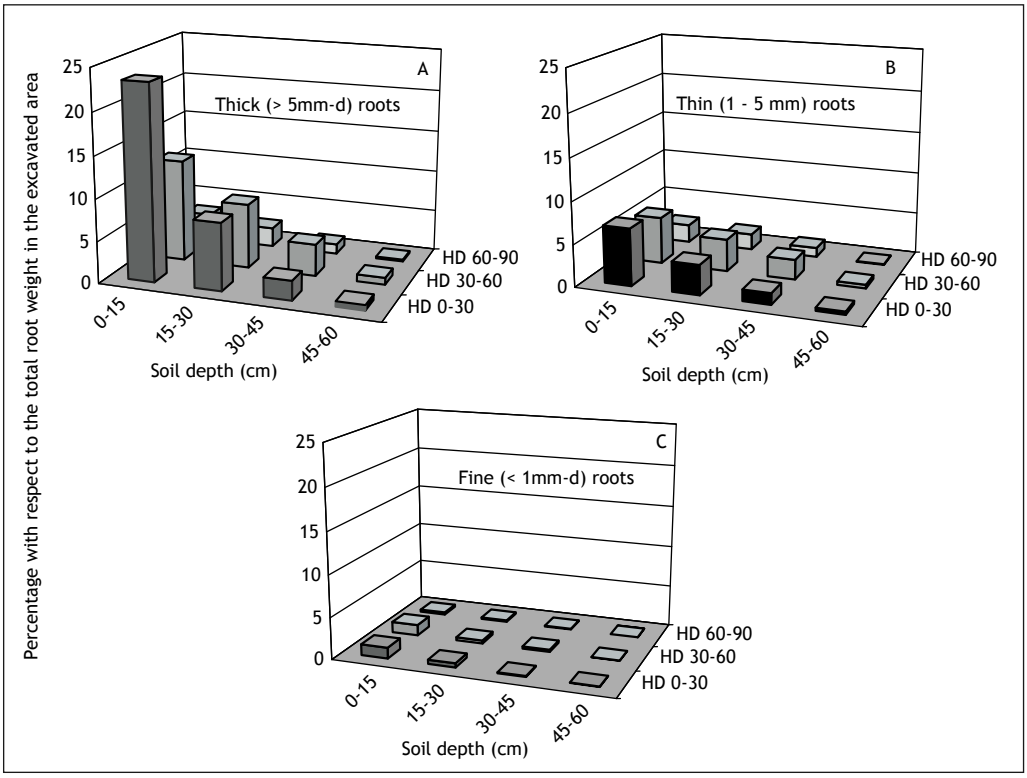


Figure 11. Vertical and horizontal distribution (%) of banana (*Musa* AAA cv 'Grande naine') roots from either chemical or manual weed control. HD= horizontal distance from the plant pseudostem. Data are means of 20 plants.

Bunches from the plot where weeds were controlled manually were 1.4 kg heavier than those from the plot with herbicide applications. No correlation was found between bunch weight and either total root weight, or root weight by thickness class or the sum of root types per soil block.

Practical implications of the stratification and spatial distribution of the banana root system

Commercial banana farms in Costa Rica are usually larger than 80 ha and in many cases it is common to observe plantations of 400 ha or more. The complete area in a given farm is treated in the same way. This means that fertilizer application, nematode, weed and black Sigatoka control, drainage and other cultural practices are equal across the farm. However, differences in plant development and yield are observed, which should give clues to managing those sites accordingly.

Independently of the research focus, the major part of the banana root system occurs in the upper part of the soil. This is in agreement with other results (Sioussaram 1968, Champion and Sioussaram 1970, Avilán *et al*. 1982, De Moura *et al*. 1986, Martinez and Ortega 1988, Soto and Ruiz 1992, Price 1995). Due to this superficial root system, mechanical cultivation should be avoided. Generally, in commercial banana farms, weed control is based on herbicide application. This reduces weed control costs compared with manual control, but according to Stover and Simmonds (1987) it increases erosion, especially in high-rainfall areas as in our study conditions. Moreover, the post-emergence herbicides should be applied with caution to prevent the product from entering the soil and killing the roots. Since herbicides have an impact on the environment and because the demand for pesticide-free products is increasing, manual weed control is becoming an alternative.

No difference in root weight between chemically and manually controlled plots indicated that weeds used as cover crops did not compete for space with the banana root system nor did they affect root stratification. Bunches from the manual weed control plot were 1.4 kg heavier compared with chemically-treated plots. This means that manual weed control did not affect yield, which is in partial agreement with other reports (De La Cruz *et al*. 2001). It is important to confirm whether this improvement in bunch weight is repeatable, because an additional yield of 2.7 Mt might be obtained, based on exportable banana production per hectare at 1.05 boxes/bunch, 1700 effective production units per hectare, a ratooning rate (number of bunches per production unit per year) of 1.4, and 25% rejected bananas. The additional yield may cover the extra expense incurred by manual weed control. A similar effect on yield was referred to by Bhattacharyya and Madhava (1987), who found that banana and sugarcane leaf trash, used as a soil cover, enhanced banana yield. This approach to weed management is being undertaken in some Colombian banana plantations (Pinilla and García 2002).

Mulched banana plantations may result in more sustained yield compared with unmulched areas. Although manual weed control appears to be beneficial for banana yield, it is a labour-intensive activity and requires a well-planned program to assure its positive effects. As with other crops, the effects of mulch on banana growth and yield may vary with physical and chemical soil properties, microclimate, and other factors. Therefore,

its introduction into a farm needs prior evaluation and a combined strategy of manual weed control and mulching is highly encouraged.

A deep rooting system should allow banana plants to better resist drought. Burgess *et al*. (1998) demonstrated a redistribution of soil water from deeper in the profile to dry surface horizons by the root system. This should maintain root viability, facilitating root growth during dry periods. Araya *et al*. (1999), working with plants with differences in vigour, found about 11% of the total root system below 60 cm depth in regular and good vigour plants. Probably, the deeper roots provided the banana plants with better resistance to drought in the months of February, March and April when precipitation was low. Additionally, a deep root system could be advantageous in the use of soil resources. It is possible to improve the depth of rooting by soil preparation in replanting either by sub-soiling, ploughing or disking according to soil requirements. Consequently, in addition to soil preparation, domes are being increasingly used in banana replanting. Pérez (1999) reported greater root mass at greater depth in plants cultivated on domes compared with those grown on flat surfaces. Robinson and Alberts (1989), working with 'Williams' banana, found most water uptake in the upper layers of the soil; up to 80% of water being taken from the upper 30 cm. In places where irrigation is used, more work is needed to assess available water and the advantages of using a specific irrigation system because water application needs to account for the amount of available water in the entire rooting zone, which depends on the rooting pattern and rooting depth.

Fertilizer application must take into consideration the distribution of roots across the soil surface. All root types were recorded at the three horizontal distances from the pseudostem. The proportion of thin and fine roots together varied between 33 and 50% of the total root system and depended on plant age, vigour and soil condition. According to Swennen *et al.* (1986 and 1988) banana feeder roots are those that are less than 5 mm diameter, and in *Musa acuminata* triploids (AAA), cultivated in hydroponics, they made up as much as 77% of the root system.

Mohan and Madhava (1988) found that plants do not draw nutrients equally from all zones in the soil through which their roots penetrated. For bananas, they stated that lateral roots bearing hairs are mainly responsible for nutrient and water uptake. These roots are distributed away from the corm and hence the placement of fertilizer should also be away from the plant (Summerville 1939). Studies of Mohan and Madhava (1988) revealed that the active zone of nutrient uptake for 2 month-old bananas was within 30 cm of the plant. However, in 5 month-old plants no large differences in the active zone were found up to 60 cm from the corm. On the basis of the findings presented here, where thin and fine roots were detected at 0-30, 30-60 and 60-90 cm from the stem, and those of Mohan and Madhava (1988) it appears advisable to apply fertilizer, taking plant development into consideration, doing broadcast applications between the plant base and up to 60-90 cm from the stem, since roots spread well. This recommendation agrees with that of Mohan and Madhava (1988), Keshava and Iyengar (1990 and 1997) and Araya *et al*. (1998). Broadcast applications should reduce the common problem of soil acidity and accumulation of specific nutrients in a small band or area affecting nutrient uptake and yield. For soil nutrient analysis, the sample must correspond with the active root zone, where fertilizer was applied.

Based on the spatial horizontal root distribution, the samples for nematode studies could be taken at any distance from the stem. Nevertheless, according to the spatial root nematode distribution detected by Araya *et al*. (1999) and Araya and De Waele (2002), samples for monitoring nematode populations should be taken within a 30 cm radius of the plant base and down to 30 cm depth from the soil surface. This allows for good sample sizes to be obtained in smaller areas (15 cm long x 15 cm wide x 30 cm depth) because of high root density. The suggested sampling point is consistent with the recommendation of Cabrales (1995) and Pattison *et al*. (1997).

Lassoudière (1978), Robinson (1996) and Serrano and Marín (1998) reported positive correlations between bunch weight or yield of dessert bananas and root mass. Calvo and Araya (2001) found good yield when root mass in nematode samplings was high. Attempts to relate the crop performance with the extent of rooting are desirable because it is known that the benefits derivable from a given investment in root dry weight depend fundamentally on root system architecture (Fitter 1996).

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3

Root physiology

Fisiología de la raíz

Factors affecting the physiology of the banana root system

D W Turner[1]

Abstract

The roots of bananas and plantains absorb nutrients and water from the medium in which they grow and transport these to the shoot. The absorption of nutrients and their loading into the stele for transport to the shoots requires energy and is very sensitive to oxygen deficiency, a component of waterlogging. In contrast, the gradient in water potential together with the conductance of the pathways of water flow, which can be influenced by the plant and its environment, determines the direction and volume of water flow. No metabolic energy is needed for this process. Under drought, roots produce signals that close stomata, allowing the banana to remain highly hydrated, but reduce carbon assimilation and yield. In addition, roots are the 'home' for micro-organisms that influence the physiology of the roots. A way forward is to integrate our knowledge into quantitative models that evaluate the most sensitive features of the root system in relation to its functions. This will point the way to improved management practices and genetic manipulation. A large gap in our knowledge is the genetic variation in physiological responses of roots to their environment, especially the rhizosphere.

Resumen - Factores que afectan la fisiología del sistema radical del banano

Las raíces de los bananos y los plátanos absorben nutrientes y agua del medio en que crecen y lo transportan a los brotes en crecimiento de la planta. La absorción de nutrientes y su carga en el cilindro vascular para su transporte a los brotes en crecimiento, requieren energía y es muy sensitivo a la falta de oxigeno, una característica del estancamiento de agua. En contraste, la gradiente en el potencial del agua junto con la conductividad del camino del flujo del agua, que puede ser influenciado por el ambiente, determina la dirección y el volumen del flujo del agua. En condiciones de sequía, las raíces producen señales que cierran los estomas, permitiendo al banano permanecer altamente hidratado, pero reduce la asimilación del carbono y la producción. Además, las raíces son "la casa" de los microorganismos que influencian la fisiología radical. Un camino hacia delante es él poder integrar nuestros conocimientos en modelos cuantitativos que evalúen las características más sensibles del sistema radical con relación a sus funciones. Esto señalara la ruta para mejorar las practicas de manejo y manipuleo genético. Un gran vació en nuestro conocimiento es la variación genética en respuestas fisiológicas de las raíces en su ambiente, especialmente en la rizosfera.

Introduction

Physiology is about how an organism works. To manage a crop requires knowledge of how that crop works at different levels. The manager is most attracted to knowledge at the whole plant level but this needs to be supported by knowledge of plant organs, their tissues and the cells that make up the tissues. Price (1995) pointed out that for bananas and plantains, "research on root physiology, metabolism and interactions with the soil and soil microorganisms is in its infancy" and Delvaux (1995) concluded that "our understanding of soil-root-microbial interactions is still embryonic". Therefore, investment in exploring the physiology of banana root systems should reward us with new insights and approaches to management.

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Draye (2002) has reviewed the banana root system with emphasis on architecture and genetics. My purpose is to draw some links between the architectural, structural and anatomical features of banana roots and their physiology. Superimposed on these links are the environmental, edaphic and biological factors that affect roots.

How well does the banana root system work?

Banana cultivars can be highly productive and in commercial plantations can produce 80 to 100 t^{-1} ha^{-1} $year^{-1}$ of fresh fruit. This approximates 16 to 20 tonnes dry matter and puts bananas in the top league among plants for productivity. Thus, the root system of bananas with its current architecture and function, and with high management inputs, can support high production. However, most banana plantations yield less because the plants, including the root system, are constrained by genetic, environmental, edaphic and biological factors.

Root length density (L_d, cm/cm^3) and specific root length (L_w, m/g) are quantitative features of the architecture of root systems. Both may be subject to genetic manipulation within *Musa*. Root length density quantifies the capacity of the root system to explore soil volume. A high L_d means that the roots absorb more of the nutrients in a volume of soil, especially those nutrients that diffuse to the root surface. Banana and plantain roots have an L_d of about 1 cm/cm^3 (Irizarry *et al*. 1981) that is similar to the root systems of trees. On the other hand, herbaceous species have an L_d, in the surface layers of soil, of 4 to 50 cm/cm^3.

Specific root length quantifies the length of root per unit of carbon invested in the root system. In bananas, the main, secondary and tertiary nodal roots and the main and secondary lateral roots have a unique L_w. The banana invests carbon in nodal roots, that arise from the rhizome (corm) and which have a much longer life than the lateral roots which absorb most of the water and nutrients. For mature plants of 'Williams' growing in sand culture the L_w varies from 0.4 m/g for the main nodal roots to 150 m/g for the secondary lateral roots (Turner and Barkus 1981). The partitioning of dry matter between nodal and lateral roots is about 50:50 but this is likely to change during plant development. In the example above, the allocation of 1 g of dry matter to main nodal roots will extend the root by 0.4 m but allocation of the same amount to secondary lateral roots will provide a total 150 m of roots. How L_w changes with genotype, plant development, climatic and edaphic conditions needs to be determined. The values of L_w for bananas can be compared with 100 to 200 m/g for the whole root system of cereals and grasses (Milthorpe and Moorby 1979). This difference in root architecture between bananas and grasses may contribute to the competitive success of grasses when they grow amongst bananas.

Root growth rates have been measured in some controlled environment experiments and in the plantation. The dry matter of the root system of 'Williams' follows an optimum curve with temperature with little growth below 13˚C or above 35˚C and an optimum of about 22˚C (Turner and Lahav 1983). For the rate of root elongation, the response to temperature may be exponential from 10 to 26˚C (Robinson and Alberts 1989) or show an optimum at about 23˚C, depending on the assumptions made in the analysis of Robinson and Alberts' data (Turner 1994). The impact of soil water deficits on root growth needs to be determined.

Oxygen supply

Roots are living entities and need oxygen for their growth and function (Armstrong 1979). Oxygen deficiency is a component of waterlogging caused by poor internal drainage in soils. Delvaux (1995) lists eight soil orders on which bananas are grown across the world and for six orders, drainage is a key management practice. Therefore, knowledge about how banana and plantain roots respond to oxygen deficiency is important for management.

Roots adapt to oxygen deficiency to various degrees by changing their anatomy and metabolism. Banana roots develop lysigenous aerenchyma in the mid cortex from about 50 mm behind the root tip, even in aerated media (Aguilar *et al*. 1999). Among cultivars, genomic constitution appears not to influence aerenchyma formation. Aerenchyma, provided it is continuous, increases gas flow axially along the root and, in waterlogged conditions, enables oxygen to move from the shoot to the roots (Aguilar *et al*. 2003). The stele of roots of 'Williams' respires (on a volume basis) six times faster than the cortex. This is about 50% higher than in maize, for example, and contributes to a rapid depletion of oxygen concentration in the stele of roots experiencing waterlogging. Even in fully aerated solution culture, oxygen concentration can be halved from the bulk medium across the root hair zone to the root surface. Further reductions inside the root mean that even a small drop of oxygen concentration, say by 3 kPa in the medium, is likely to cause the stele to become anoxic and reduce nutrient loading into the stele. Under laboratory conditions, net nutrient loading begins to fall soon after the imposition of hypoxia and after 4 hours is 36% of its original rate. Lateral roots consume oxygen that flows longitudinally from the shoot (Aguilar *et al*. 2003). They reduce the amount of oxygen that can then flow to the apex but are essential for the root to explore large volumes of new soil. The density of the short secondary lateral roots is within the range to classify them as cluster roots, however we should be careful in assuming they are physiologically similar until data are available on their function. Lack of oxygen kills root tips (Aguilar *et al*. 2003) with subsequent branching behind the dead apex. This is commonly seen in the plantation and may indicate an earlier waterlogging event.

Roots as a "home" for microorganisms

Roots provide an environment for microorganisms, such as fungi and nematodes. The aerenchyma provides a suitable habitat for Fusarium (Aguilar *et al*. 2000a). Indeed, hyphal connections between the aerenchyma and the stele may be necessary for Fusarium, as the hyphae in the aerenchyma can absorb oxygen for transport to the stele, which may be anoxic. In addition, the hyphae in the stele can absorb nutrients for transport to the hyphae in the aerenchyma. Beckman *et al*. (1961) proposed that physical barriers and physiological responses are essential for resistance to Fusarium. Temporary blockage of the fungus at the vessel endings in the stele, for example, would provide time for physiological responses to be effective. However, aerenchyma, if present, may provide a by-pass for the fungal hyphae around barriers in the stele. Mycorrhizae increase the acquisition of phosphorus and potassium in banana coming from micropropagation (Declerck *et al*. 1994) and there is an interaction between the species of mycorrhizal fungi and cultivar (Knight 1988). Fungi and nematodes obtain nourishment from the root system and this represents a carbon cost for the plant.

Microorganisms alter the physiology of the roots they invade. *Fusarium oxysporum* f. sp. *cubense* (*Foc*) increases the activities of enzymes involved in phenol metabolism in roots and so does exposure to hypoxia, more so in cultivars resistant to *Foc* (Aguilar *et al*. 2000b). These interactions are fascinating but complex and make it difficult to predict what might happen in the field.

Nutrient uptake by root systems

The efficiency with which the root system transfers nutrients from the soil to the plant is a gross measure of root function. The apparent root transfer coefficient, α, proposed by Nye and Tinker (1969), evaluates this efficiency and it is suitable for longer term (weeks or months) studies. The plant uptake rate for a nutrient, R_p, is influenced by the root dry weight, W_r, the concentration of the nutrient at the root surface, C_0 and α. This approach includes growth and nutrient components and is calculated from Nye and Tinker (1969):

$$\alpha = (W/W_r)(C_m/C_0)(R_W + R_C) \qquad 1.$$

Where W is plant weight, C_m is the nutrient concentration in the plant, R_W is the relative growth rate and R_C is the relative change in nutrient concentration over time. In equation 1, W/W_r and R_W are growth components and the nutrient components are C_m/C_0 and R_C. To increase plant uptake rate of a nutrient we increase either root weight (e.g. improve soil conditions for roots), or the concentration of nutrient at the root surface (e.g. add fertilizer). The α can be influenced by environment and nutrient supply. For example, Turner and Lahav (1983) studied the effect of temperature on the growth of 'Williams' banana plants in the vegetative stage in controlled environments over 12 weeks. As temperature increased from 25/18˚C (day/night) to 33/26˚C, the root dry weight, W_r, fell by almost two thirds. This could be expected to reduce K uptake. However, temperature increased the apparent root transfer coefficient α of K so that it more than compensated for the reduced W_r and plant uptake rate was increased by 50% (Turner and Lahav 1985).

Earlier, Turner and Barkus (1981) evaluated the effect of K supply on α in a sand culture experiment lasting three crop cycles. Low K supply reduced yield and K deficiency reduced the effectiveness of the root system, α, in absorbing N, P, Ca, Mn, Na, and Zn but had no effect on the α of K, Mg or Cu. These differences were caused by the marked effect of K on growth, and in the case of K, Mg and Cu there were compensatory changes in the concentration components.

In summary, the environmental factor, temperature, generally increases root system effectiveness for all nutrients from 13 to 30˚C, overriding some of the negative effects on root growth above 22˚C. Potassium deficiency reduces the effectiveness of the root system for absorbing most nutrients, mainly through its effect on reduced growth. However, a deficiency of K does not reduce the effectiveness of the root system in absorbing the K that is available, despite the reduction in growth and yield.

Water uptake and banana roots

Roots absorb and conduct water. The radial hydraulic conductivity, L_{Pr}, measures the capacity of the roots to transport water from the epidermis to the stele and can be

measured using a root pressure probe (Steudle *et al*. 1987). For young nodal roots of 'Williams', grown in solution culture, the L_{Pr} is 1.8 x 10^{-6} m s^{-1} MPa^{-1}, which is three times higher than for the primary roots of maize under the same conditions. The L_{Pr} of maize (Gibbs *et al*. 1998) and banana (Aguilar *et al.* 2003) roots, determined hydrostatically, decreases temporarily in response to oxygen deficiency. Gibbs *et al*. (1998) argue that therefore a significant flow occurs through the protoplastic pathway, even under hydrostatic gradients. This means, the measured L_{Pr} is an integrated value of all pathways of water flow. Within the protoplastic pathway, at the level of the membranes, the activity of water channels (aquaporins) is likely to change L_{Pr} (Zhang and Tyerman 1999).

Laboratory measurements, such as the above, allow maximum control. However, the question as to what happens in the field comes to mind. Sap flow technology, adapted for use in banana by Lu *et al*. (2002), could evaluate the hydraulic conductivity of the whole root system in the field. Miniature sap flow sensors used on fine roots of trees in field studies (Coners and Leuschner 2002) may be suited to roots of bananas and plantains.

Root signals

Banana plants have a reputation for being very sensitive to soil water deficit and there are numerous field experiments, summarized by Robinson (1996), that support this view. Banana leaves remain highly hydrated, even under drought (Shmueli 1953, Turner and Thomas 1998) and so the closure of stomata caused by soil water deficits is likely to be linked to a signal from the roots rather than water deficits in leaves. Thomas (1995), in a split root experiment, observed that drying part of the root system had no effect on leaf water status but closed stomata. Severing the roots on the dry side caused the stomata to re-open. These observations support the view that the roots produce a signal that is transported to the leaves. This mechanism conserves the plant's water, but reduces carbon assimilation and productivity. It explains why the banana is very sensitive to soil water deficit and responsive to irrigation. A challenge will be to modify the root system so that it is less sensitive to drying soil. This would allow the plant to draw more water from the soil before growth is restricted and would increase the efficiency of water use.

Studies in root**:**shoot signals in bananas need to consider mycorrhizae, that can improve water uptake, and allow more water to be extracted before the root generates the signal indicating that the soil is drying. In addition, when soils dry, soil strength increases. The increased mechanical impedance may influence root signals (Masle 2002). In bananas, as soil bulk density increases, across soil types, from 0.6 to 1.2 g/cm^3 root density decreases exponentially (Delvaux and Guyot 1989). Thus mechanical impedance will be an issue in studies of root signals.

Embolisms, or cavitation of xylem vessels, cause malfunction of the conducting tissues reducing the supply of water to the shoot. Embolisms occur in the roots (Shane pers. comm.) where up to 70% of the conducting vessels may be affected, even in mild climatic conditions. Stopping transpiration prevents embolisms occurring and allows those present to be refilled, presumably by root pressure, which is known to be high in bananas (Davis 1961). Modelling studies of water flow in plants and soils, reviewed

by Sperry *et al.* (2002), show that the amount of soil water used by a plant, especially in loamy soils, can be increased if the resistance to cavitation is increased. Studies on the sensitivity to cavitation in bananas across genotypes would establish whether this approach is likely to lead to gains in water use efficiency.

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Ion absorption and proton extrusion by banana roots

Bruno Delvaux, Gervais Rufuikiri and Joesph Dufey[1]

Abstract

For growth and fruit production, bananas require large amounts of nutrients, which are only partly covered by soil supply. Research on the mineral nutrition has a long history. It was first devoted to the description of symptoms of plant deficiency and the determination of fertilizer rates in a range of soils (1920s-1970s). In a second stage (1960s-2000), it focused on both the role played by nutrients in banana growth and development, and the fate of some major nutrients in soil, particularly N and K. The very high nutrient demand of bananas is expected to strongly affect soil properties in its rhizosphere wherein crucial processes occur. Surprisingly, direct interactions between banana roots and the surrounding rhizosphere have been investigated only recently. At that scale, a first step in the study of soil-plant feedback concerns ion absorption by banana roots from the liquid phase.

Calcium uptake is governed by simple convection (mass flow). Magnesium uptake seems to be only convective at low water uptake rate. Potassium, NO_3^-, NH_4^+, P and Mn uptake rates clearly depend on active mechanisms. For most microelements (Fe, Mo, B), exclusion mechanisms can take place in roots when supply is greater than demand.

The net proton excretion by banana roots is quantitatively related with excess uptake of cations over anions. So, the large uptake of K^+ and NH_4^+ ions induces strong release of acidity by banana roots.. Excretion of protons by plant roots promotes the dissolution of aluminosilicate minerals present in the surrounding rhizosphere. This dissolution liberates bio-available nutrients (Ca, Mg, Fe) as well as silicon and toxic elements such as Al. Aluminium uptake by banana roots significantly decreases plant transpiration rate, hence decreases the uptake rate of Ca and particularly Mg. This means that banana roots are able to extract a toxic element from soil minerals and take it up. The total concentration of Al is well correlated with the cation exchange capacity of banana roots. The fixation of Al on root exchange sites did not occur to the detriment of Ca but to that of Mg. The Al/Mg ratio on roots is thus a better indicator of Al-toxicity than the Al/Ca ratio. The former is significantly larger in banana roots collected in acid soils than in the ones sampled in non-acid soils.

These recent findings illustrate interactions between the soil solid phase, soil solution and banana roots. They may open a large field of research aimed at understanding the relationship between banana roots and their rhizosphere environment.

Resumen - Absorpción de iones y extrusión de protones por las raíces del banano

La planta de banano requiere de grandes cantidades de nutrientes para su crecimiento y producción de frutos, los cuales son parcialmente suministrados por el suelo. La investigación sobre nutrición mineral tiene una larga historia. En sus inicios, ésta se dedicó a la descripción de síntomas de deficiencias y a la determinación de cantidades de fertilizantes para un rango de suelos (1920-1970). En una segunda fase (1960-2000) se investigó el rol de los nutrientes en el crecimiento y desarrollo del banano y el destino de algunos macronutrientes en el suelo, particularmente N y K. Se espera que la alta demanda de nutrientes del banano afecte grandemente las propiedades del suelo y de su rizosfera y micorrizosfera, donde ocurren procesos cruciales. Es de notar, que las investigaciones sobre las interacciones directas entre las raíces del banano y el suelo de la rizosfera que las rodean

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son muy recientes. A esa escala, un primer paso de interés en el estudio de las respuestas suelo-planta sería la absorción de iones por las raíces del banano en la fase líquida.

La absorción de calcio es controlada por simple convección (flujo de masas). La absorción de magnesio parece ser únicamente convectiva a una baja rata de absorción de agua. La absorción del Potasio, NO_3^-, NH_4^-, P y Mn depende claramente de mecanismos activos. Para la mayoría de microelementos (Fe, Mo, B), los mecanismos de exclusión pueden ocurrir en las raíces cuando hay mayor oferta que demanda.

La excreción neta de protones de las raíces de banano está cuantitativamente relacionada con un exceso de absorción de cationes sobre los aniones. De esta forma, la alta absorción de iones K^+ y NH_4^+, induce una fuerte descarga de acidez por las raíces de banano. La excreción de protones por las raíces de la planta promueve la disolución de minerales aluminosilicados presentes en la rizosfera vecina o adyacente. Esta disolución libera nutrientes biodisponibles (Ca, Mg, Fe) así como silicón y elementos tóxicos como el Al. La absorción de aluminio por las raíces del banano disminuye significativamente el ritmo de transpiración de la planta decreciendo así el ritmo de absorción de Ca y particularmente de Mg. Esto implica que las raíces de banano son capaces de extraer un elemento tóxico de los minerales del suelos y absorberlo. La concentración total de Al está bien correlacionada con la capacidad de intercambio de cationes de las raíces de banano. La fijación de Al en los sitios de intercambio en la raíz no sucedió en detrimento del Ca sino del Mg. De esta manera, la relación Al/Mg en las raíces es un mejor indicador de la toxicidad por Al que la relación Al/Ca. Lo anterior es significativamente mayor en raíces de banano recolectadas en suelos ácidos que en las muestreadas en suelos no ácidos.

Estos últimos descubrimientos ilustran las interacciones entre la fase sólida del suelo, la solución del suelo y las raíces del banano y pueden abrir un amplio campo de investigación para comprender la relación entre las raíces del banano y el ambiente de su rizosfera.

Introduction

Research on the mineral nutrition of bananas first involved the description of symptoms of plant deficiency and the determination of fertilizer rates in a range of soils (1920s-1970s) (Lahav 1995). In the second stage (1960s-1990), it focused on the role played by nutrients in banana growth and development (Lahav 1995), on soil-plant relationships with respect to cationic balance (Montagut *et al.* 1965, Martin-Prével and Montagut 1966), and on the fate of potassium and inorganic nitrogen in soil (Godefroy and Lossois 1966, Godefroy and Dormoy 1983, Fontaine *et al.* 1989).

The very high nutrient demand of bananas is expected to strongly affect the soil rhizosphere wherein crucial processes occur, for example, water and nutrient uptake, root exudation of acidity and organic substances, invasion of roots by soil borne pathogens, establishment of mycorrhizal symbiosis (Hinsinger 1998). In particular, nutrient uptake may rapidly induce the weathering of minerals close to plant roots (Hinsinger *et al.* 1992). Despite of this, direct interactions between banana roots and their surrounding environment have been investigated only recently.

The aim of this paper is two-fold. First, we will report on recent studies involving interactions between banana roots, the surrounding solution and clay minerals. Second, we will point to the need for further studies on the banana rhizosphere to better understand soil – banana plant interactions.

Material and methods

The first steps in the understanding of soil-banana interactions at the rhizosphere scale concern basic knowledge on root-liquid and root-liquid-solid interactions.

Young banana plantlets from tissue culture are convenient for such studies carried out in controlled conditions. We used five varieties (AAA 'Grande naine', ABB 'Kayinja', AAB 'Agbagba', AAB 'Obino l'ewaï' and AAA 'Igitsiri'). The plantlets were supplied by Vitropic or produced by us in the INIBAP *Musa* Germplasm Transit Centre located at KULeuven. Experimental procedures have been described in previous papers. Briefly, as illustrated in Figure1, plantlets (6 repetitions) were each grown during 45 days in a 2.5 L-vessel receiving a complete nutrient flow of low ionic concentration and known composition at a continuous rate of supply (104 ml hr^{-1} $vessel^{-1}$) (Rufyikiri *et al.* 2000a). Water and nutrient uptake were measured twice a week over 24h, by weighing inlet/outlet solutions and assessing their mineral concentrations, respectively. After pH measurement, the outlet solutions were filtered at 0.45 µm. The concentrations of Ca, Mg, Fe, Mn, Cu, Mo, B and Al were determined by direct current plasma (DCP) spectrometry. Potassium concentration was measured by atomic absorption spectrophotometry (AAS). NO_3^--N and NH_4^+-N were measured by Kjeldahl distillation. The net release of H^+/OH^- ions by roots was assessed from pH values on the basis of pH buffering curves established for inlet solutions. Plant height and leaf area were measured weekly. Dry matter was assessed after drying plant material at 60°C for 1 week. The material was ashed at 450°C for 1 day, followed by dissolution in concentrated HNO_3. Elemental contents were measured as above (DCP, AAS, Kjeldahl). The cationic composition of root exchange sites was assessed (Rufyikiri *et al.* 2002) by extracting cations with $CuSO_4$ (Dufey and Braun, 1986) and measuring them as above (DCP, AAS). Data obtained in hydroponics were compared with field data from bananas grown in a nutrient depleted Acrisol (pH_{water} = 4.2) and in a base-saturated Andosol (pH_{water} = 6.0). The cation exchange capacity of banana roots was measured on root axis tips and thus involved young root tissues (Dufey and Braun 1986).

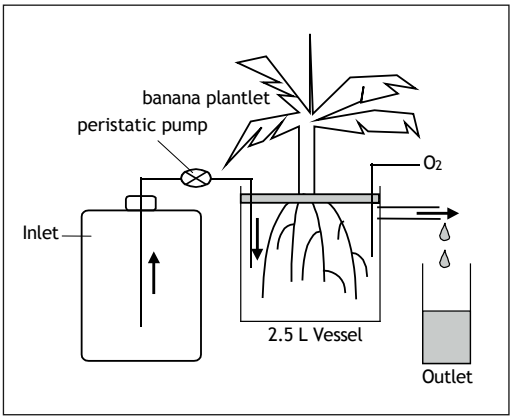


Figure 1. Sketch out of the experimental design involving the continuous nutrient supply (adapted from Rufyikiri *et al*. 2000a).

Finally, root-liquid-solid interactions were studied in an experimental rhizosphere (Hinsinger *et al.* 1992) involving an intimate contact between roots of 'Grande naine' plantlets and clay minerals incorporated in agarose gel, namely Georgia kaolinite and Wyoming smectite (Rufyikiri *et al.* 2004). The crystal formulae of these clay minerals (previously saturated by Sr^{2+} cations) were:

$$\text{kaolinite: } \{Si_2Al_2O_5(OH)_4\}Sr_{0.001}$$

$$\text{smectite: } \{[Si_{3.96}Al_{0.04}]\ [Al_{1.52}Fe_{0.19}{}^{III}Mg_{0.27}]\ O_{10}(OH)_2\}\ Ca_{0.01}K_{0.01}Sr_{0.14}.$$

Results and discussion

The results presented here are compiled from previous studies carried out by our group (Rufyikiri *et al*. 2000a, b, 2001, 2002, 2004).

Nutrient uptake

Calcium uptake by banana plantlets was governed by simple convection (mass flow) (Figure 2). Magnesium uptake seemed to be only convective at low water uptake rate, whereas active transport processes took place at high water uptake (not illustrated). Potassium, NO_3^-, NH_4^+, P and Mn uptake rates clearly depended on active mechanisms (illustrated for K, Figure 3). For most microelements (Fe, Mo, B), exclusion mechanisms could have taken place in roots when supply was greater than demand (not illustrated). The increase of ammonium uptake by banana roots resulted in a significant decrease of magnesium and the development of Mg deficiency symptoms (Rufyikiri *et al*. 2000a). Ammonium was selectively absorbed against nitrate, as NO_3^- was weakly taken up in the presence of NH_4^+ ions. Yet, upon NH_4^+-depletion in the nutrient solution, NO_3^- uptake by banana roots significantly increased (not illustrated).

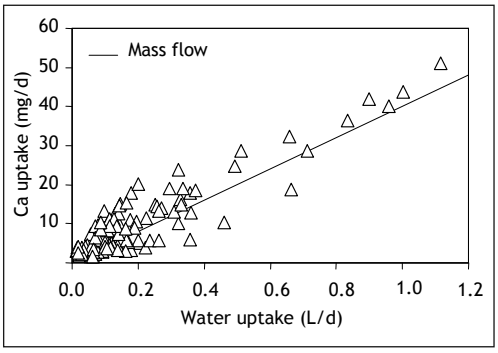


Figure 2. Calcium uptake as plotted against water uptake (convective Ca uptake as predicted from water uptake and Ca concentration in the inlet solution) (adapted from Rufyikiri *et al*. 2001).

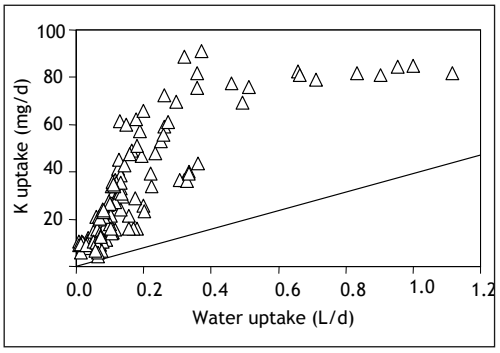


Figure 3. Potassium uptake as plotted against water uptake (convective K uptake as predicted from water uptake and K concentration in the inlet solution) (adapted from Rufyikiri *et al*. 2001).

Proton excretion

The net proton excretion by banana roots was quantitatively related to excess uptake of cations over anions (Figure 4). So, the large uptake of K^+ and NH_4^+ ions induced a strong release of acidity by banana roots. In particular, the increase of the fraction $[NH_4^+/(NH_4^+ + NO_3^-)]$ from 0 to 0.30 in the inlet solution at constant N supply decreased pH of from 6.5 to 3.8 in the outlet solution (not illustrated). The NH_4^+/NO_3^- balance thus directly influenced charge balance and proton excretion by banana roots, as it is well known for other plant species (Marschner 1995). However, banana plantlets were remarkable in the amplitude of H^+-excretion as assessed by pH measurement in the outlet solution, since the above-mentioned increase of NH_4^+/NO_3^- involved an increase of proton activity of three orders of magnitude (pH 6.5-3.8) in the outlet solution. This was likely due to both the large uptake of cations (K^+, NH_4^+) and the rapid growth of banana plantlets in controlled conditions (Rufyikiri *et al*. 2001).

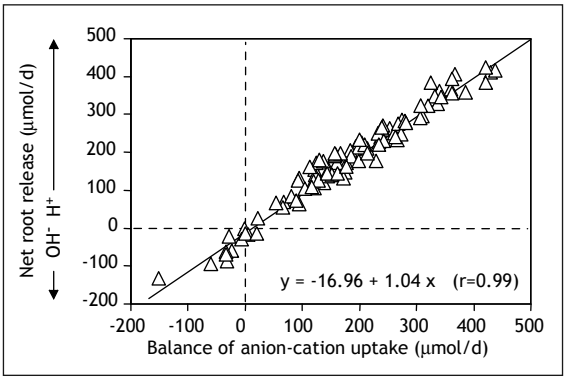


Figure 4. Relationship between net H+/OH- release by banana roots and cation-anion balance of uptake (adapted from Rufyikiri *et al*. 2001).

Mineral dissolution around roots

Excretion of protons by plant roots promotes the dissolution of aluminosilicate minerals present in the surrounding rhizosphere (Hinsinger 1998). This dissolution liberates bio-available nutrients (Ca, Mg, Fe) as well as silicon (Hinsinger *et al*. 2001).

As reported by Rufyikiri *et al.* (2004), protons excreted by banana roots were neutralised by the dissolution of clay minerals such as kaolinite and smectite. However, H^+ neutralization was much more effective through smectite dissolution because this mineral was less stable than kaolinite in the experimental conditions that prevailed. The root induced dissolution of clays released Al from kaolinite and smectite, but also released Mg from smectite. These elements were readily taken up by banana roots over time (Figure 5). This means that banana roots were able to extract toxic Al from clays and absorb it.

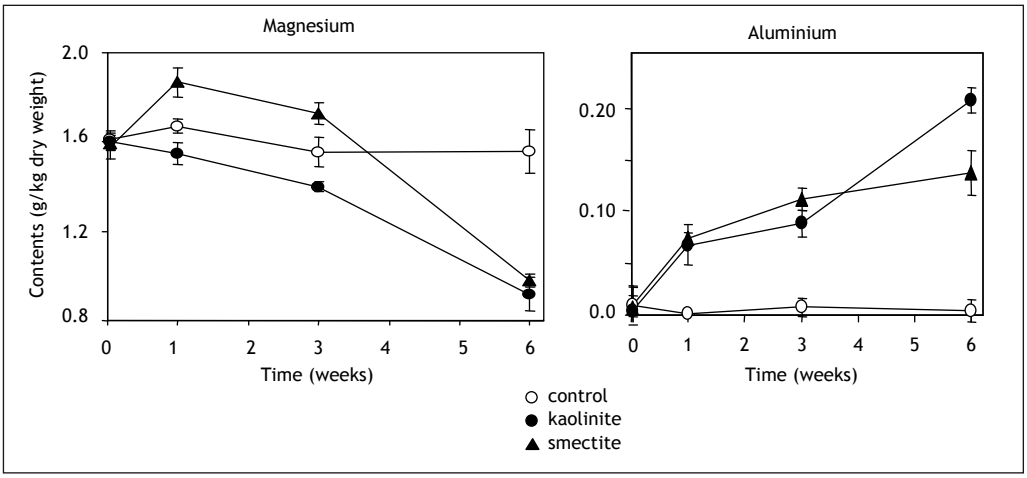


Figure 5. Week variation of the Mg and Al contents of banana roots growing in the close vicinity of smectite and kaolinite clay minerals (adapted from Rufyikiri *et al*. 2004).

Ion adsorption on root exchange sites

For the five banana varieties investigated, the cation exchange capacity of roots (CECR) differed between root axes (23 ± 4 cmol/kg root) and lateral roots (34 ± 3 cmol/kg root) (Rufyikiri *et al.* 2002). This was likely to be related to the lower contribution of secondary walls to dry matter in small lateral roots.

Aluminium was selectively adsorbed on banana root exchange sites against divalent cations. However, Al fixation on root exchange sites did not occur to the detriment of Ca, but to the detriment of Mg (Rufyikiri *et al*. 2002, Rufyikiri *et al*. 2003). The Mg proportion dropped from 40% to 5% when Al was competing for ion exchange on root sorbing sites, whereas the Ca proportion remained at about 60% (Figure 6). Similarly, the proportion of Al on root exchange sites was larger for banana roots sampled in the nutrient-depleted Acrisol than in the base-saturated Andosol. These observations may explain why Mg-deficiency symptoms associated with the 'bleu magnésien' occur preferentially in acid soils (Montagut *et al.* 1965; Martin-Prével and Montagut 1966).

In the base-saturated Andosol, the sum of Cu-extractable cations (Al, Ca, Mg) amounted up to 32 $cmol_c$/kg root because of higher pH (6.0 against 4.2 in the Acrisol). Despite this pH value, Al was readily sorbed on exchange sites of roots (Figure 6), and thus likely mobilised from mineral dissolution in the vicinity of plant roots. Moreover, this also indicates that Al is very efficient in competing with other cations for root exchange sites despite the low Al concentrations usually found in soil solutions (Dufey *et al*. 2001).

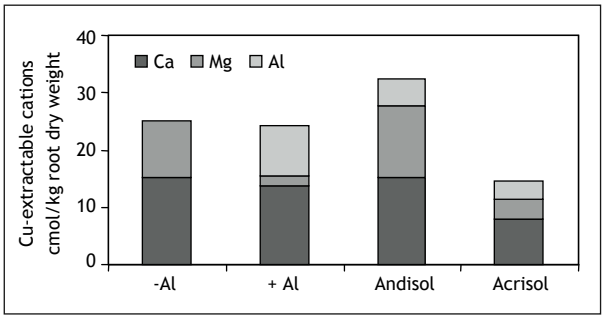


Figure 6. Cu-extractable contents of Al, Mg, Ca of banana root exchange sites from bananas cultivated in controlled conditions (continuous flow device: Figure 1) as well as in field conditions (Andosol, Acrisol) (adapted from Rufyikiri *et al*. 2002, 2003).

Al uptake and toxicity

Aluminium uptake by banana roots significantly decreased plant transpiration rate, hence decreased the uptake rate of Ca and particularly Mg, which are transferred to plants chiefly by mass flow. The toxicity of Al to bananas significantly reduced dry matter, stunted the roots and induced Mg deficiency (Rufyikiri *et al*. 2000a, Rufyikiri *et al*. 2001).

Arbuscular mycorrhizal fungi (AMF) might alleviate Al toxicity to bananas. The *in vitro* symbiotic association of AMF (*Glomus intraradices*) and micropropagated banana plants of 'Grande naine' indeed increased plant growth and dry matter, water and nutrient uptake, whereas it involved a decrease in Al concentration of plants as well as a delay in appearance of Al-induced leaf symptoms (Rufyikiri *et al*. 2001).

Conclusions

The large nutrient demand of banana represents a very strong potential for soil net acidification, which is directly governed by the balance of cation-anion uptake. In par-

ticular, the large uptake of potassium and the selective absorption of ammonium against nitrate play a major role in acid excretion by banana roots.

Protons excreted by banana roots dissolve secondary soil minerals that commonly occur in soils (kaolinite, smectite). Clay minerals as stable as kaolinite can be dissolved over short time periods (weeks). Proton excretion exceeds the acid neutralizing capacity of the clay minerals close to banana roots. Mineral dissolution liberates Al and Mg previously occluded in crystal structures. Aluminium uptake by banana roots reduces water uptake, nutrient uptake and particularly Mg uptake. Selective Al fixation on banana root exchange sites has a strong detrimental effect on Mg sorption, and hence uptake. Aluminium toxicity to bananas might be alleviated by symbioses involving arbuscular mycorrhizal fungi.

Perspectives

The recent findings presented in this paper illustrate a few of the interactions between soil solid phase, soil solution and banana roots. They may open a large field of research aimed at understanding the relationship between banana roots and their rhizosphere.

With respect to the scope of this symposium, this paper modestly contributes to the need for pursuing deeper investigations on the rhizosphere of banana plants. As shown above, banana roots may exert a strong influence on their surrounding environment. Intensive banana cropping systems, particularly in prolonged monocultures, may thus exhaust soils on a presently little-known scale.

The rhizosphere environment is very unique in terms of physicochemical properties and processes. Interactions between these properties/processes and biotic processes and constraints are poorly known in soils long influenced by intensive banana cropping. Unpublished data show that both the pathogenic nematode *Radopholus similis* and fungus *Cylindrocladium* spp. penetrate the root between the apex and the first lateral root as well as through the locations of extrusion of lateral roots. *R. similis* preferentially invade banana roots excreting alkalinity, i.e. taking up large amounts of NO_3^- over NH_4^+ (Declerck *et al*. 1998). *Cylindrocladium* spp. preferentially invade roots of Mn-deficient banana plants (unpublished data). In this respect, the continuous solution flow device allows us to study root-liquid-solid interactions in controlled conditions. This system is convenient for studying symbiotic interactions at the scale of the 'experimental rhizosphere' in controlled conditions of plant nutrition. It is also promising for the study of root-pathogen interactions in controlled conditions. Yet, *in vitro* studies are best coupled with field investigations. In this respect, we need a reproducible and standard procedure to accurately sample the banana rhizosphere

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4

Soils and root development

Suelo y desarrollo radical

Soil physical properties and banana root growth

Roque Vaquero M[1].

Abstract

The physical properties of the soil regulate the conditions in which banana roots grow; therefore, they should be among the criteria evaluated to determine the soil's potential for banana production. Under adequate nutritional conditions and with a good water supply (rain or irrigation), banana roots require aeration and low mechanical resistance for normal growth. Therefore, the physical characteristics that affect the water-air balance and soil consistence (the resistance of a soil to mechanical stress at various water contents), are manifested in the growth of the plant root system and consequently in crop productivity.

Resumen - Propiedades físicas del suelo y desarrollo del sistema radical

Las propiedades físicas del suelo regulan las condiciones del medio en que crecen las raíces del banano, por lo que se deben incluir dentro de los criterios para valorar el potencial del suelo para el cultivo. Bajo condiciones nutricionales adecuadas y con un suministro apropiado de agua (lluvia o riego), las raíces del banano necesitan aireación y baja resistencia mecánica, que les permitan un crecimiento normal. Por lo tanto, el efecto de las características físicas que afectan el balance agua-aire y la consistencia del suelo (la resistencia del suelo al stress mecánico en varias condiciones de humedad), se refleja en el crecimiento del sistema de raíces de la planta y por consiguiente en la productividad del cultivo.

Introduction

Texture, compaction and drainage are the main physical soil characteristics that influence banana growth and development; they can limit effective soil depth or the conditions of water supply and aeration in the rhizosphere. According to Stover and Simmonds (1987), studies carried out in bananas indicate that root distribution, in relation to soil depth, is determined by soil type and drainage conditions and that root growth is stopped or reduced by hardpans, impermeable layers, high clay content or waterlogged areas.

Layers or horizons within the coarse textural class (sandy soil) and the very fine (clayey, with more than 60% clay) hinder the development of the banana root system, due to their effect on water retention capacity, permeability and the water-air balance. The presence of coarse fragments (above 15% by volume) is also considered a limiting factor in banana root growth. Compact soil layers limit root growth and affect the properties related to water and air movement. Soil structure and consistence are related to compaction and an adequate field evaluation of them facilitates the diagnosis of the physical conditions of the root environment.

Horizons in the soil profile that indicate high water saturation, either permanent or temporary, are indicators of conditions that restrict root growth and can cause necrosis and rotting during very wet spells (Lara 1970 cited by Soto 1990, Dorel 1993, Stover and Simmonds 1987).

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Soil texture and root growth

Commercial banana farms are located in humid climates with a relatively flat topography. The most extensive farms are on alluvial plains, with some exceptions in dry climates. The rest are located in small areas in soils of volcanic origin or of varied mineralogy, on irregular topography, others on peat over clay. In other areas bananas are planted on bench terraces with transported soil (Stover and Simmonds 1987).

In the American tropics, in alluvial areas, soil texture has been one of the principal factors used to select the soil for the crop (Stover and Simmonds 1987). The spatial variability of soil texture in alluvial lands is determined by the gradient in particle size that varies transversally and longitudinally according to the location of the stream flow where it originated. Close to the stream and on higher grounds, the soil is of coarse texture or with higher sand content and lower clay content than those that are found downstream or further from the riverbank. Therefore, the best areas for the crop on alluvial plains are in medium-textured soils near streambeds. Soils with high sand or clay contents have low potential or are inadequate for bananas. The former due to their low water retention capacity and natural fertility and the latter due to their low permeability and because they are generally found in low areas, that consequently, present drainage problems.

However, there are banana plantations in clayey soils and low-lying areas that have excellent growth and reach high production. It is evident that the dominating effects of clay-sized particles, the fine fraction, can be outweighed by a moderate to strong structure and a high potential fertility due to their material of origin deposited on some river floodplains (as observed in Costa Rica, Panama, and in some areas of Guatemala). According to Soto (1990), the best soil textures for obtaining high banana production go from very fine and fine sandy loam to clay loam, meanwhile finer or coarser textures lead to management problems. Soto also points out that light textures are favourable in the subsoil to assist with drainage, and that plants in medium to finer textured soils with good structure and porosity, develop a more extensive and deeper root system.

At the commercial banana plantation at EARTH University, in the Atlantic region of Costa Rica, the author made soil descriptions and root mapping, in profiles 1.5 m wide and 1.0 m deep, in semicircles 50 cm from the base of the banana plant, in front of the sucker and at the time of shooting, selecting the sites based on the soil classification made by Sanchez (1994). One of these tests was on a class IV soil with 17% of the roots located below 50 cm, while better root distribution was noticed in a plant from the same clone planted on a class II soil, with more than 30% of the roots below 50 cm. The plant surpassed, by more than 15%, the plant in class IV soil, in height and circumference of the pseudostem at shooting (Table 1).

There was a higher root density in loam to silty loam soils, decreasing as the sand content increased to textures like sandy loam (Figure 1). Lower root densities were observed in soils with higher clay content (clay loam) and a finer texture (silty clay).

Table 1. Vertical root distribution, in front of banana plants of the 'Williams' clone, at flowering, in two soils with different banana production potential. EARTH commercial Farm, September 2003.

Depth (cm)	Soil Class II			Soil Class IV		
	Roots		Texture*	Roots		Texture*
	Quantity	%		Quantity	%	
0-25	173	42	L	148	45	CL
25-50	114	28	L	124	38	C
50-75	72	17	SL	31	9	C
75-100	55	13	LS	25	8	C
Plant height (cm)	345	299				
Pseudostem circumference (cm)	74	65				

* L = loam; SL = fine sandy loam; LS = fine loamy sand; CL = clay loam; C = clay.

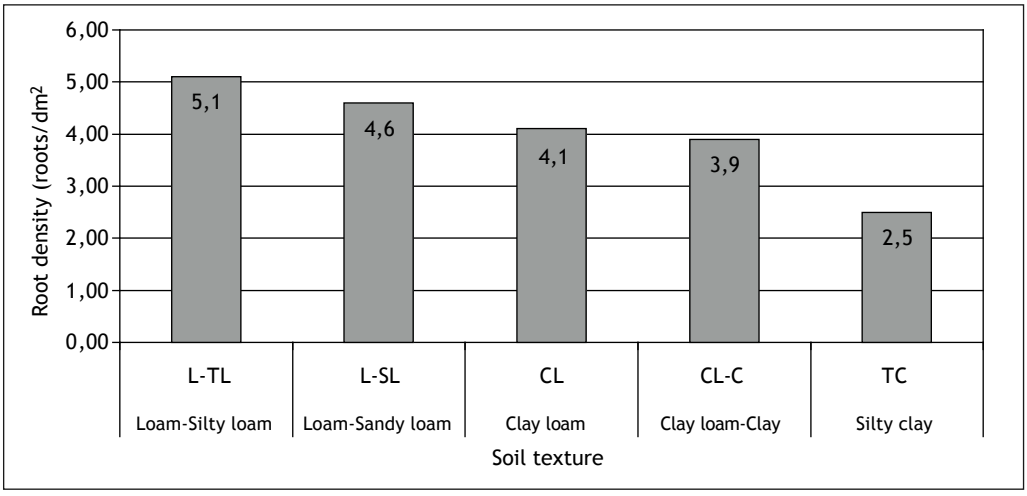


Figure 1. Average root density on vertical cut of the first 25 cm of soil depth, with different textures, sampled in front of a sucker of a flowering banana plant. EARTH commercial farm, 2003.

Soil compaction and root growth limitations

Soil compaction results when the mass, upon compression, occupies part of the volume of the air spaces. Thus, one of the major effects of compaction is manifested in decreased soil permeability and increased physical resistance.

Most of the research work that relates soil physical properties to banana root growth has been done in Guadeloupe and Martinique. The studies carried out by Gousseland (1983) established the relation between bulk density and root growth under controlled conditions, finding a direct relationship between them. Work done by Delvaux and Guyot (1989), in different soil types with bulk density between 0.7 and 1.1 g/cm^3 indicates that when the bulk density of a soil is above 0.95 g/cm^3, root density is significantly reduced. The author has obtained data on bulk densities above 1.15 g/cm^3,in fine texture soils, and 1.35 g/cm^3 or more in medium to medium-coarse textured alluvial soils in the Sula Valley, Honduras, derived from sediments of varied mineralogy. And there, banana plantations do not show the effects of soil compaction problems.

Dorel (1993) argues that although it is difficult to evaluate the effect of soil compaction on banana production, soil compaction reduces plant and bunch size, delays flowering and reduces sucker emergence. Experiments carried out in andosols in Martinique demonstrate that compaction reduces aeration and leads to root death due to lack of oxygen and its immediate effect is reflected in the decline in the number of roots and, consequently, nutritional imbalances in the plant, because of a reduced capacity of the root system to absorb nutrients.

Mechanical penetration resistance of the soil is a result of the consistence and compaction of the soil horizons. Some empirical values have been established for samples taken with a pocket penetrometer, Soiltest CL-700A. When the soil is at field capacity, penetration resistance values of 2.0 kg/cm^2 or lower, are associated with a friable to very friable soil consistence, which is adequate for banana root growth. Values higher than 2.0 kg/cm^2 and close to 3.0 kg/cm^2 are associated with a firm soil consistence and indicate a higher soil compaction and a certain degree of root growth limitation. Meanwhile, values close to, or higher than 3.5 kg/cm^2 have been obtained for firm to very firm soil consistence that severely limits banana root growth.

The author's experience in different soil types in Honduras and Belize has shown that penetration resistance can be utilized as a parameter to evaluate soil compaction, taking into consideration that the degree of compaction is affected by other variables, like soil texture, structure and water content. The conversion of the penetrometer reading to relative values is also adequate to explain the difference in banana root growth in different sites and soil profiles. There is a relationship between soil consistence and the penetration resistance values measured with a penetrometer (Soiltest CL-700A) (Table 2). A range of soil consistence and a range of soil penetration resistance and bulk density at each depth in the soil profile can identify the principal cause of the lower values of root density (Table 3). Root density of banana plants is higher in friable to very friable soils with low bulk density and penetration resistance values (<2.5 kg/cm^2) (Table 3). But, root density is drastically reduced in areas with high penetration resistance values (>2.5 kg/cm^2) associated with a firm or very firm soil consistence and bulk density above 1.2 g/cm^3. In alluvial soils the author has used a different approach to evaluate the problem of compaction by considering the relation between structure development and soil consistence (Table 4).

Table 2. Penetration resistance (kg/cm^2)* for different soil texture and consistence conditions in vertical profiles utilized for root description. EARTH commercial farm, 2003.

Soil texture	Soil consistence			
	Very friable	Friable	Firm	Very firm
Coarse	0.9 – 1.5	**	4.3 - > 4.5	**
Medium coarse	1.8 – 1.3	**	2.8 – 3.5	> 4.5
Medium	0.3 – 1.3	0.5 – 1.5	**	**
Medium fine	0.8 – 1.5	0.6 – 2.5	**	**
Fine	**	0.8 – 2.5	2.3 – 3.5	**

* Reading ranges from a pocket penetrometer (Soiltest CL-700A) down to 25 cm depth, with readings at intervals of 5 cm. ** These conditions were not present.

Table 3. Root density (R_d roots/dm^2), soil consistence C, penetration resistance (R_p kg/cm^2) and soil bulk density (D_b g/cm^3) in soil layers, each with a 25 cm depth, for EARTH commercial farm, 2003.

Depth (cm)	R_d	C*	R_p **	D_b***	Minimum value of root density related to:
0-25	2.5 - 5.1	vFr - Fr	0.4 – 2.5	0.72 – 1.17	Fine texture
25-50	0.9 – 3.3	vFr - Fr	0.4 – 1.8	0.62 – 1.12	Indicates poor drainage
50-75	0.5 - 2.5	vFr - vFir	0.25 - >4.5	0.93 – 1.11	Compaction and poor drainage in medium texture; fine texture
75-100	0 - 1.7	vFr - Fir	0.91 - >4.5	0.91 – 1.24	Poor drainage, consistency and compaction

* vFr = very friable; Fr = friable; Fir = firm; vFir = very firm. ** Penetration resistance; reading range with a pocket penetrometer (Soiltest CL-700 A). *** Bulk density of the soil.

Table 4. Scores for interpreting the interaction between soil consistence and structure. d.a. = does not apply

Soil consistence	Structure development grade			
	Strong	Moderate	Weak	Massive
Loose	d.a.	d.a.	d.a.	d.a.
Very friable	1	1	1	2
Friable	1	1	1	2
Firm	2	2	3	4
Very firm	3	3	4	4
Extremely firm	3	3	4	4

Interpretation of the soil consistence x structure scores

Score	Interpretation	General actions
1	Low or unnoticed	No corrective measures are expected, but measures should be undertaken to maintain these conditions
2	Moderate	Requires some soil/water management practices (mechanized preparation, organic matter incorporation, drainage, use of cover crops and green manure, amongst others)
3	Severe	Requires specific soil/water management practices (plowing and sub soiling, incorporating high amounts of organic matter, alternate crop cycle with fallow and cover crops to break compact layers, incorporate green manure, intensive drainage practices, special irrigation control, and others)
4	Very severe	Even if intensive management practices are put in place, conditions might not improve, therefore species, cultivation system, physical inputs and agricultural techniques must be precisely selected

Soil drainage and root growth

Saturated soil and shallow water tables reduce the number of roots, root system growth and banana plant productivity (Ghavami 1976, Holder and Gumbs 1983, cited by Stover and Simmonds 1987). In the American tropics, bananas are grown in regions with medium to high precipitation leading to temporary or permanent problems of

waterlogging in the soil profile. In these areas, excessive runoff is produced and the water table rises to a depth that directly affects plant root depth and density.

Some research indicates that water tables in banana farms should not be shallower than 120 cm. They also show that deeper water tables are associated with a better performance of production variables (Ghavami 1976, Sancho 1991), because the air-water balance is improved, which facilitates root growth. Stover and Simmonds (1987) argue that banana crops require good surface and internal drainage and that the watertable should preferably be below 1.2 m deep. They also report that watertable fluctuations cause damage when the water rises to the dense rhizosphere and remains there for more than 24 hours. According to Stover and Simmonds (1987) root horizon profiles are good indicators of poor drainage or compact subsoil, and low permeability and that, in Central America, it is clear that there are factors that limit root growth (mainly drainage) when the percentage of roots below 60 cm is less than 25% of the plant root system.

In recent root readings done by the author and mentioned before, a lower density was found in soils with drainage problems and in horizons with evidence of temporary water saturation, due to low permeability caused by compaction (Table 5). Water saturation on a permanent (hydromorphic horizons) or variable (mottled horizons of low permeability) basis represent a huge limitation for root growth (Table 5). Soil profiles that do not reveal signs of poor drainage in the first meter of depth have a better root distribution with depth. Additionally, because the majority of the banana root system is located in the first 30 - 50 cm and, due to its high susceptibility to water excess or deficit, it is important to avoid ponding and waterlogging that can lead to root necrosis by lack of oxygen or toxicity by some chemical compounds that are more soluble under these conditions.

Table 5. Root density in soil profiles with different drainage conditions. EARTH commercial farm, 2003.

	Soil profile number and drainage			
Depth (cm)	**2, poor**	**5, good**	**3, good**	**4, moderate**
	Root density, root/dm^2			
0-25	2.5	4.1	4.6	5.1
25-50	0.9	2.8	3.0	2.6
50-75	0.5	2.5	1.9	1.7
75-100	0.0	1.7	1.5	0.0

Profile 2: class III, poor drainage, water table at 1.10 m, hydromorphic horizons below 75 cm; clayey on the surface and clay loam in the subsoil; grey and red mottling along the profile; firm layer from 50 – 75 cm in depth.

Profile 3: Class II, well drained, deep; loam to fine sandy loam; friable to very friable; higher sand content below 50 cm.

Profile 4: Class III, moderate drainage with evidence of temporary water saturation below 50 cm and a firm layer with low permeability at a depth of 75 – 100 cm.

Profile 5: Class II, well drained up to 1.10 m, below hydromorphic layer; clay loam, friable to very friable, with a firm layer (5 cm thick) below 85 cm depth.

Final remarks

Soil texture, the degree of compaction and the drainage conditions affect banana root growth and density. The effects of these variables cannot be addressed on an individual basis because of the multiple interactions they have on the root stratum. The efforts that are undertaken to analyze the soil's physical characteristics in order to evaluate its potential for this crop, are intended to help locate areas that can guarantee high production with a reasonable investment, minimizing the risks of this activity. Research and the development of techniques to evaluate and solve soil compaction problems, improve structural conditions, soil stratum consistence and porosity that allow the plant root system to develop are ways to introduce improvements to increase productivity in cultivated areas.

Finally, the development of strategies and schemes to avoid surface ponding through soil conformation or surface drainage, and proper design of major drainage infrastructure to prevent watertables from rising to the root zone, can help guarantee a healthy and deeply-developed root system and, as a consequence, high production.

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Interrelations between the soil chemical properties and the banana plant root system

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Abstract

The relationship between the solid phases, organic and non-organic, liquid (soil solution) and the banana plant root system have been found to influence soil chemical conditions that determine commercial yields. The role that the minerals, found in clay soils that are planted with bananas in Latin America, have on the activity of the elements and substances in soil solution and their availability to the banana plant is examined. Some of the most important chemical properties are: the availability of phosphorus in the allophanic soils of the Pacific coast of Central America; saline, sodic and saline-sodic soil conditions of the Santa Marta, Colombia zone; and the highly available iron, manganese and exchangeable aluminum concentrations in the soils along the Atlantic coasts of Costa Rica and Urabá, Colombia. The importance of improving knowledge about the banana plant rhizosphere as a key factor to better root health management and improve yields is highlighted. Technologies such as mycorrhizae (VM) offer opportunities to substantially improve banana root systems in sub-optimal soil conditions.

Resumen - Interrelaciones entre las propiedades químicas del suelo y el sistema radical del banano

Las interrelaciones entre las fases sólida, orgánica e inorgánica coloidal, liquida (solución del suelo) y el sistema radical del banano son conocidas por inferir en las condiciones químicas del suelo que afectan el rendimiento comercial del cultivo. Se examina el papel que juega la mineralogía de suelos arcillosos sembrados con banano en América Latina en la actividad de elementos y sustancias de la solución del suelo y su disponibilidad a la planta del banano. Algunas de las propiedades químicas mas importantes son: la disponibilidad del fósforo en los suelos con contenidos altos de alófano en las costas del Pacifico Centroamericano; las condiciones que presentan los suelos sódicos, salinos y salino sódicos en la zona de Santa Marta, Colombia; y la alta disponibilidad del hierro, manganeso y el contenido de aluminio intercambiable en los suelos de la Costa Atlántica de Costa Rica y Urabá, Colombia. Se destaca la importancia de incrementar el conocimiento de los diferentes componentes de la rizosfera del banano como un factor para mejorar el manejo de la salud del sistema radical y la producción. Las tecnologías como el uso de las micorrizas (MVA) ofrecen oportunidades para mejorar sustancialmente el desempeño del sistema radical del banano en condiciones de suelos deficientes.

Introduction

The relationship between soil chemical properties and the banana root system has great practical importance. Unfortunately, this relationship has not been fully understood and its economic impact has not been accurately estimated due to the complexity of its multiple components. This lack of understanding brings negative economic consequences since accurate and effective soil management programs cannot be designed; thus limiting crop yields to different degrees, depending upon the severity of the limitation.

A fair level of understanding has been reached to predict the behavior of nitrogen, magnesium, copper, zinc, boron, sodium and soluble salts, given the relative simpli-

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city of their reactions in the soil system. However, the level of understanding of the relationship between soil reaction, exchangeable aluminum, iron, manganese, organic substances, potassium and phosphorus is more limited. Nevertheless, it is known that each of them has a high degree of complexity in the interaction between the soil (organic and inorganic colloids), liquid (soil solution) and the rhizosphere of the banana and plantain (Table 1).

It is clear that a thorough understanding of these interactions will lead to more accurate and effective programs that will substantially increase yields. Actually, due to the lack of specific studies in bananas and plantains, many predictions and recommendations are based on more general knowledge of soil-plant relationships.

Table 1. Level of understanding of the relationship between the chemical soil properties and the root system of the banana plant.

Satisfactory level of understanding	Partial level of knowledge	Complex factors necessary to understand the soil-root system relationship
Nitrogen	pH	Complexity of the causes of acidity or different sources of alkalinity
Magnesium Copper	Kinds and contents of organic matter	Lack of good and cheap methods to characterize organic compounds and their physic-chemical processes
Zinc	Potassium	Behavior and availability of potassium with different types of clay
Boron Sodium Soluble salts	Phosphorus	Complexity of phosphorus reactions with the different primary minerals of the soil, iron and magnesium oxides and hydroxides, changes in pH and clay contents.
	Aluminum	Susceptibility of the different banana varieties to the possible toxicity of aluminum and understanding of the processes at the cellular level in the banana plant
	Iron and Manganese	Oxidation states of iron and magnesium in the soil and the level of susceptibility of the different banana varieties
	Cation Exchange Capacity	pH dependent charges, different composition of the solid fraction of the soil phase (clay and organic matter)

Soil phases and the banana plant root system

The solid phase

The inorganic component: primary minerals

Soils devoted to banana production in Latin America (including Martinique and Guadeloupe) are composed of parent materials with diverse primary minerals. Those, such as the slightly weathered minerals from the active volcanic zones, metamorphic or sedimentary rocks rich in quartz, feldspar and mica weathered to various degrees, and calcium carbonate from areas rich in limestone, have the greater influence on the relationship between soil chemical properties and the banana plant rhizosphere (Table 2).

The release of sodium from albite (sodium feldspar) bears special importance in the soils of the banana zones of Santa Marta, Colombia, the alluvial soils of the Yaque del Norte River in the Dominican Republic and south of Maracaibo Lake in Venezuela. This causes high contents of exchangeable and soluble sodium in many soils that, in

Table 2. Predominant soil mineralogy of the main banana production zones of Latin America.

Geographic zone	Minerals of the coarse fraction of the soil	Secondary minerals
Alluvial valleys of Honduras	Quartz, feldspar and calcium carbonate	Smectite, vermiculite, kaolinite and illite
Atlantic coast of Colombia Santa Marta Urabá	Quartz, degraded muscovite and sodium feldspar (albite) Quartz	Illite, vermiculite, smectite and kaolinite Kaolinite, vermiculite, illite and smectite
Atlantic coast of Costa Rica	Quartz, volcanic amorphous materials and calcium carbonate	Allophane, imogolite, kaolinite, vermiculite and sesquioxides
Atlantic coast of Guatemala	Quartz, feldspar and degraded muscovite	Kaolinite, vermiculite and smectite
Atlantic coast of Panama	Quartz	Vermiculite, kaolinite, illite and allophane
Dominican Republic	Quartz, calcite and sodium feldspar (albite)	Vermiculite and smectite.
Pacific coast of Guatemala	Recent primary minerals	Allophane
Pacific coast of Nicaragua	Recent primary minerals	Allophane
Martinique and Guadeloupe	Recent primary minerals and calcium carbonate	Allophane and smectite
Venezuela, Golf of Maracaibo	Degraded muscovite, sodium quartz and sodium feldspar (albite)	Illite, vermiculite, smectite and kaolinite

turn, cause severe toxicity problems in bananas and plantain. Soils formed from volcanic sediments (Andisols) rich in allophane are notorious for fixing phosphorus. These soils are typical of the Pacific Coasts of Central America and large parts of Martinique and Guadeloupe. Limestone soils, rich in calcium carbonate, also fix considerable amounts of phosphorus and restrict the availability of micronutrients and result in magnesium and potassium imbalances. Large areas of such soils are common in the northwest alluvial valleys of Honduras, Belize, some areas of the Dominican Republic, Santa Marta in Colombia and Martinique.

In this way, primary minerals regulate the availability of phosphorus, magnesium, potassium and most micronutrients for plant uptake. These specific cases have not been widely studied in bananas and plantains; however, the crop response to the application of specific nutrients highlights the importance of the reactions indicated above in the geographic areas of interest.

The inorganic fraction: phyllosilicates

Together with humus, phyllosilicates (clay fraction of soils and sediments) determine the kind and quantity of elements entering the soil solution that eventually can be taken up by plants. High contents of smectite restrict the availability of phosphorus and potassium in the soils of the Sula Valley in Honduras (Table 3). In the case of phosphorus, this is aggravated by the relatively high calcium carbonate content of these soils. Besides, it also alters the (Ca+Mg)/K and Ca/Mg ratios and the availability of most

Table 3. Relevant relationships between the solid and liquid phase in the banana Zones in Latin America.

Geographic zone	Element or compound in the soil solution	Key environmental factors or components of the soil solid phase	Known effect on the root system of the banana plant
Alluvial soils of the northwest of Honduras	Restricted concentration of P, Mg and micronutrients	Relatively high calcium carbonate contents	None
Atlantic coast of Guatemala, Costa Rica and Urabá, Colombia	High concentrations of soluble Fe and Mn, exchangeable aluminum >30%	Temporary soil saturation, permanent watertables and strongly acid pH	Poor root development becoming short and thin
Pacific coast of Guatemala and Nicaragua	Low concentration of P	Allophane in the clay fraction of the soil	None
Santa Marta, Colombia	High soluble salt contents	Very limited rainfall, elevation above sea level, poor internal soil drainage, high watertable	Weak and injured roots
Lake of Maracaibo, Venezuela	High concentration of exchangeable sodium in soil solution	Minerals rich in sodium in the coarse soil fraction, elevation over sea level and climate	None
Machala, Ecuador	Very low concentration of K	Degraded micas and illite in the clay fraction	

micronutrients. The same condition is common in some areas of the Yaque del Norte River in the Dominican Republic and Trois-Ilets in Martinique, and to a lesser extent in the Machala and Los Rios provinces in Ecuador. The very low potassium concentration in the colluvial-alluvial soils of the Sierra Nevada in Santa Marta, south of Maracaibo Lake (Venezuela), and some soils of the Machala and Los Rios provinces of Ecuador is determined by high contents of illite in the soil clay fraction (Table 3). This condition is aggravated in soils with high clay content since the higher the clay content the higher their potassium fixing potential.

High contents of allophane occur in the soils of the Pacific coast of Central America. Besides fixing phosphorus, the cation exchange capacity is highly dependent on the pH of the soil solution. Thus, when fertilizers are applied and the pH of the soil solution changes, the cation exchange capacity of the soil is altered, resulting in changes in the nutrient availability for plants. A special case occurs in the extensive alluvial system of the banana zones of Ecuador where sediments originate from various sources. In this particular case, the allophane originating from the volcanic areas of the Andes Mountains is mixed with limestone or metamorphic rock sediments that contain different minerals. Thus the effect of allophane on nutrient availability in these soils is less important than in other geographic locations. The mineralogy of the clay fraction of the Atlantic coast of Costa Rica is variable. However, there are some areas of localized importance where allophane predominates in the clay fraction. This significantly affects the phosphorus concentration in the soil solution, and thus also affects its availability

for plant uptake. This condition is more common in the foothills of the central mountain range of the country.

The relatively high concentrations of iron and aluminum oxides and hydroxides in the soils formed in highly weathered sediments also restrict the phosphorus concentrations in the soil solution. This condition is common in the soils of the gently rolling hills of Pocosí and La Sierpe in Limon Province of Costa Rica. The cation exchange capacity/clay ratio of subsoil horizons suggests significant amounts of halloysite and possibly kaolinite; thus, given the rainfall regime of the area, nutrient leaching can be significant.

Aluminum, iron and manganese

Bananas can be grown in soils with a wide pH range, 5.5 to 7.7 (Stover and Simmonds 1987). Actually, this range is wider - reaching values slightly higher than 8 and lower than 4.7. This also implies a wide range of aluminum and manganese concentrations in the soil solution. The symptoms of iron and manganese toxicities in bananas have been described by Lopez *et al.* (2001), but they were not associated with a significant decrease in yield or plant development. Similar symptoms have been reported by Norman *et al.* (1995). Production experiences indicate that in soils with a pH range from strongly to extremely acid, exchangeable aluminum concentrations are greater than 30%, and together with high soil manganese concentrations, yields are reduced, usually to less than 2,000 boxes/ha/year. It has not been clearly established whether this is due to high soil Al, Mn and Fe concentrations or to low Ca, P, K, Mg, Zn and B concentrations, that are usually very low in soils with these characteristics. Short, thin, branched roots and shallow corms are found in soils with different physical characteristics but similar Al, Fe and Mn contents. Microscopic tissue studies related to this condition have not been reported. The response of bananas to liming has been inconsistent, probably due to inadequate rates (soil-incorporated or applied to the soil surface), soil water content and mesh size of the liming materials used. High lime and dolomite applications can alter the Ca/Mg, Mg/K ratios and decrease the availability of phosphorus and micronutrients. It has been suggested that bananas have a certain degree of tolerance to aluminum toxicity (Lahav and Turner 1992). Production experiences also suggest differences in tolerance among the commercial banana varieties currently used. Often, banana producers point out that the 'Valery' variety shows more resistance than 'Williams' and in turn this variety more than 'Grande naine' under the soil chemical conditions previously indicated. It is clear that this subject demands more research taking into consideration possible differences among the various banana varieties.

The organic fraction: humic acids

Climatic conditions and the different plant species that occupied a given area before cultivation of banana or plantain determine the kinds of organic acids found in the soil. Thus, a wide variety of organic acids can be expected in soils devoted to banana production. The physical and chemical characteristics of humic substances are quite different (Varani and Pinton 2001). The effect of humic substances on the interactions discussed in this work can range from weak to strong depending upon their concentration in the soil system, mainly concerning the exchange reactions between the solid and liquid soil phases. Production experiences indicate that plant responses are different in

soils that have similar morphological, physical and chemical characteristics, including organic matter contents, but that had different plant species before banana cultivation. This explains differences in response to the application of organic matter, humic substances, and crop residues after long fallow periods with different plant species. Organic matter composition also determines the population and kind of soil microorganisms in the rhizhosphere. This issue has been little studied in banana cultivation; however, it is of considerable importance and deserves much more investigation in the future. The chelating role of humic substances has also been widely recognized to offer significant opportunities for future research.

The liquid phase

The equilibrium between phases

Nutrient uptake by banana plants, as any other higher plant, depends on the concentration and activity of the ions in the soil solution. Thus, the equilibrium of the nutrients in the soil solution at the time of plant uptake determines the rate of their uptake (Barber 1995). This situation becomes very complex under field conditions since the soil is an open system subjected to changing imports and exports of matter and energy in the root zone. This prevents the establishment of a long-term equilibrium between the solid and the liquid phase; and, therefore alters the supply of nutrients to the rhizosphere of the banana plant.

The practical applications of this concept can be significant for banana production, considering the fact that the concentration of soluble salts in the soil solution is constantly altered by the addition of fertilizers like KCL, nitrates and sulfates. This effect is not the same throughout the year due to soil water conditions in the various banana zones of Latin America. It is obvious that salt concentration in the soil, due to the addition of fertilizers, is less important in rainy areas with uniform rain distribution than in dry zones. This implies that a key aspect of banana plant nutrition in rainy areas is to maintain an adequate nutrient concentration in the soil solution. This highlights the importance of frequent fertilizer applications in banana zones of high and uniform rainfall throughout the year such as the Atlantic coast of Costa Rica, Panama, and Urabá in Colombia.

The climatic factor

The effect of soluble salts generated by fertilizer applications is stronger in areas with well-defined dry and rainy seasons even though the areas may be irrigated. Irrigation systems are usually designed to prevent significant leaching. In these areas, the effect is relieved during the rainy season such as in the North coast of Honduras and the Pacific coast of Nicaragua due to natural leaching of the soil profile. However, in areas where evapotranspiration exceeds rainfall for long periods, the soluble salt concentration generated by fertilizers or weathered salt containing rocks can affect banana yields significantly over time.

Cations in the soil solution

As previously pointed out, potassium and to a lesser extent magnesium concentrations in the soil system depend to a large extent on the kinds and content of the clay minerals in the soil. The equilibrium reactions are altered by leaching, fertilizer applications, and the kinds and content of humic substances. On the other hand, the sodium ion con-

centration in the soil solution depends on the soil content of albite (sodium feldspars), the cation exchange capacity, rainfall and internal soil drainage. The effect of high sodium concentrations in the soil solution is better understood when it is expressed as the Sodium Absorption Ratio (SAR) and the Exchangeable Sodium Percentage (ESP). In banana production, values greater than 5 and 7%, respectively, limit yields and retard vegetative growth. Under field conditions, banana roots are short and thin and have black or dark brown epidermal lesions when soil sodium is at the concentrations indicated above.

Necrosis along the margin of the leaves and slow growth are better field diagnostic criteria than the symptoms shown by roots. Field observations indicate that the mechanisms by which sodium affects banana plants are similar to those found in other susceptible plant species as described by Maas and Nieman (1978) and Hale and Orcutt (1987). Typical cases of this situation occur in the banana zones of Santa Marta in Colombia, South of the Maracaibo Lake in Venezuela, and the Dominican Republic. High soil sodium concentration occurs in low-lying areas influenced by high tides such as on the Pacific Coasts of Mexico, Guatemala, and Machala (Ecuador), where the watertables are high and leaching rates are low. Given how difficult it is to drain the soil effectively and wash sodium out of the root zone in these areas, compounds that may increase the cation exchange capacity of the soil can lower the sodium ion activity in the soil solution substantially. Among these substances are humic acids, highly decomposed compost and synthetic polymers with high negative charge.

Soluble salts

Soils devoted to banana production with relatively high soluble salt concentrations with or without high sodium contents, occur in areas where evapotranspiration greatly exceeds precipitation most of the year (Santa Marta in Colombia, northern Dominican Republic and the southern Maracaibo Lake area in Venezuela), and soil leaching is limited or where elevation is not high enough above sea level to allow effective soil drainage (several areas on the Pacific coasts of Guatemala, El Salvador and Ecuador). Electrical conductivities above 5 dS/m affect banana production; however, the kind of soluble salt is more important to banana plant yields than the concentration itself. Sodium chloride strongly affects crop production due to the toxic action of both ions. Sodium is especially damaging compared with calcium sulfate, calcium carbonate or magnesium sulfate. The effect caused by calcium carbonate in banana production is more indirect; high soil solution pH strongly affects the availability of phosphorus and most micronutrients and alters the balance among calcium, magnesium and potassium. On the other hand, very high magnesium and sulfate concentrations could potentially cause severe damage to the crop as has been found in other higher plants (Fitter and Hay 1987). However, this condition has not been reported in bananas specifically.

As previously indicated, temporary high soluble salt contents in the rhizosphere can occur as a result of using large amounts of high salinity index fertilizers. Symptoms observed in the field indicate that the effects of soluble salts in banana plants, and the root system in particular, are generally the same as those described by Marschner (1995) for susceptible higher plants. In practice, the improvement of the rhizosphere affected by high soluble salt concentrations depends on the availability of enough good

quality water to wash the soluble salts out of the soil root zone and of a drainage system that will allow leaching to take place.

Soil solution reaction

The bioavailability of most nutrients is strongly influenced by the pH of the soil solution and the changes that it undergoes with the application of fertilizers and other compounds. The solubility of the various compounds used greatly affects the magnitude of changes in the soil solution pH. Fertilizers that are applied through the irrigation system are more advantageous in lowering the soluble salt concentration than hand-applied fertilizers since the rate of fertilizers applied by hand are usually higher due to the lower application frequency.

Without doubt, the application of fertilizers via the irrigation system improves plant nutrient uptake. It is almost impossible to attain the relative stability of the soil solution when the cation exchange capacity of the soil is strongly pH dependent as is typical of the Andosols of the Pacific coasts of Central America, Martinique and Guadeloupe. The effect of fertilizer additions in these soils make matters more complex as the soil solution pH changes frequently causing the Cation Exchange Capacity (CEC) of the soil to change frequently as well. The almost constant changes in the CEC make the behavior of Andosols less predictable than the non-volcanic soils of other banana producing zones in Latin America. This perhaps partially explains the inconsistent responses to the application of certain nutrients in these soils.

Redox reactions

Different states of redox potential occur with the variation of oxygen concentrations in the soil system, as a consequence of fluctuations in the watertable or the occurrence of perched watertables that are very common throughout the banana zones of Latin America. Also, long periods of rainfall associated with cold fronts on the Atlantic Coasts of Guatemala, Honduras and Costa Rica commonly result in saturation of the soil profile and changes in its redox-potential. Changes in the solubility of iron and manganese and their affects on banana production rank among the most important consequences of this phenomenon. To what extent this negatively affects the banana root system has not been clearly established, since the consequences of soil saturation are multiple and always negative for the crop. The toxic effects of iron and manganese have not been clearly established since the active uptake of nutrients stops after oxygen has been depleted from the rhizosphere. It is of great commercial importance to establish the differences among cultivars in tolerance to high concentrations of iron and manganese. This information may play an important role in planning planting strategies on a regional level.

It is also important to recognize that the temporary saturation of the entire soil profile, due to long and intense periods of rainfall, sometimes negatively affects the banana root system more than permanent and static watertables. Banana roots grow during the dry season in soil horizons that will be saturated in the rainy season when many roots die.

The rhizosphere

This is the zone of interaction in the soil-plant relationship; thus it is the most complex component of the system (Pinton *et al.* 2001). In particular, this component has been

little studied in bananas. Judging by the level of understanding reached in other species, it can be inferred that it is also vital to banana production that progress be made in innovative technologies to improve the rhizosphere. The banana industry has recently recognized the need to improve the conditions of the rhizosphere. Its physical, chemical and biological components have been improved in the last decade. This has involved a wide spectrum of technologies among which humic substances, the application of fertilizers through the irrigation system, the use of hormones, soil physical conditioning, mycorrhizae inoculation, and lately precision agriculture are the most relevant. All these technologies are aimed at improving the conditions of the rhizosphere.

Root system performance has been substantially improved by mycorrhizae inoculations under physically, chemically and biochemically adverse soil conditions. Inoculation with mycorrhizae has resulted in greater uptake of P, K, S, and Cu in the 'Galil 7' variety (Solis 2003), and Cu, Mn, and Zn in cv. 'Williams' (Medina 2003) under greenhouse conditions. Faster growth of inoculated plantain plants has been reported under greenhouse conditions, 18 days faster than for the control plants. In the same experiment, inoculation of banana roots with mycorrhizae, Mycoral ®, resulted in greater production of dry matter, but not in a faster growth rate. The results of the tests showed a 46% increase in dry weight and a 56% increase in root volume in cv. 'False horn' plantain and a 43% increase in dry weight in cv. 'Williams' banana. In all cases, there was an increase in the uptake of phosphorus, sulfur, potassium, zinc, copper and iron (Zamorano Biotechnology Unit 2003).

These findings suggest that future advances in similar technologies will allow for a wider range of soils to be planted with bananas at lower production costs under limited soil conditions.

Conclusions and recommendations

The relationship between soil chemical properties and the banana root system needs more basic and applied research to design more efficient programs to improve rhizosphere conditions that will result in higher yields and a sustainable soil management system. Basic research should include microscopic tissue analyses, physiology of the banana plant root system as it is related to potentially toxic ions in various soil systems and climates, the effect of humic substances and mycorrhizae in improving rhizosphere performance. On the other hand, applied research should include the effect of chelating agents on nutrient availability for plant uptake, the possible effect of humic substances in reducing the activity of toxic ions in the soil solution, kinds and rates of liming materials, and the relationship between physical, chemical and biological conditions and their effect on crop yield.

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Banana soil acidification in the Caribbean coast of Costa Rica and its relationship with increased aluminium concentrations

Edgardo Serrano[1]

Abstract

The relationship among soil acidity, pH and aluminium was studied in plantations of different ages located in the areas east and west of the Reventazón River, Costa Rica. Mini-trenches were dug to study, both physically and chemically, the three horizons in the upper 60 cm of the soil profile in the area under the influence of fertilizers. The surface horizon (Ap) ranged from 8 to 12 cm deep, had accumulated humic organic matter and its chemical and physical properties were more likely to be affected by the applications of agrochemicals. The next horizon (Bw_1) ranged from 20 to 30 cm deep, and was characterized by a change in colour, structure and/or texture. The third soil horizon (Bw_2) from 28 to 32 cm deep, also differed from the first horizon in colour, texture and/or structure. In the Western zone (n=75), an increasing linear effect was found between crop age, soil acidity and aluminium concentration in the Ap, Bw_1 and Bw_2 horizons. The soil pH decreased linearly with age of plantation in each of the three horizons. The same effect was observed in the Eastern zone (n=165) but only in the Ap and Bw_1 horizons. By sampling the same production units for three crop cycles, a decrease in pH from 6.5 to 5.1 and an increase in acidity from 0.07 to 1.16 cmol(+)/L was observed in the andosols west of the Reventazón river. This acidification was induced by the acid reaction of the fertilizers used. In most of the world's tropical areas where soils are acid, aluminium toxicity limits crop production.

Resumen - Acidificación de los suelos bananeros en la región Caribe de Costa Rica y su relación con el incremento en las concentraciones de aluminio

La relación entre la acidez, el pH y el Aluminio se estudió en fincas de diferente edad, ubicadas en la zona Este y Oeste del río Reventazón. Se utilizaron mini calicatas para describir química y físicamente los tres horizontes presentes en los primeros 60 centímetros del perfil del suelo, en el área de influencia de los fertilizantes. El horizonte superficial (Ap) osciló entre 8 y 12 cm, acumuló materia orgánica humificada de la cual derivó su color oscuro y sus propiedades físico-químicas fueron alteradas por la adición de agroquímicos. El siguiente horizonte (Bw_1) mostró una amplitud de 20 a 30 cm y se caracterizó por un cambio de color, estructura y/o textura. El tercer horizonte (Bw_2) osciló entre 28 a 32 cm y se separó del anterior por un cambio nuevamente en el color, estructura y/o textura. En la zona Oeste (n =75) se encontró un efecto lineal creciente entre la edad del cultivo y la acidez con la concentración de aluminio en los horizontes Ap, Bw_1 y Bw_2. El pH del suelo decreció linealmente con el tiempo en cada uno de los 3 horizontes. El mismo efecto se observó en la zona Este (n = 165) pero solo en los horizontes Ap y Bw1. Muestreando las mismas unidades de producción durante tres ciclos de cultivo, en andisoles de la zona oeste del río Reventazón, se encontró que el pH en la banda de fertilización disminuyó de 6,48 a 5,07 y la acidez aumentó de 0,07 a 1,16 Cmol(+)/L. Esta acidificación fue inducida por el efecto de los fertilizantes de reacción ácida que se usan en la actividad. En la mayor parte de las áreas tropicales del mundo donde los suelos son ácidos, la toxicidad por aluminio limita la productividad del cultivo.

Introduction

The banana root system is affected by abiotic and biotic factors. Among the biotic factors are plant parasite nematodes, opportunistic fungi that cause root rot, micro-

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organisms associated with the accelerated biodegradation of nematicides, and foliage pests (insects and fungi) that damage leaves at flowering and harvest, affecting the root system balance. Within the abiotic factors there are water excess and deficits, extreme temperatures (low and high), low incidence of photosynthetically active radiation, soil compression, poor drainage (internal and superficial), and soil acidification which results in toxic concentrations of soluble Al^{+3} (Avilán *et al*. 1982, Sancho 1993, Serrano and Marín 1998, López and Espinosa 2000, Serrano 2002, Moens *et al*. 2003).

Al^{+3} is not considered a nutrient for banana since it is not essential for the plant to complete its life cycle (Lahav and Turner 1992). The problem lies in the possible toxic effects of soluble Al^{-3} created in the soil when increased amounts of ammonium based fertilizers decrease soil pH (López and Espinosa 2000, Serrano 2002). In studies with acid nutrient solutions (78 µM Al), Rufyikiri *et al.* (2000, 2001) observed a decrease in total plant dry weight, in the number and diameter of roots, in the Ca and Mg contents, and in the total water and nutrient absorption of 'Grand naine' plants. Rodríguez *et al.* (1985) classified the 'Grande naine' banana cultivar and 'Maricongo' plantains as tolerant to a high Al^{+3} saturation. Nevertheless, these results are difficult to transfer directly to the banana soils of the Caribbean coast of Costa Rica. Rodriguez's results were obtained in ultisols and oxisols; orders of acid soils that practically do not exist in the alluvial zones of Costa Rica that are used to cultivate bananas. The majority of soils in Costa Rica's Caribbean Zone are andosols and inceptisols, that are not naturally acid (López 1963, Jiménez 1972, López and Solís 1991, Nieuwenhuyse *et al*. 1993, Stoorvogel and Eppink 1995, Mata 2000).

This paper examines acidity induced in the fertilization band, pH and Al^{+3} in the cultivated banana soils in Costa Rica's Caribbean coast.

Main sources of soil acidity

There are various natural processes and crop management procedures (Thomas and Hargrove 1984, Lora 1994, Espinosa and Molina 1999, López and Espinosa 2000, Matsumoto, 2002) that increase soil acidity and decrease soil pH.

Among the most important are:

a) **Nutrient removal**. This occurs when the crop roots absorb cations (K^+, Ca^{+2} and Mg^{+2}) and release H^+, to maintain ionic balance.

b) **Nitrogen based fertilizers**. When nitrogen fertilizers that either contain or form ammonium (NH_4^+) are used, the ammonium changes to nitrate by means of nitrification and produces an excess of H^+ that acidifies the soil (Equations 1 and 2).

$$2NH_{4+} + 3O_2 \xrightarrow[\text{Nitrosomes}]{} 2NO_{2-} + 4H^+ + H_2O \quad (1)$$

$$2NH_{4+} + O_2 \xrightarrow[\text{Nitrobacter}]{} 2NO_{3-} \quad (2)$$

The soils where bananas are grown are intensively fertilized with N. Between 375 and 450 kg of N/ha/yr are applied to satisfy the crop need, usually using ammonium based

fertilizers that, to a greater or lesser degree, acidify the soil. This residual or induced acidity is measured through the physiological acidity index, which indicates the amount of $CaCO_3$ that could neutralize the acidity caused by 100 kg of fertilizer. The higher the net value of this index, the greater the residual effect that the fertilizer produces (Table 1). To supply 387 kg of N/ha/yr on the farms east of the Reventazón River, 1402 kg of raw material is used, of which 81% are nitrogen sources that either have or produce ammonium (Table 1).

Table 1. Sources of nitrogen fertilizers used in banana plantations of the zone east of the Reventazón river.

Nitrogen fertilizers	N kg ha^{-1} yr^{-1}	Fertilizer kg ha^{-1} yr^{-1}	Physiological acidity index*
Ammonium sulfate $(NH_4)_2SO_4$	72	342	-112
Ammonium nitrate $(NH_4)_2NO_3$	130	388	-63
Urea $(NH_4)_2CO$	92	200	-84
Diammonium phosphate [(NH4)2HPO4]	37	203	-74
Calcareous ammonium nitrate	57	269	0
Total	388	1 402	

*Physiological acidity index = (-) kg CaCO3/100 kg of fertilizer.

c) **Organic matter mineralization**. This is a natural process that produces NH_4^+ as a final product of organic matter decomposition. This NH_4^+ source also acidifies the soil, although more slowly than the addition of ammonium based fertilizers.

d) **Soluble aluminium hydrolysis**. Aluminium is the third most abundant metal in the earth's crust, and it exists in the soil in an insoluble form as aluminosilicates and oxides. When fertilizers that are applied to the soil, lower the pH to less than 5.3, a soluble form of Al exists as octahydro-hexahydrated $[Al(H_2O)_6^{+3}]$, frequently abbreviated to Al^{+3}. Hydrolysis occurs when the charge/size ratio of the cation is sufficiently large to break the H-O links. The result is hydrate ionization which produces hydrogen ions. Reactions (3), (4) and (5) were abbreviated and are as follows:

$$Al^{+3} + H_2O \longrightarrow Al(OH)^{2+} + H^+ \quad (3)$$

$$Al(OH)^{2+} + H_2 \longrightarrow Al(OH)_2{}^{+} + H^+ \quad (4)$$

$$Al(Oh)^{+} + H_2O \longrightarrow Al(OH)_3{}^{0} + H^+ \quad (5)$$

Each reaction releases H^+ and contributes to soil acidification. This acidity increase promotes the presence of Al^{+3} which is ready to react again. According to the charge/size ratio of the different soil cations, the affinity for hydrolysis that causes acidification is as follows, in decreasing order: $Al^{+3}(44)>Fe^{+3}(36)>Mg^{+2}(14)>Cu^{+2}(14)>Zn^{+2}(14)>Mn^{+2}(13)>Ca^{+2}(10)>Na^{+}(2)$.

Sampling methodology

A total of 14 farms located in the alluvial plain of the Caribbean coast of Costa Rica were sampled: 5 farms of different ages west of the Reventazón River, distributed among Sarapiquí, Guácimo and Pocosí counties; and 9 farms east of the Reventazón River in Siquirres, Matina, Limón and Talamanca counties. Seventy five mini-trenches were dug in the zone west of the river on farms that had been planted for 1, 10, 12 or 30 years, while 165 mini-trenches were dug on the eastern zone on farms that had been planted for 1, 3, 4, 7, 10, 11, 17 or 30 years.

The sampling was done following the methodology described by Jaramillo and Vasquez (1990), which consists in excavating a 60 cm wide x 60 cm long x 60 cm deep ditch (mini-trench) in the fertilization band of recently flowered banana plants. In each mini-trench at least three soil horizons (Ap, Bw_1 and Bw_2) were studied. The surface horizon (Ap) ranged from 8 to 12 cm deep, had accumulated humic organic matter, from which its dark colour was derived, and its chemical and physical properties were more likely to be affected by the applications of agrochemicals. The next horizon (Bw_1) ranged from 20 to 30 cm deep, and was characterized by a change in colour, structure and/or texture. The third soil horizon (Bw_2), from 28 to 32 cm deep, also differed from the first horizon in colour, texture and/or structure (Figure 1). To measure soil pH, exchangeable acidity and Al^{+3}, samples were taken from each horizon. The pH was determined in water using the McLean (1982) procedure with a 1:2.5 soil:water ratio. The readings were taken with an Orion Research 701 A potentiometer. To determine exchangeable acidity, 1N KCl was used as the extracting solution, titrating it with NaOH according to the procedure described by Thomas (1982).

The effect of plantation age on soil acidification

It was observed on the western farms (n = 75) that as plantation age increased, the acidity and the Al^{+3} increased linearly in the Ap, Bw_1 and Bw_2 horizons (Table 2). The pH decreased linearly in all three horizons. Similarly, it was observed that as plantation (n = 165) age increased in the eastern zone, the acidity and the aluminium increased and

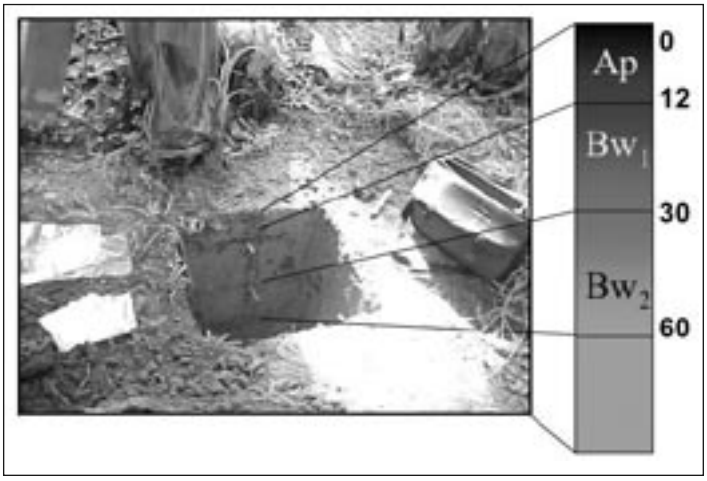


Figure 1. Sampling methodology based on mini-trenches.

Table 2. Relationship between plantation age and soil acidity, pH and aluminium in three soil horizons in banana plantations of the zone west of the Reventazón river (n = 75).

Variable	Horizon	Plantation age (years)				Linear effect*
		1	10	12	30	
	Ap	5.83	5.00	4.78	4.26	dec.**
pH	Bw1	6.29	5.31	5.33	4.76	dec.**
	Bw2	6.21	5.81	5.54	5.21	dec.**
Exchangeable	Ap	0.70	1.76	1.64	4.35	inc.**
acidity	Bw1	0.19	1.45	0.24	4.39	inc.**
cmol(+)/L	Bw2	0.12	0.58	0.14	4.72	inc.**
	Ap	0.64	1.01	0.89	2.72	inc.**
Al	Bw1	0.17	0.81	0.04	2.49	inc.**
cmol(+)/L	Bw2	0.11	0.28	0.02	2.76	inc.**

*The linear effect is the significance of the linear regression between the variable and plantation age. ** P<0.01. dec = negative slope, inc = positive slope.

pH decreased, in a linear manner but only in the Ap and Bw_1 horizons (Table 3). The acidity in the deeper horizon (Bw_2) of the western soils could be related to a greater leaching of the nitrogenous fertilizers towards the deeper horizons. The western zone has soils that are moderately deep, with medium and moderately fine textures, and a greater infiltration rate and hydraulic conductivity than the eastern zone soils (Serrano and Marín 1998, Alvarado *et al*. 2001). Additionally, in the period between 1987 and 2002 the annual average precipitation on the western side of the Reventazón river was 4152 mm in comparison with 3547 mm on the eastern side.

Sampling the same Andisol production units west of the Reventazón river during three crop cycles, it was observed that pH in the fertilization band decreased from 6.48 to 5.07 and acidity increased from 0.07 to 1.16 cmol(+)/L, with a consequent increase of Al^{+3} from 0.02 to 0.99 cmol(+)/L in a two year period. The induced acidification

Table 3. Relationship between plantation age and pH, soil acidity, and aluminium in three soil horizons of banana plantations located in the zone east of the Reventazón river (n = 165).

Variable	Horizon	Plantation age (years)								Linear effect*
		1	3	4	7	10	11	17	30	
	Ap	5.50	5.25	5.08	4.26	4.95	4.45	4.38	4.41	dec.**
pH	Bw1	6.41	5.94	6.01	5.63	5.83	5.50	5.27	4.96	dec.**
	Bw2	6.63	6.35	6.14	5.84	6.15	5.96	5.96	5.25	N.S.
Exchangeable	Ap	1.57	3.55	0.79	2.41	3.73	4.70	2.21	3.96	inc.**
acidity	Bw1	0.34	0.26	0.17	0.25	0.63	1.18	1.03	2.11	inc.**
cmol(+)/L	Bw2	0.34	0.13	0.09	0.16	0.48	0.95	0.20	1.08	N.S.
	Ap	0.85	1.65	0.40	1.12	2.05	2.27	0.55	4.69	inc.**
Al	Bw1	0.18	0.09	0.05	0.07	0.23	0.55	0.75	2.45	inc.**
cmol(+)/L	Bw2	0.09	0.00	0.00	0.00	0.30	0.62	0.14	0.33	N.S.

*The linear effect is the significance of the linear regression between the variable and plantation age. ** P<0.01, N.S.= not significant, dec = negative slope, inc = positive slope.

is cumulative in the fertilizer application band, which is consistent with the increase in plantation age. When pH decreases to 5.3, the Al^{+3} becomes soluble and as a direct consequence of this there are fewer roots and less water and nutrient absorption by the banana crop (Lora 1994, Rufyikiri *et al.* 2000, 2001).

The soils and drainage section of CORBANA in Costa Rica, recommends some crop management practices to diminish the impact of induced acidification, such as:

- Application of calcium amendments as calcite (calcium carbonate) and dolomite (calcium carbonate and magnesium) to precipitate Al^{+3} and to contribute Ca and Mg.
- Application of decomposed or semi-decomposed organic matter to adsorb Al^{+3}.
- Application of fertilizers in lesser quantities but more often (increasing from 17 to 26 cycles of fertilizer application/yr).
- Application of fertilizer in a 90 cm radius around the follower.

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Banana root and soil health project - Australia

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Abstract

The banana plant forms an adventitious root system that is dependent on soil physical, chemical and biological properties to function efficiently. A pot experiment demonstrated that increasing soil compaction was able to significantly reduce the weight of banana roots and shoots. However, in the presence of *Radopholus similis* the effects of soil compaction were obscured, due to the significant reduction in root weight caused by the nematode.

The use of a basic set of soil quality indicators that can be readily used by farmers, was linked to soil nematode indicators to determine relationships between soil properties. In a survey of banana fields in North Queensland, different diameter root classes were affected differently by changing soil properties. Banana roots greater than 5 mm diameter were positively correlated with aggregate stability and negatively correlated with soil bulk density. Banana roots less than 1 mm were positively correlated with electrical conductivity. Specific interactions between soil properties become apparent as crop production systems become more uniform. This allows farmers to prioritise management options to improve the most deficient soil health indicators.

The addition of organic amendments is one possible method of correcting degrading soils. The use of amendments with high carbon contents, such as grass hay, banana trash and alfalfa hay, were able to significantly suppress *R. similis* in the roots of banana plants relative to untreated soil. Due to banana production being located near environmentally sensitive areas there is an increasing need to monitor and modify soil management practices. However, this needs to be linked with a framework that allows the integration of all soil components with a system to allow continual improvement in soil management to allow banana production to have minimal impact on the surrounding environment.

Resumen - Proyecto sobre salud del suelo y raíces de banano - Australia

La planta de banano forma un sistema radical adventicio que depende de las propiedades físicas, químicas y biológicas del suelo para su buen funcionamiento. Un experimento en macetas demostró que el aumento de la compactación del suelo fue capaz de reducir significativamente el peso de las raíces del banano y de los rebrotes. Sin embargo, en presencia de *Radopholus similis* los efectos de la compactación fueron dudosos debido a la significante reducción en el peso radicular causada por los nematodos.

El uso de un grupo básico de indicadores de calidad del suelo, que puede ser fácilmente usado por los agricultores, fue correlacionado a indicadores de nematodos en el suelo para determinar las relaciones existentes entre las propiedades del suelo.

En un diagnóstico de suelos bananeros en el norte de Queensland, diferentes clases de diámetro de raíces fueron afectadas diferentemente al cambiar las propiedades del suelo. Raíces de banano con diámetros mayores a 5 mm fueron correlacionadas positivamente con la estabilidad de los agregados del suelo y negativamente correlacionadas con la densidad total. Raíces de banano menores de 1 mm

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fueron correlacionadas positivamente con la conductividad eléctrica. Interacciones específicas entre las propiedades del suelo se hicieron más aparentes a medida que los sistemas productivos de los cultivos fueron más uniformes. Esto permite a los agricultores priorizar las opciones de manejo, para mejorar los indicadores de salud del suelo más deficientes. La aplicación de enmiendas orgánicas es un posible método para corregir suelos degradados. El uso de enmiendas con alto contenido de carbono, tales como heno de pasto, residuos de banano y heno de alfalfa, fueron capaces de suprimir significativamente a *R. similis* en las raíces de las plantas de banano en comparación con suelos no tratados. Debido a que la producción de bananos está localizada cerca de áreas ambientalmente sensibles, existe una necesidad creciente de monitorear y modificar las prácticas de manejo de suelos. Sin embargo, esto necesita estar ligado a un marco de referencia que permita la integración de todos los componentes del suelos en un sistema que permita el continuo mejoramiento del manejo de suelos para asegurar que la producción bananera tenga un impacto mínimo en el ambiente que le rodea.

Introduction

The banana plant forms an adventitious root system that is wide spreading, unbranched, shallow and gives rise to a dense mat (Blake 1969, Price 1995). The function of banana roots is to provide anchorage, absorption of water and nutrients and synthesis of some plant hormones (Price 1995). The growth of roots is an important factor contributing to banana productivity and is dependent on soil physical, chemical and biological properties (Delvaux 1995). It is suggested that increased size and altered architecture may improve both resource acquisition and anchorage of banana plants, creating a more efficient root system (Price 1995). The condition of the soil has large impact on the development of the root system, with heavy or compacted soils restricting root growth (Araya and Blanco 2001, Price 1995). There are also biological constraints to the development and function of the banana root system such as *Radopholus similis* (Gowen and Queneherve 1990, Gowen 1995, Fogain 2001, Moens *et al*. 2001).

Delvaux (1995) suggested that soil fertility (health), was a poorly defined concept that not only relied on soil chemical, physical and biological properties, and their interaction with the plant community, but on management practices, farming skills and economics. Doran and Parkin (1996) defined soil health as "the capacity of a soil to function within an ecosystem and land use boundary, to sustain biological productivity, maintain environmental quality and promote plant and animal health". Van Bruggen and Semenov (2000) suggested a healthy soil is a stable soil with resilience to stress, high biological diversity and internal cycling of high amounts of nutrients. Knowledge of the function of the soil ecosystem is a basic requirement for soil stewardship (Ferris *et al*. 2001).

Nematodes are a component of the soil ecosystem that interacts with biotic and abiotic soil factors (Yeates 1979). Because of this interaction, nematodes are excellent bio-indicators of soil health, because they form a dominant group of organisms in all soil types, have high abundance, high biodiversity and play an important role in recycling within the soil (Neher 2001, Schloter *et al*. 2003). Nematodes are heterotrophs, higher in the food chain than micro-organisms and so serve as integrators of soil properties related to their food source, predators and parasites (Ferris *et al*. 2001, Neher 2001). Nematode diversity tends to be greatest in ecosystems with the least disturbance (Yeates 1999). The disturbance to the soil by environmental or land management practices changes the composition of nematodes (Bongers 1990, Yeates and Bongers 1999, Ferris *et al*. 2001). There are a number of indices derived from nematode community analysis that

can be used to determine the impact of management changes on the soil ecosystem (Bongers 1990, Yeates and Bongers 1999, Ferris *et al*. 2001).

However, the use of nematodes as indicators of soil ecosystem health and banana management is not a practical tool for farmers, as it requires specialised knowledge and equipment (Neher 2001). Doran (2002) suggested linking "science to practice" in assessing the sustainability of land management practices, by the use of simple indicators of soil quality and health that have meaning for farmers. To embrace changes in environmental management of their land, farmers need to understand why they need to change (Marsh 1998). The best way to achieve this is by the use of participatory research strategies using simple on-farm techniques (Freebairn and King 2003, Lobry de Bruyn and Abbey 2003). A basic set of soil quality indicators was developed by J.W. Doran (USDA-ARS, Lincoln, NE), and developed into an on farm test kit (http://soils.usda.gov/sqi/soil_quality/assessment/kit2.html). The basic set of soil parameters has been used to measure the effects of changes in soil management on agricultural crops (Sarrantonio et al. 1996, Stamatiadis et al. 1999) but not on bananas.

If advances are to be made in improving the efficiency of the banana root system there needs to be a link between indicators and more complex soil processes. Nematodes as integrators of soil properties, linked with chemical, physical and biological indicators may increase our understanding of soil management to improve the efficiency of the banana root system. The Banana Root And Soil Health (BRASH) project aims to highlight for farmers limits of the present banana soil management techniques, provide tools and indicators to measure soil health and potential solutions to overcome soil limitations to create a more efficient banana root system.

Materials and methods

Impact of soil compaction

A pot experiment was designed to determine the impact of soil compaction on the roots of banana plants (*Musa* AAA cv. 'Williams'). The density of soil in 10 L plastic pots was adjusted by adding perlite to field soil to achieve a bulk density of 1.00 and 1.25 g/cm^3 or compacted by compressing moist field soil in the pots around a banana plant to achieve a bulk density of 1.50 and 1.75 g/cm^3. Half of the plants were inoculated with 2390 motile *R. similis*, 7 days after planting. Each treatment was replicated 8 times in a completely randomized design. The plants were maintained in the glasshouse at 20-30^{o}C and were watered by misting twice daily for 15 minutes. The banana plants were fertilized by adding 5 g of Osmocote Plus Mini™ (16.0:3.5:9.1 + trace elements, Scotts Australia Pty Ltd) at planting.

The banana plants were harvested after 12 weeks. Plant growth parameters, including shoot dry weight, were measured by drying the shoots at 70^{o}C for three days at harvest. A transverse section through the soil next to the plant was made and the number of roots greater than 2 mm in diameter originating from the corm were counted. The roots were then washed free of soil and the fresh root weight determined for different root diameter classes, > 5 mm, 1-5 mm and < 1 mm diameter (Araya and Blanco 2001). Nematodes were extracted from the root system in a misting cabinet for seven days (Hooper 1986) and quantified under a compound microscope.

Banana soil health survey

Soil health measurements

A soil health survey method was developed using basic soil quality indicators (Sarrantonio *et al.* 1996, http://soils.usda.gov/sqi/soil_quality/assessment/kit2.html). On site evaluation of water infiltration was measured with aluminium infiltration rings (150 mm d x 125 mm) inserted 75 mm into the soil. The ring was placed 100 mm from the follower sucker of the banana plant, so that it was in line with the follower sucker and the mother plant. Soil respiration was measured from the head space of the covered infiltration rings for 30 min using CO_2 gas sampling tubes (0.01-2.6%, 126SA, Kitigawa, Japan) before determining water infiltration rates. The ring was then inserted level with the soil surface and excavated. All roots within the ring were washed free of soil and banana roots were divided into classes, > 5 mm, 1-5 mm and < 1 mm diameter (Araya and Blanco 2001) and expressed as the weight of root in one litre (dm^3) of soil.

A second aluminium ring (75 mm d x 125 mm) was inserted into the soil until level with the soil surface. The ring was excavated from the soil and the soil within the ring was used in the laboratory determination of soil bulk density, gravimetric water content and aggregate stability (Sarrantonio *et al*. 1996). Additionally, soil pH and electrical conductivity (EC), were determined in a 1:1 soil-water mixture. Soil nitrate-N was determined from the filtered extract of the soil water mixture using test strips (Aquacheck™, Hach company, Loveland, USA). A 200 g sub-sample was used for nematode community analyses by placing the sub-sample on a single ply of tissue in water for 1 day (Whitehead and Hemming 1965). The community structure was determined using the method described by Yeates (2001). The nematodes were further subdivided into functional guilds and nematode indices calculated (Yeates and Bongers 1999, Ferris *et al*. 2001).

Further observations made in the field included soil temperature (100 mm depth), presence or absence of earthworms, finger number per bunch (Turner *et al*. 1988), leaf emergence rate and height increase of the follower sucker and the amount of banana trash on the soil surface around the banana plant.

Paired site survey

A survey compared soil and plant measurements (described above) made around banana plants with undeveloped plant systems, such as rainforest and pasture. Four sites in north Queensland were compared, located at East Palmerston, Mission Beach, Tully and Kennedy. The sites represented the major banana growing regions and soil types used in banana production in north Queensland. An organic farm was also included in the survey at the Mission Beach site. At each site, five samples were taken from each plant system.

Banana farm survey

Twenty-one banana fields were surveyed using the methods described above, in the major banana production zone of north Queensland. At all sites sampled, banana farms were more than three years old and the cultivars were members of the Cavendish subgroup (*Musa* AAA). In each farm, five samples were collected.

Banana field survey

An eight year old banana field (*Musa* AAA cv. 'Williams') near Innisfail, north Queensland was surveyed nine times beginning in October 2002. The sampling occurred monthly and five banana plants were sampled on each occasion.

Soil amendments

A pot experiment was established in 10 L plastic containers using three soils from different banana growing areas of north Queensland. The soils were amended with the equivalent of 40 tonnes/ha of grass hay, alfalfa hay, banana trash, mill mud, mill ash (by-products of sugar cane processing), paunch (cattle rumen contents), bio-solid, or municipal waste compost (MW compost). Additional treatments of 120 t/ha of mill ash, 5 t/ha of wolastonite (calcium silicate) and 300 L/ha of molasses were compared with an untreated control. The chemical composition of the amendments was determined (Table 1).

A banana plant (*Musa* AAA cv. 'Williams') was grown in each pot. Half of the pots were inoculated with 860 motile *R. similis* 3 days after planting the bananas. All treatments were replicated four times in a randomized block design. The plants were maintained in the glasshouse at 20-30^{o}C and were watered by misting twice daily for 15 minutes. Trays were placed at the base of the pots and water collected in the trays returned to the soil surface. The banana plants were fertilized by adding 5 g of Osmocote Plus Mini™ at planting.

The plants were harvested after 12 to 15 weeks from planting. The shoot dry weight was determined as described previously. The fresh root weight was determined by washing the soil from the roots and allowing the roots to drain on absorbent paper. Nematodes were then extracted from the root system in a misting cabinet for seven days (Hooper 1986) and quantified under a compound microscope.

Statistics

Nematode numbers from pot experiments were transformed, ln(x+1), before conducting analysis of variance. Means were separated using the least significant difference (LSD) method and presented as back transformed values. Linear correlations between soil properties were determined for the three surveys. Soil health properties that were significantly correlated (P<0.05) were linked using a concept map. All statistical analyses were performed using Genstat 6 (version 6.1.0.205)

Results

Impact of soil compaction

The weight of banana roots and shoots declined significantly as the soil bulk density increased (Figure 1). However, the addition of a disease-causing organism such as *R. similis* obscured the effects of soil compaction causing a significant (P<0.05) reduction in the weight of banana roots (Figure 1). The difference in root weight caused by *R. similis* was greater at lower than higher bulk densities (Figure 1). There was a significant decline in shoot weight of bananas with increasing soil bulk density in the absence of *R. similis*. However, when *R. similis* was present there was no significant relationship

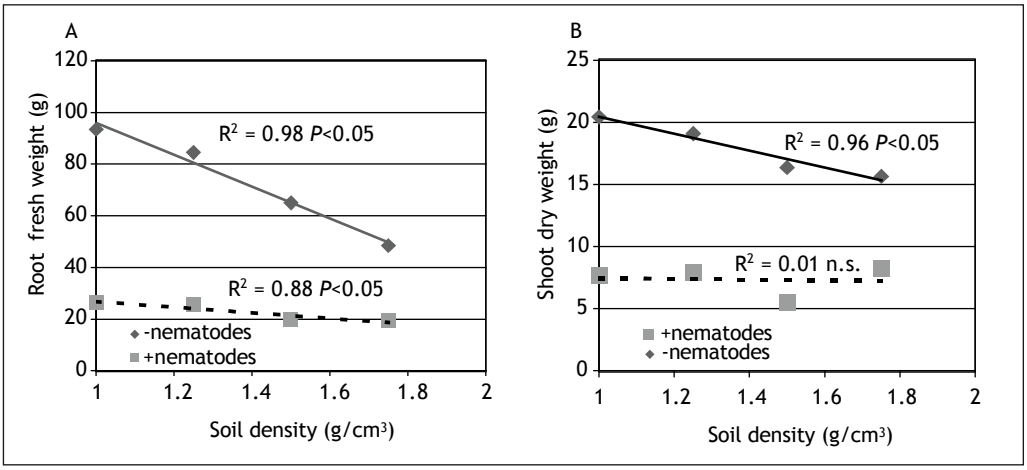


Figure 1. Effects of increasing soil density on banana root fresh weight (A) and shoot dry weight (B) in the presence and absence of *R. similis*.

between shoot weight and soil bulk density (Figure 1). The weight of roots less than 5 mm in diameter were reduced with increasing soil bulk density (Table 2). Similarly, the number of roots greater than 2 mm in diameter originating from the corm was reduced with increasing soil bulk density (Table 2).

Banana soil health

Paired site survey

Banana soils tended to be dominated by plant-parasitic nematodes relative to undeveloped plant systems (Table 3). This contributed to the lower nematode diversity (H′) in the soil (Figure 2). Aggregate stability tended to be lower on banana producing soils relative to soils in the undeveloped plant systems (Table 3). Aggregate stability was negatively correlated with the amount of nitrate-N in the soil (Figure 2), with banana farms tending to have high soil nitrate-N relative to undeveloped sites, except at the Mission Beach site (Table 3). Electrical conductivity (EC) appeared to be a central indicator of many soil properties (Figure 2). Higher EC was evident on banana farms relative to undeveloped sites, except at Mission Beach (Table 3). Lower EC favoured fungal domination in the soil with nutrients being decomposed by fungal pathways, determined by the channel index (determined by the nematode community analyses as a resource decomposition pathway, Ferris *et al*. 2001)(Figure 2).

Banana farm survey

The soil properties on the banana farms exhibited a greater number of significant relationships than comparing different plant systems (Figures 2 and 3). Again, the soil nematode community on banana farms was dominated by plant-parasitic nematodes and low nematode diversity (Table 4). The proportion of plant-parasitic nematodes in the soil was negatively correlated with other nematode feeding types, nematode diversity and increased the nematode dominance index (Figure 3).

Table 1. Chemical composition of amendments applied to soil before growing bananas in pots.

Soil amendment	Nutrient (%)								C:N ratio	Nutrient (mg/kg)						
	N	P	K	Ca	Mg	S	Na	C		Cu	Zn	Mn	Fe	Al	B	Si
Biosolid	0.81	0.39	1.50	0.97	0.77	0.64	2.24	7.1	8.7	14.9	95	180	330	90	54	1.38
MW compost	1.85	0.28	0.15	32.0	0.19	0.13	0.05	29.0	15.7	56.8	120	83	670	2200	11	15.86
Mill Mud	1.44	0.39	0.54	6.30	0.23	0.40	0.52	19.8	13.7	248.0	460	270	13000	11000	< 0.3	15.7
Mill Ash	0.30	0.27	0.28	0.70	0.16	0.05	0.01	19.4	64.7	32.4	76	930	13000	38000	< 0.3	25.35
Banana trash	1.82	0.35	2.00	1.50	0.72	0.10	0.40	46.8	25.7	59.3	110	1300	24000	55000	< 0.3	2.31
Grass hay	2.28	0.29	3.20	0.49	0.16	0.54	0.76	44.7	19.6	9.0	22	190	170	140	5.9	1.29
Alfalfa hay	3.16	0.25	1.70	1.70	0.52	0.35	0.30	45.8	14.5	6.1	15	61	880	700	45	0.63
Molasses	0.50	0.06	3.80	0.72	0.25	0.43	0.04	-	-	2	8.8	70	350	110	2.7	-

Table 2. Banana root measurements in soil at different soil bulk densities.

Soil bulk density (g/cm^3)	Fresh root weight (g/L)				Corm root number
	>2 mm	Total roots	>5 mm	1-5 mm	<1 mm
1.00	60.0 c	0.3 n.s.	30.2 b	29.4 b	5.1 bc
1.25	54.9 bc	0.9 n.s.	27.8 b	26.2 b	5.8 c
1.50	42.4 ab	0.1 n.s.	19.8 a	22.5 ab	4.0 b
1.75	33.9 a	0.3 n.s.	17.3 a	16.2 a	2.1 a

Means with the same subscript within a column are not significantly different at the 5% level. Values are the means of 16 plants with and without *R. similis*.

Table 3. Properties (mean ± standard error) of soil quality indicators and nematode communities comparing banana cultivation to undeveloped plant systems at four locations in north Queensland.

Location	East Palmerston		Mission Beach			Tully			Kennedy	
Vegetation	**Banana**	**Pasture**	**Banana**	**Organic**	**Rainforest**	**Banana**	**Rainforest**	**Pasture**	**Banana**	**Rainforest**
Indicators					*Chemical*					
NO3-N (kg/ha)	24±7	6±1	15±2	16±1	43±10	109±42	60±4	28±14	76±36	31±7
pH	6.5±0.2	5.4±0.1	5.2±0.1	5.5±0.3	4.6±0.1	5.5±0.3	4.3±0.2	4.1±0.1	4.3±0.3	5.2±0.1
EC soil (dS/m)	0.25±0.04	0.04±0.00	0.11±0.02	0.30±0.03	0.22±0.02	0.38±0.09	0.13±0.01	0.07±0.01	0.40±0.162	0.21±0.01
					Physical					
Temperature (C°)	24.6±0.1	26.1±0.1	20.9±0.2	20.9±0.1	20.4±0.1	18.9±0.1	18.5±0.3	20.2±0.1	19.4±0.2	19.6±0.0
Infiltration rate (s)	11±4	161±16	82±13	65±6	49±20	791±359	1195±320	1800±0	122±23	39±13
Soil water (g/g)	0.39±0.02	0.34±0.01	0.25±0.01	0.32±0.01	0.29±0.01	0.30±0.010	0.33±0.01	0.42±0.01	0.15±0.02	0.14±0.01
Bulk density (g/cm^3)	0.86±0.02	0.91±0.01	1.12±0.01	1.04±0.02	1.07±0.02	1.12±0.06	1.03±0.02	1.06±0.01	1.24±0.01	0.92±0.05
Aggregate stability (%)	62±1	66±3	62±2	76±1	78±2	20±4	71±4	74±3	41±5	80±5
					Biological					
Soil Respn (kg $CO_2.ha^{-1}.d^{-1}$)	7.3±0.7	12.6±1.13	5.1±0.47	4.5±0.21	6.1±0.56	7.1±1.00	8.7±0.39	15.2±1.60	5.9±0.37	5.1±0.32
Root weight (g/L)	11.3±3.2	21.0±3.5	9.0±1.1	16.0±3.3	19.8±5.7	9.4±4.9	11.3±1.1	35.1±5.3	13.6±5.1	26.8±2.8
Soil surface trash (g/m^2)	40±16	79±8	1.3±1.0	83±27	47±15	159±37	21±2	--	135±29	154±14
					Nematode proportions					
Plant parasitic (%)	82±5	44±4	91±3	28±7	18±1	55±6	57±3	19±4	74±9	14±5
Bacterial feeding (%)	13±4	20±2	6±2	18±3	33±3	23±6	13±2	26±2	17±6	47±4
Fungal feeding (%)	2±1	11±2	1±0	15±4	9±1	3±1	7±1	8±2	4±1	11±2
Predatory (%)	0±0	2±1	1±0	23±4	7±1	5±1	9±1	5±1	1±1	6±1
Plant associated (%)	0±0	12±2	0±0	2±1	14±1	7±1	7±1	30±7	3±2	10±1
Omnivorous (%)	3±2	10±1	2±1	15±4	20±2	6±3	7±2	12±3	2±1	12±2
					Nematode indices					
Shannon-Weiner (H')	1.39±0.10	1.93±0.08	0.76±0.15	1.76±0.08	2.24±0.08	1.80±0.10	2.21±0.07	2.00±0.05	1.39±0.19	2.23±0.07
Dominance (λ)	0.33±0.03	0.23±0.03	0.10±0.08	0.17±0.01	0.13±0.01	0.20±0.03	0.09±0.02	0.18±0.02	0.35±0.04	0.15±0.02
Bacterial.$(Bact+Fung)^{-1}$	0.78±0.08	0.50±0.06	0.68±0.06	0.37±0.05	0.53±0.03	0.69±0.08	0.46±0.05	0.56±0.04	0.70±0.07	0.67±0.03
Structural index	50±10	62±5	73±9	84±5	85±1	62±15	79±4	77±6	43±13	68±3
Enrichment index	63±5	51±5	82±4	67±5	83±3	82±5	66±6	82±4	70±5	77±3
Channel index	9.1±2.6	38.3±4.2	6.3±3.1	28.8±7.6	9.4±1.5	8.1±4.0	30.1±9.1	10.9±2.3	15.6±4.5	10.4±1.5

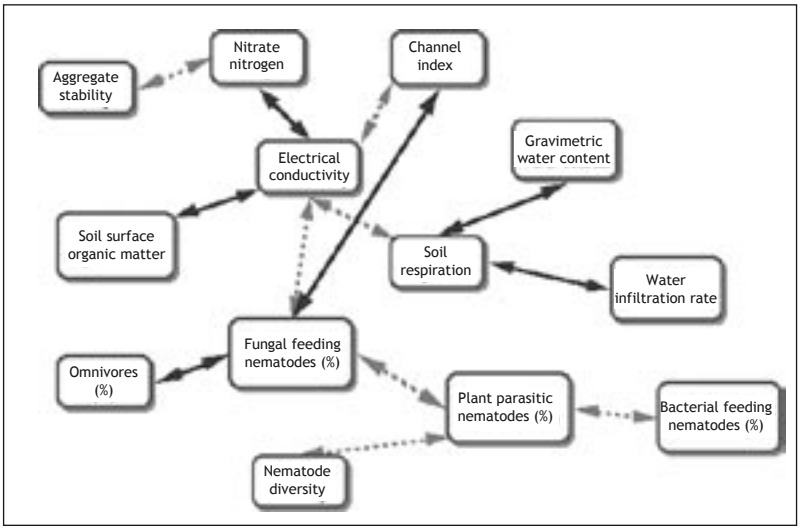


Figure 2. Significant (P<0.05) correlations between soil properties and nematode community analysis comparing banana cultivation with undeveloped plant systems in north Queensland. Dashed lines (---) depict a negative relationship, solid lines (____) depict a positive relationship.

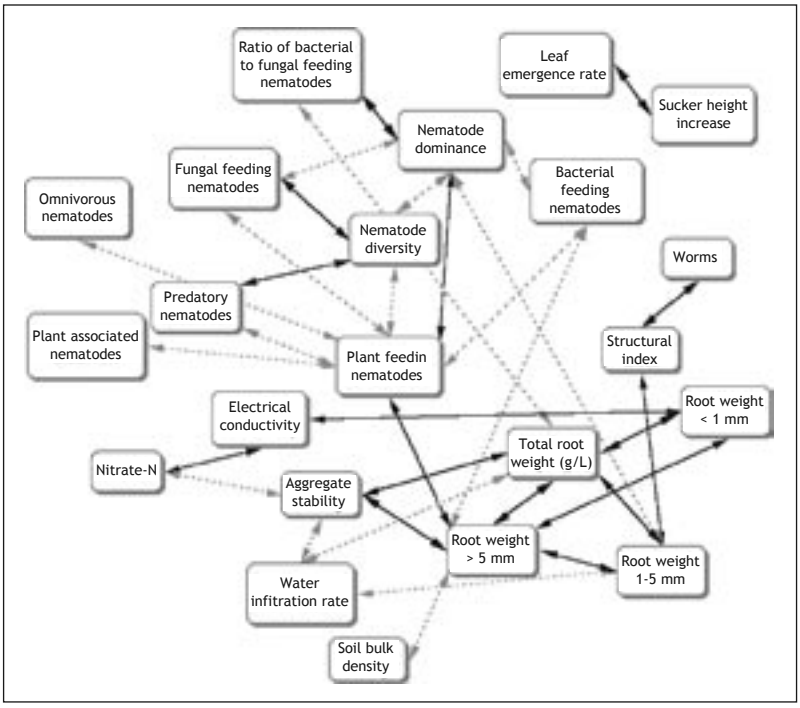


Figure 3. Significant (P<0.05) correlations between soil properties and nematode communities within 21 banana fields in north Queensland. Dashed lines (---) depict a negative relationship, solid lines (____) depict a positive relationship.

The total weight of banana roots was made up of the different root diameter classes (Figure 3). However, roots of different diameters were affected by different soil properties. Roots greater than 5 mm were negatively correlated with soil bulk density and the proportion of bacterial feeding nematodes, but were positively correlated with aggregate stability and the proportion of plant feeding nematodes in the soil (Figure 3). The weight of roots 1-5 mm was positively correlated with the structure index (deter-

mined by the nematode community analyses as a measure of the trophic layers and potential for opportunists, Ferris *et al*. 2001), but negatively correlated with nematode dominance and water infiltration rates (Figure 3). Roots less than 1 mm in diameter were positively correlated with electrical conductivity (Figure 4). Aggregate stability was again negatively correlated with nitrate-N amounts in the soil (Figure 4). There was

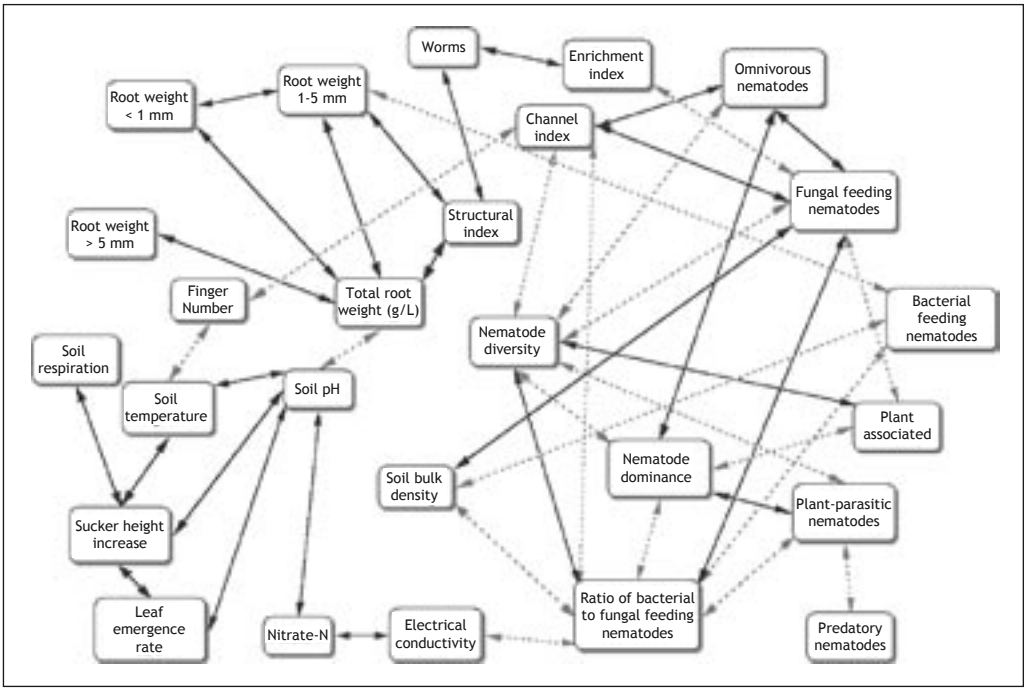


Figure 4. Significant (P<0.05) correlations between soil properties and nematode communities within a banana field in north Queensland sampled monthly 9 times since October 2002. Dashed lines (---) depict a negative relationship, solid lines (____) depict a positive relationship.

no correlation between soil factors and plant production parameters (Figure 4), which suggested that farmer management of the crops may be able to obscure poor soil and root characteristics.

Banana field survey

In a single banana field there was an increasing number of relationships between soil properties (Figure 4). Plant parasitic nematodes were not the dominant trophic nematode group at this site (Table 5). The structure index (Ferris *et al*. 2001) was positively correlated with the total weight of roots and the weight of roots between 1-5 mm (Figure 4). The channel index (33) was almost double the banana industry average (19), which suggested that fungi were more important in the recycling of nutrients even though bacterial feeding nematodes dominated the nematode community (Table 5). The site also had low soil nitrate-N (14 kg NO_3-N.ha^{-1}), approximately half of the north

Table 4. Properties (grand mean ± standard error) of soil quality indicators and nematode communities of 21 banana fields in north Queensland, n=105.

Soil property	Mean	±Standard error
Physical properties		
Soil temperature (°C)	24.2	0.5
Water infiltration rate (secs)	448	108
Gravimetric soil water (g/g)	0.25	0.02
Soil bulk density (g/cm^3)	1.11	0.03
Aggregate stability (%)	43.9	4.2
Chemical properties		
Electrical conductivity (dS/m)	0.25	0.04
pH	6.13	0.16
No_3-N (kg/ha)	32.9	6.6
Biological properties		
Soil respiration (kg CO_2-C ha^{-1} d^{-1})	6.53	0.30
Worms (0=absent, 1=present)	0.4	0.1
Banana measurements		
Finger number per bunch	133	9
Leaf emergence rate (leaves/week)	0.50	0.04
Sucker height increase (m/week)	0.06	0.01
Total root weight (g/L)	8.19	0.83
Root weight >5 mm (g/L)	3.19	0.40
Root weight 1-5 mm (g/L)	2.45	0.24
Root weight <1 mm (g/L)	2.56	0.41
Surface trash (t/ha)	8.1	1.1
Soil nematodes		
Plant parasitic nematodes (%)	61.7	4.8
Bacterial feeding nematodes (%)	21.5	2.5
Fungal feeding nematodes (%)	4.5	1.1
Predatory nematodes (%)	4.2	0.9
Plant associated nematodes (%)	2.0	0.9
Omnivorous nematodes (%)	6.1	1.1
Nematode indices		
Shannon-Weiner diversity index H′	1.11	0.09
Dominance λ	0.37	0.04
Bacterial.(Bacterial+Fungal)$^{-1}$	0.82	0.03
Structural index	60.3	3.1
Enrichment index	68.3	2.6
Channel index	18.6	4.3

Queensland industry mean (33 kg NO_3-N.ha^{-1}), which meant that recycling of nutrients is more important to supply nitrogen for crop production at this site (Tables 4 and 5).

The site was measured over different environmental conditions and soil temperature was positively correlated with the increase in follower sucker height and soil pH and negatively correlated with bunch finger number (Figure 4). This suggested that seasonal fluctuations may impact more on crop production than on soil characteristics and obscure effects of soil health on crop production.

Table 5. Properties (grand mean ± standard error) of soil quality indicators and nematode communities within a banana field in north Queensland sampled 9 times at monthly intervals from October 2002.

Soil property	Mean	±Standard error
Physical properties		
Soil temperature (°C)	25.5	0.8
Water infiltration rate (secs)	350	129
Gravimetric soil water (g/g)	0.27	0.01
Soil bulk density (g/cm3)	1.13	0.01
Aggregate stability (%)	47.6	2.4
Chemical properties		
Electrical conductivity (dS/m)	0.18	0.02
pH	6.47	0.29
NO3-N (kg/ha)	13.6	1.9
Biological properties		
Soil respiration (CO_2-C ha^{-1} d^{-1})	5.6	0.4
Worms (0=absent, 1=present)	0.4	0.1
Banana measurements		
Finger number per bunch	101	6
Leaf emergence rate (leaves/week)	0.7	0.1
Sucker height increase (m/week)	0.07	0.02
Total root weight (g/L)	6.59	0.89
Root weight >5mm (g/L)	1.77	0.47
Root weight 1-5mm (g/L)	2.53	0.38
Root weight <1mm (g/L)	2.29	0.36
Surface trash (t/ha)	5.2	0.7
Soil nematodes		
Plant parasitic nematodes (%)	23.6	2.7
Bacterial feeding nematodes (%)	37.0	4.6
Fungal feeding nematodes (%)	19.2	3.6
Predatory nematodes (%)	7.0	1.8
Plant associated nematodes (%)	1.8	0.8
Omnivorous nematodes (%)	11.3	2.1
Nematode indices		
Shannon-Weiner diversity index H′	1.56	0.09
Dominance λ	0.24	0.02
Bacterial.(Bacterial+Fungal)$^{-1}$	0.65	0.07
Structural index	67.7	5.5
Enrichment index	61.8	4.3
Channel index	33.1	7.7

Means are calculated from 45 samples.

Soil amendments

The addition of mill mud (40 tonnes/ha) or mill ash (120 tonnes/ha) significantly increased the weight of banana roots relative to the untreated control (Table 6). However, only the addition of mill mud was able to significantly increase the shoot weight (Table 6). The addition of biosolids to the soil significantly reduced the weight of banana roots and shoots (Table 6).

R. similis numbers within the roots of bananas were significantly suppressed when grass hay, alfalfa hay, mill mud and banana trash were added to the soil (Table 6).

Table 6. Effects of applications of soil applied amendments on R. similis numbers in the roots of bananas and the weight of banana roots and shoots.

Amendment	Rate (t/ha)	Nematodes in 100 g root	Shoot dry weight (g)	Root fresh weight (g)
Untreated	-	10 046 d	17.8 bcd	53.8 bc
Bedminster	40	7 449 d	18.1 bcd	54.8 bcd
Biosolid	40	3 935 bcd	11.6 a	36.0 a
Grass	40	1 734 b	21.2 cde	61.4 bcde
High ash	120	3 931 bcd	22.0 de	71.4 de
Low ash	40	5 452 cd	21.1 cde	52.9 abc
Lucerne	40	569 a	15.7 ab	50.5 abc
Mill mud	40	2 121 bc	25.9 e	75.9 e
Molasses	300 L/ha	8 847 d	16.6 bc	46.1 ab
Paunch	40	4 354 bcd	17.5 bcd	45.6 ab
Trash	40	1 778 b	24.5 e	66.9 cde
Wolastonite	5	9 661 d	16.8 bc	56.4 bcd

Means with the same letter within a column are not significantly different at the 5% level.

There was no interaction between soil type and the amendments, which suggested that the effects of the amendments would be the same on banana growth and *R. similis* in banana producing soils of north Queensland.

Discussion

The health of the banana root system is linked to the conditions of the soil in which the plants grow. Complex interactions between soil physical, chemical and biological properties can be mapped to gain a greater understanding of the interactions of crop production and soil health under specific soil conditions. As the cropping systems and conditions in which the plants are grown become more uniform, the interactions within the soil become more distinct. This was seen in moving from a survey of different plant systems, to a survey of banana growing systems finally to a single banana field (Figures 2, 3 and 4).

Skilful farm management can mask the deterioration of the soil and obscure interactions of soil components to obtain profitable banana production. It is not until the plant is placed under stress that soil degradation becomes apparent within the banana production system. The time needed for the soil to respond and overcome an imposed stress may be one method of determining the health of the soil (van Bruggen and Semenov 2000). Damage to banana roots by *R. similis* can be interpreted as a stress on the soil ecosystem. The nematode is capable of significantly reducing the root system of banana plants even in favourable physical soil conditions (Figure 1). Therefore, improved biological and chemical management of the soil appear as important in suppressing nematode damage to banana roots as developing an extensive root system.

Tools and indicators are needed to measure changes in soil properties to prevent soil degradation. The basic soil quality indicators (Sarrantonio *et al.* 1996, http://soils.usda.gov/sqi/soil_quality/assessment/kit2.html) used in the BRASH project

showed relationships with nematode indicators (Yeates and Bongers 1999, Ferris *et al*. 2001). This suggested that simple tools can indicate more complex soil processes. The tools can be used to depict how farmer's soil management decisions can have 'flow on' effects that are not easily recognisable. In the survey of banana farms in north Queensland the accumulation of soil nitrate was positively correlated with EC and negatively correlated with aggregate stability (Figures 2 and 3). Aggregate stability in turn was negatively correlated with water infiltration rates, which were negatively correlated with the total weight of banana roots (Figure 3). As EC increased so did the weight of roots less than 1 mm diameter. It could be proposed that as EC increased the banana plant produced more fine roots, possibly to absorb the readily available nitrate-N. Therefore, the use of nitrate-N fertilisers in the short term may produce higher yields, however, the long-term effects may lead to soil degradation as aggregates become less stable. Excessive soil nitrogen has also been linked with increased soil-borne diseases in crops due to the lack of microbial diversity (van Bruggen and Termorshuizen 2003). This requires further investigation in banana production.

Abawi and Widmer (2000) suggested that soil-borne diseases are most damaging when soil conditions are poor as a result of inadequate drainage, poor soil structure, low organic matter, low soil fertility and high soil compaction. However, effects of soil health on the suppression of soil-borne diseases need to be extrapolated to the banana field. Management of the soil microbial environment may be able to reduce the susceptibility of bananas to soil-borne diseases. Increasing the nematode diversity in the soil was negatively correlated with the proportion of plant-parasitic nematodes (Figures 2, 3 and 4). The addition of soil amendments high in carbon was found to suppress *R. similis* in a pot experiment (Tables 1 and 6). Similarly, Stirling *et al.* (2003) found that amendments with high C:N ratios are the most effective in enhancing biological control activity against plant-parasitic nematodes. One possible mechanism for the suppression of plant parasitic nematodes is that there are a variety of nematode parasitic fungi in the soil that use nematodes as a source of nitrogen (Stirling *et al*. 2003). Conditions in the field need to be manipulated to increase soil organisms that suppress plant-parasitic nematodes. This has been promoted as longer control than the use of chemicals (Widmer *et al*. 2002) and may promote a more efficient banana root system.

One important soil characteristic that is not easily measured is soil organic carbon. Widmer *et al.* (2002) suggested that maintenance of high concentrations of organic matter, especially the active fraction, greatly improves the physical, chemical and biological properties of soils leading to increased productivity. Tropical soils used in banana production tend to have high soil water contents and high soil temperatures, which are favourable for organic matter decomposition (Sikora and Stott 1996). Additionally, intensive cultivation of the soil in preparation for planting bananas in north Queensland may also be reducing soil carbon. A simple on farm test to determine soil organic carbon is needed to allow monitoring and linking in to other soil health indicators.

The commercial production of bananas in monoculture, using the same clone, makes commercial bananas susceptible to pests and diseases due to the lack of diversity. Yeates (1999) found that plant communities were responsible for dictating soil nematode communities. The use of ground-cover plants may be one method of increasing the diversity around the banana root system and improving soil physical, chemical and biological

properties. The mechanized method of banana cultivation in north Queensland would allow mowing of ground-cover plants to return organic matter to the banana soil ecosystem. The choice of species is important and ideally would be deep rooted, allowing the capture of nutrients that escape the banana root system, shade tolerant and capable of withstanding waterlogging and traffic.

The use of soil health indicators needs to be linked with a framework of continual crop and environmental improvement, to support management decisions if farmers are to make advances in environmentally responsible soil management. However, soil management issues may be specific to individual farming systems. Heisswolf *et al.* (2003) designed a process that valued farmer's motives, knowledge and experience, was participative and encouraged farmers to identify their own environmental issues within an economic perspective. This process could be linked with the tools and indicators used in monitoring soil health and allow farmers to understand the effects their management is having on soil health. However, soil management must be seen as a holistic system, made up of physical, chemical and biological components that cannot be separated.

The health of the banana root system is strongly reliant on soil health determined by soil physical, chemical and biological properties. The soil properties are linked within the soil ecosystem, so that subtle management changes can have long-term effects leading to soil degradation and future problems with banana production. The BRASH project aims to involve farmers in changing soil management practices by demonstrating the impact that soil degradation, such as soil compaction, has in reducing banana root development. BRASH develops simple tools for farmers to monitor the trends in soil health and provides solutions to correct adverse trends, such as the use of soil amendments. However, due to complex interactions occurring in the soil and the long time frame needed to detect changes in soil indicators, a framework for integrating and managing all of the components is required if sustained changes in environmental management practices are to occur. Most banana production world-wide is in environmentally sensitive of areas. Therefore, responsible soil management is needed to ensure that banana production remains socially and economically viable with minimal impact on the surrounding environment.

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5

Pathogen - root interactions

Interacciones patógeno - sistema radical

The potential use of microbial communities inside suppressive banana plants for banana root protection

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Abstract

Research has demonstrated that plants lose up to 33% of their assimilates to the soil. Why does a plant, in this case banana, exert large amounts of energy to produce nutrients that land unused in the soil? We believe that: (1) roots are damaged by pests and diseases and the plant cannot utilize the nutrients produced in the shoot; and/or (2) the plant has evolved a health support system made up of "rhizosphere specific microbial communities" (RSMC) that live on these nutrients in symbiotic and/or mutualistic associations. These RSMC are not enhanced by standard banana production systems even though they are important for root health and growth. Research has shown that the interactions between banana and certain endophytic fungi are important for root health and growth. This interaction has been studied in detail and these forms of microbial communities have evolved concomitantly with the plant over evolutionary time. We have shown that specific fungi, and probably even bacteria, that have plant health promoting abilities are important for root health. When an ecological state is reached in which RSMC are well established and are functioning properly, we believe this leads to a disease or pest suppressive agro-ecosystem. Such a system was studied in Guatemala. The research indicated that: 1) pest nematodes are suppressed in certain areas of the Motagua Valley, Guatemala; 2) endophytic fungi play a major role in this suppressive system, and 3) endophytic *Fusarium oxysporum* and *Trichoderma atroviride* suppress *Radopholus similis* in banana roots.

Resumen - Uso potencial de las comunidades microbianas en plantas supresivas de banano para proteger las raíces del banano

Investigaciones han demostrado que las plantas pierden hasta un 33% de sus asimilados en el suelo. ¿Porqué una planta, en este caso banano, utiliza grandes cantidades de energía para producir nutrientes que se pierden en el suelo? Nosotros creemos que: (1) las raíces son dañadas por plagas y enfermedades y no pueden utilizar los nutrientes producidos en en la parte aérea de la planta; y/o (2) la planta ha desarrollado un sistema de apoyo a la salud con "comunidades microbiales específicas de la rizosfera" (CMER) que viven en asociaciones simbióticas y/o mutualísticas con la planta y que se alimentan con esos nutrientes. Las CMER no se mejoran mediante los sistemas de producción estándar de banano, aún cuando éstas son importantes para el crecimiento y la salud de la raíz. La investigación ha mostrado que la interacción entre el banano y hongos endofíticos específicos son importantes para la salud y el crecimiento de la raíz. Esta interacción ha sido estudiada en detalle y estas formas de comunidades microbiales se han desarrollado en concomitancia con la planta sobre un tiempo evolucionario. Hemos demostrado que hongos específicos y probablemente aún bacterias que tienen la habilidad de promover la salud de la planta, son importantes para la salud de las raíces. Creemos que cuando se alcanza un estado ecológico en el cual las CMER están bien establecidas y funcionando apropiadamente, da como resultado un agro-ecosistema supresivo de enfermedades o plagas. Un sistema de este tipo fue estudiado en Guatemala. La investigación indicó que: 1) nematodos parásitos son suprimidos en algunas sitios en el Valle Motagua en Guatemala; 2) hongos endofíticos son importantes en este sistema supresivo, y 3) aislados endofíticos de *Fusarium oxysporum* y de *Trichoderma atroviride* suprimen *Radopholus similis* en las raíces del banano.

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Introduction

The idea that susceptible plants can survive in a field heavily infested with an economically important pest or disease because they have acquired high levels of microbial-based suppression is fascinating, but not impossible. The banana is a perennial plant that, under commercial and subsistence production remains in a soil for up to 25 years. This exerts selection pressure not only on pests and diseases but also on beneficial microorganisms in the soil surrounding the root. Under banana growing conditions, the selection of these important groups of organisms out of the total soil biodiversity is a 24 hour, 365 day and multiple year process that leads either to more disease or more antagonistic potential (Sikora 1992, 2002).

The presence of suppressive soils is well known in other crops. In banana it has been overlooked due to the devastating effect of the burrowing nematode, *Radopholus similis*, on banana root health. It has also gone unnoticed because of the multiple and yearly applications of nematicides on banana plantations. This masks the existence of pest suppression and ultimately the detection of this important phenomenon. In other cropping systems, it has been shown that monoculture can lead to the development of high levels of antagonists in the soil and finally to suppression, or a virtual elimination of a pest nematode from the soil (Kerry *et al.* 1982). Rhizosphere and endorhiza specific microbial communities are selected by root exudates (Curl and Truelove 1986, Vilich and Sikora 1998). However, this does not mean that every plant in a field will have the exact same microbial community, as microorganisms are not equally distributed. This is another reason why plants suppressive to a pest have been overlooked.

If we hope to reduce the use of nematicides in banana production, we either need a plant with durable resistance or we need to increase the plant's defences against that pest. Resistance is without doubt a priority, but increasingly aggressive races of *R. similis* are likely to develop under the constant pressures of monoculture. Therefore, additional tools are necessary to sustain yield, protect plant resistance, lower pesticide use and reduce overall costs. We believe a biological system management strategy (Sikora 1997) that integrates an understanding of the cropping system, the pest and the biological factors that can limit infection is the right approach.

Suppression has been equated with "The Edge of Chaos", which is the dynamics of an ecosystem in which individual microbes optimize themselves until they reach sustained fitness (Sikora and Reimann 2004). In our opinion, "The Edge of Chaos" is the norm and not the exception in a banana plantation. However, it does not exist on every plant or it would have been detected long ago. Constant and prolonged selection of rhizosphere specific microbial communities is the rule in and around a banana plant. As stated above, all plants secrete certain exudates that select specific microbial communities in the soil. Therefore, root exudates specific to a banana cultivar select a rhizosphere- and endorhiza-specific microbial community, which is involved in susceptibility, tolerance and/or resistance to pest infection. It must be made clear that these communities can be detrimental or beneficial to the plant with a balance between the two being the most common case. The question is: can we manipulate this state to the benefit of the banana plant?

Questions that banana producers need to ask themselves are:

1. Does suppressiveness exist in or on a banana plant or in banana plantations?
2. Can plant-beneficial nematode-antagonistic microorganisms, living in the rhizosphere or endorhiza, be isolated from the microbial community?
3. Is it possible to detect specific microbes in banana that are highly effective in reducing or suppressing nematodes in banana roots?
4. :Can some form of suppression be established in banana using these beneficial microbes?
5. Can full suppression be achieved either by using a single microorganism or by a multi-trophic inundative system?
6. Is enhancement of banana planting material an effective means of attaining biological system management in the field?

We believe that the answer to all six questions is a firm *yes*! We believe this response to be valid based on past experience in banana research. This has been demonstrated in research results obtained in over 15 years of work on the antagonistic potential of microorganisms for nematode, insect and disease control with banana in cooperative research with ICIPE, IITA and INIBAP. The concepts, methods and results that cover the development of this biological system management approach will not be reviewed here but have been published elsewhere (Sikora and Schuster 1998). As part of the ongoing research to detect suppressive plants and associated microorganisms, a survey of endophytic fungi from banana and the screening of their nematode-antagonistic potential was carried out in Central America in 1998 (Niere *et al.* 1998, Pocasangre *et al.* 2000). Following this study, reports of nematode suppressive soils in Guatemala focused our attention on the Motagua Valley. Such areas, where natural suppression of pathogens occurs, represent an ideal source of potential bio-control organisms (Dicklow *et al.* 1993). To study this area, a research programme was established in Guatemala and Costa Rica with the cooperation of INIBAP, CATIE and BANDEGUA, during the 2001-2002 growing season. The research programme had the following goals:

1. To verify if the three main plant parasitic nematodes affecting banana are suppressed in the banana production districts of the Motagua Valley, Guatemala;
2. To isolate and identify the endophytic fungi present in the root tissue of bananas from these districts;
3. To screen endophytes *in vivo* for antagonistic effects toward *R. similis*.

Materials and methods

Sampling took place in randomly selected plots on one farm per banana growing district in the Motagua Valley of Guatemala; namely on El Real farm in the Panchoy district, Maya in Motagua A, Creek in Motagua B, and Lourdes in Bobos. Material came only from 'Grande naine' (AAA) banana plants that had flowered within 14 days of sampling. Sampling was done according to the method described by Speijer and Gold (1996) and restricted to the area between the base of a mother plant and its follower

sucker. Composite root samples were made up of the excavated roots of ten plants encountered in a plot.

Sampling took place on two days, farms in the Motagua A and Motagua B districts were sampled on 22 October 2001, and farms in the Bobos and Panchoy districts were sampled on 26 October 2001. Root necrosis was assessed by washing the total fresh root sample with tap water, weighing it and dividing the roots into necrotic and healthy roots. The necrotic roots alone were then weighed and the percent of necrotic roots (%NR) calculated using the following formula:

%NR = (fresh weight of necrotic roots/fresh weight of total roots) x 100

As composite samples of ten plants were collected, the weight of functional roots per plant was calculated by dividing the fresh weight of functional roots per composite sample by ten.

The method used to extract plant-parasitic nematodes from the roots was based on the maceration-sieving method described by Speijer and De Waele (1997). To assess the nematode densities in the roots, a 25 g sub-sample of healthy root tissue was removed from each sample. Roots were chopped and macerated in a kitchen blender with approximately 200 ml tap water for 12 s at low speed. The sample was then transferred to four nested screen filters with apertures of 600 μm, 150 μm and two of 45 μm, filtered and washed with tap water. The contents of the final two screens were poured into a clean 1000 ml-graduated cylinder that was filled with tap water. The contents of the cylinder were shaken well and 2 ml removed for counting using a nematode counting slide. All nematodes present in the sub-sample were identified and counted, and the number of nematodes per 100 g root estimated.

To determine and compare the endophytic fungal populations of the four production areas, endophytic fungi were isolated from roots by placing surface sterilized root pieces on selective growth media. Three to 5 cm-long healthy root segments were sterilized in 1.5% NaOCl solution for 5 minutes, washed with sterile water and dried on sterile filter paper. The ends of each root segment were trimmed and the segment cut lengthwise. Five such lengthwise cut pieces, each from a different root segment, were plated on 90 mm Petri plates with 10% potato dextrose agar (PDA) plus antibiotics (4 g PDA, 16 g agar, 150 mg Penicillin G and 75 mg Streptomycin Sulphate per litre distilled water). Plates were stored in a dark incubator at 25°C and regularly checked for fungal growth. All fungal colonies encountered over a six-week period were described, pure cultures produced on fresh 10% and 100% PDA plates, and later identified. A selection of the endophytes recovered was screened for antagonistic effects towards *R. similis*.

Twelve endophyte isolates were selected for screening of antagonistic activity towards *R. similis* on micropropagated banana plantlets of the cultivar 'Grande naine'. Micropropagated plantlets were obtained from a commercial biotech company in San Jose, Costa Rica. The test was set up in a totally randomized block design with seven replications of 14 treatments: 12 fungal isolates and 2 controls. The controls consisted of an entry without fungi, but inoculated with *R. similis* (Control); and the absolute control, free of fungi and nematodes (AC). Since the effect of the fungi on nematode density in plant roots was the primary objective of this test, no controls with plants inoculated exclusively with fungi were used.

The selected endophytic *Fusarium* and *Trichoderma* isolates were grown on 100% PDA plates until they produced sufficient conidia: about 8 days in the case of *Fusarium* spp., and 3-5 days in the case of *Trichoderma* spp. Under a laminar-flow hood, conidia were removed from plates by pouring sterile, distilled water onto the agar surface and gently moving the water over the surface with a cool, flame-sterilized glass scraper. The resulting conidia stock solution was poured through sterile gauze into sterile 50 ml Erlenmeyer flasks and capped with aluminium foil. Conidia concentrations of the stock solutions of each isolate were determined with the help of a Neubauer haemocytometer. For each fungal isolate screened, 300 ml of inoculation suspension with 1 x 10^5 conidia/ml were prepared with calculated volumes of distilled water and stock solution, in 500-ml beakers. In the greenhouse, the roots of micro-propagated 'Grande naine' plantlets ~12 cm tall were immersed and gently shaken in the inoculation solution for 5 minutes, and immediately planted in 1 L pots containing a 1:1 mix of sterile river sand and soil. The roots of the two sets of controls were immersed in distilled water for 5 minutes. All plants were left to harden under greenhouse conditions for two weeks (temperature: 25ºC ± 2ºC, natural light conditions, daily irrigation with tap water, no fertilizer). They were then inoculated with 500 *R. similis* nematodes extracted from carrot disks, provided by T. Moens from CORBANA. After eight weeks, the plants were removed from pots and shoot and root fresh weight recorded. Nematodes were extracted from roots according to the method described by Speijer and De Waele (1997). Nematodes in two 3 ml aliquots per plant were counted and the total number of nematodes per 100 g root was calculated.

Results

The total number of nematodes recovered per 100 g root differed significantly from farm to farm (Figure 1), and supported the designation of El Real and Maya farms as suppressive, of Creek farm as moderately suppressive and of Lourdes farm as

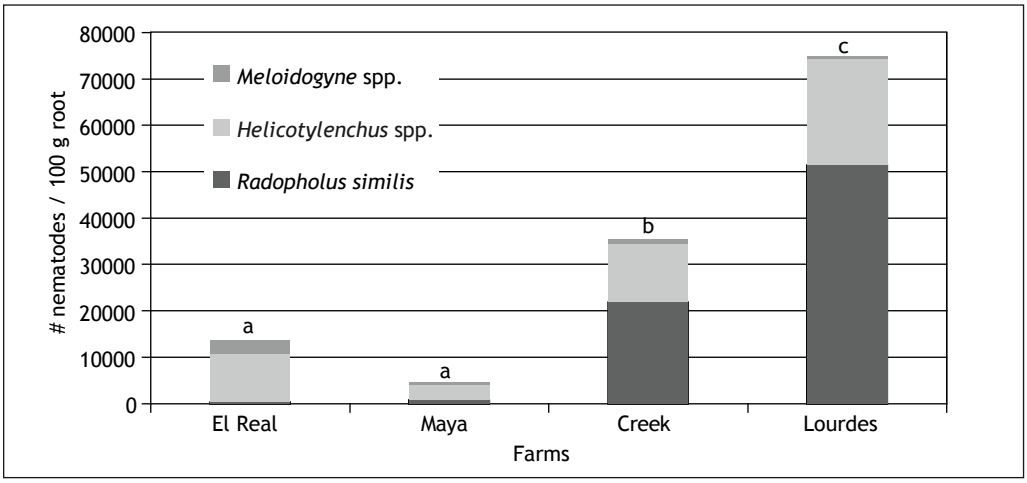


Figure 1. Total number of nematodes recovered from banana roots from sampled farms in October 2001. Columns with different letters are significantly different at P ≤ 0.05, using the one-way ANOVA test in StatsGraphics Plus 3.1.

non-suppressive. *Meloidogyne* spp. populations neither differed significantly between farms, nor did their size indicate an important infestation (Table 1). The same can be said for the *Helicotylenchus* spp. populations, though their numbers were significantly greater on the Lourdes farm. However no suppression was expected nor observed in this area, so the results support the assumption that suppression is only present in certain areas of the Motagua Valley. Root health indices verify that the roots of the suppressive plants from El Real and Maya farms are larger and significantly less necrotic than those from Creek or Lourdes farms.

Table 1. Number of nematodes recovered from banana roots from sampled farms in October 2001[1] and root health indices.

Origin (Farm)[2]	Number of nematodes recovered per 100 g root[3]			Root health indices	
	Radopholus similis	*Helicotylenchus* spp.	*Meloidogyne* spp.	Weight of functional root (g)	% necrotic root
El Real	400a	10 500a	2 800a	90b	3a
Maya	800a	3 200a	600a	132c	4a
Creek	21 800b	12 600a	1 000a	72ab	12b
Lourdes	51 400c	22 900b	500a	69a	22c

1 Numbers followed by the same letter in a column are not different according to the one-way ANOVA test in StatsGraphics Plus 3.01 ($P \leq 0.05$).

2 Farms are presented in order of suppressiveness: El Real – suppressive (SS); Maya – suppressive (SS); Creek – moderately-suppressive (MS); and Lourdes – non-suppressive (NS).

3 All life stages of nematodes were included in the count and only functional roots were used for nematode extraction.

Table 2. Genus and number of fungi and their proportion of the population isolated from banana roots from four farms.

Genus of fungal isolate	Sampled farms and their suppressive status							
	El Real - SS1		Maya - SS		Creek - MS		Lourdes - NS	
		(%)		(%)		(%)		(%)
Fusarium	2	5	22	41	54	61	53	69
Trichoderma	2	5	11	20	7	8	4	5
Penicillium	2	5	4	7	3	3	4	5
No ID or Lost[2]	8	20	10	19	24	27	16	21
Arthrobotrus	1	3	-	-				
Aspergills	-	-	1	2				
Basiptospora	-	-	1	2				
Candida	4	10	-	-				
Chrysosporium	12	30	-	-				
Gleosporium	1	3	2	4				
Gliocephalis	1	3	-	-				
Gliodadum	1	3	-	-				
Gliodium	1	3	-	-				
Paecilomyces	-	-	1	-				
Torula / Wallemia	-	-	1	-				
Trichotechium	3	8	1	2				
Tritirachium	1	3	-	-				
Verticillium	1	3	-	-				
Total	40	(100)	54	(100)	88	(100)	77	(100)

Further identification of isolates from Creek and Lourdes was not carried out, as no nematode suppression was observed in these farms

1 SS: Suppressive; MS: Moderately suppressive; NS: Not suppressive. 2 Isolates lost to bacterial contamination were considered lost and not identified.

The predominant genera identified were *Fusarium* and *Trichoderma* (Table 2). Though more *Chrysosporium*, *Candida* and *Trichotechium* were recovered from roots from El Real farm, these genera are known saprophytes, and were not considered endophytic. Only *Fusarium* and *Trichoderma* isolates that demonstrated good growth *in vitro* were selected for screening.

The screening of 12 selected endophytes revealed that all had some antagonistic effects on the reproduction of *R. similis* in the roots of 'Grande naine' plantlets over a two-month period (Table 3). Additionally, most endophytes positively influenced plant growth, as indicated by increased root and shoot fresh weight. The four most effective endophytes, the *Fusarium* isolates MF-25 and MF-40, and the *Trichoderma* isolates MT-20 and ET-35, were later identified as *Fusarium oxysporum* and *Trichoderma atroviride* isolates, by Dr Helgard Nirenberg from the BBA, in Berlin, Germany.

Table 3. Screening of 12 fungal endophyte isolates for antagonistic activity towards *Radopholus similis* on micropropagated plantlets of the cultivar 'Grande naine' (AAA)[1].

Isolate code	Number of *R. similis*[2]	Reduction %	Root weight g[3]	Shoot weight g[4]
Control[5]	18 694 a	-	8.3 b	20.0 bc
MF-50	14 707 a	-21	10.8 ab	17.9 c
MF-22	14 025 ab	-25	11.3 ab	19.9 bc
MF-30	12 931 ab	-31	13.3 ab	19.1 bc
MF-10	11 171 abc	-40	10.3 ab	22.7 abc
EF-39	7 890 bdc	-58	14.5 a	28.3 a
MF-49	7 417 dc	-60	14.2 a	26.3 abc
MF-6	6 764 dc	-64	10.3 ab	25.4 ab
MF-12	6 601 dc	-65	12.4 a	25.2 abc
MF-40	5 505 de	-71	13.5 ab	27.5 ab
ET-35	4 856 de	-74	14.8 a	27.6 ab
MF-25	4 793 de	-74	14.1 a	28.3 a
MT-20	3 271 e	-83	14.0 a	24.9 abc
AC[6]	-	-	12.6 ab	26.5 abc

[1] Numbers followed by the same letter in a column are not different according to the Tukey test ($P \leq 0.05$) in SAS.

[2] Number of vermiform *R. similis* nematodes/100 g root recovered from root system at time of evaluation (2 months after inoculation with 500 *R. similis*).

[3] Root weight: fresh weight of root system of plant at time of evaluation.

[4] Shoot weight includes the fresh weight of corm, pseudostem and leaves of plants at time of evaluation.

[5] Control inoculated with *R. similis*, but without fungal endophyte spores.

[6] AC: absolute control (no endophytes, no nematodes).

Discussion

This latest study confirms that nematode suppression exists in banana plants and in banana plantations. Nematodes are strongly suppressed in the Panchoy and Motagua A districts in the Motagua Valley. Additionally, we managed to isolate a variety of plant-beneficial nematode-antagonistic microorganisms living in the endorhiza. Among

them, *Fusarium* and *Trichoderma* spp. were most commonly encountered endophytes. All those endophytes screened for antagonistic effects were effective in reducing or suppressing *R similis* in banana roots. *F. oxysporum* and *T. atroviride* isolates exhibit strong antagonistic activity towards *R. similis*. This is the first time this type of behaviour has been observed for *Trichoderma*, confirming its biological control potential in banana. We were able to establish suppressiveness in micropropagated banana plantlets by inoculating them with conidia of these fungi before planting, indicating that this enhancement of banana planting material can be an effective means of attaining biological system management in the field. While micropropagated plants provide producers with guaranteed nematode-free planting material, they are also free of non-pathogenic microorganisms such as beneficial endophytic microorganisms (Pereira *et al.* 1999). This makes them an easy target for soil-borne diseases and nematodes. Therefore, the use of endophytic fungi as biocontrol agents of *R. similis* and other plant-parasitic nematodes has great potential on such planting material. By inoculating micropropagated plants with endophytes before planting, they are provided with tailored and "on site" protection. The use of endophytes also eliminates a major problem associated with the use of soil microbial biocontrol agents to control nematodes: the inoculation of "problem" soils with biocontrol organisms (Rodríguez-Kábana 1991). By placing the biocontrol agent directly inside the root, it is at least partially protected from other microorganisms present in the soil. This ensures a high density of biocontrol activity. Nevertheless, the non-pathogenic nature of the promising biocontrol endophytes toward banana and other crop species has to be investigated before field experiments can be undertaken.

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Effect of arbuscular mycorrhizal fungi (amf) and other rhizosphere microorganisms on development of the banana root system

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Abstract

Despite its influence on plant growth, root architecture has not been studied as much as it should be. Root architecture and morphology provide a lot of useful information about plant species and their ability to take up nutrients from the soil. Energy flow can also be examined in these studies. Several soil factors, such as nutrients and microorganisms, greatly affect root development. Soil microbiota interactions, especially with those organisms that colonize the rhizosphere, have also been reported to affect plant health and soil quality. Microbiota help the host plant under limiting conditions provoked by abiotic and/or biotic factors. Arbuscular mycorrhizal fungi (AMF) and plant-growth promoting bacteria (PGPBs) are among these beneficial rhizosphere microbes. Mycorrhizal symbiosis significantly improves plant nutrition under low fertility soil conditions. Mycorrhizal hyphae are more efficient than roots alone in nutrient uptake, since they increase the root absorption area. Recently, it has been reported that AMF are even able to change root architecture. Bananas (*Musa acuminata* Colla AAA) show a great ability to establish symbiotic associations with both AMF and PGPBs. Two experiments were conducted: one to evaluate the effect of AMF (*Glomus intraradices)* on banana root architecture of micropropagated 'Grande Naine' plantlets, in an 80-day sequential study. The second experiment was conducted to determine the effect of the interaction between AMF and PGPBs on root morphology. In this case, three micropropagated banana cultivars ('Grande Naine', 'Dwarf Cavendish' and ITC #1283 from the INIBAP gene bank), were inoculated with *Glomus manihotis* and with a mix of rhizosphere *Bacillus* spp. From these experiments it can be concluded that the rhizosphere microorganisms studied (AMF and PGPBs), promote positive banana root system development that leads to an improvement in plant nutrition and health. Thus, these microorganisms could be used in future alternative biotechnologies for banana production systems.

Resumen - Efecto de los hongos micorrícicos arbusculares (HMA) y de otros microorganismos de la rizosfera en el desarrollo del sistema radical del banano

La arquitectura de las raíces ha sido poco estudiada en los trabajos de fisiología vegetal, a pesar de su gran importancia para el desarrollo de las plantas. Conocer la arquitectura y morfología de un sistema radical, nos proporciona información útil acerca de la especie en estudio, y su capacidad para absorber nutrientes del suelo. El flujo de energía también puede ser espinado en estos estudios. Existen muchos factores del suelo, tales como los nutrientes y los microorganismos que influyen en el desarrollo de la raíz. Las interacciones microbianas en la rizosfera inciden notablemente en la salud vegetal y calidad del suelo. Las interacciones de la microbiota del suelo, especialmente con los organismos que colonizan la rizosfera, han sido reportadas influenciando la salud y calidad de los suelos. La microbiota ayuda a la planta hospedera a adaptarse a situaciones de estrés de tipo hídrico o nutricional e incluso, a aquéllas originadas por patógenos del sistema radical. Los hongos formadores de micorrizas arbusculares (MA) y las bacterias promotoras del crecimiento vegetal (PGPBs), pertenecen al grupo de microorganismos que cohabitan en el entorno rizosférico. La simbiosis micorrícica mejora significativamente la nutrición en suelos de baja fertilidad. Las hifas de estos hongos son más eficaces en la captación de nutrientes que las propias raíces, incrementando el área de absorción radical. Recientemente se sabe que los hongos micorrícicos son capaces de alterar

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la arquitectura de la raíz y propiciar una mayor eficiencia para la toma de nutrientes en las plantas micorrizadas. El banano (*Musa acuminata* Colla AAA) muestra una gran capacidad para beneficiarse de la simbiosis micorrícica y de la actividad de ciertas PGPBs. Se desarrollaron dos experimentos: uno para comprobar el efecto de los hongos MA *Glomus intraradices* ,sobre la arquitectura radical del banano (vitroplantas de 'Gran Enana'), evaluando el efecto a lo largo de 80 días. El segundo experimento, tuvo como objetivo determinar el efecto de la interacción entre hongos MA y PGPBs sobre la morfología radicalen tres cultivares de banano micropropagado ('Gran Enana', 'Pequeña Enana' y el ITC #1283 del INIBAP), tratados con inóculo de *Glomus manihotis* y un cóctel de la bacteria rizosférica *Bacillus* spp. Ambos trabajos nos permiten concluir que los microorganismos rizosféricos estudiados (hongos MA y PGPBs), promueven el desarrollo del sistema radical del banano, lo cual mejora la nutrición y salud de las plantas. Se propone su utilización en los sistemas de producción del banano como una alternativa biotecnológica de futuro.

Introduction

Despite its influence on plant growth, root architecture has not been studied as much as it should be. Root architecture and morphology provide a lot of useful information about plant species and their ability to take up nutrients from the soil. Energy costs, involved in this nutrient uptake as a consequence of environmental adaptation, can also be examined in these studies. Indeed, the successful establishment of some crops depends on the adequate development of the root system of the plant. Survival rates during the *post vitro* phase of micropropagated material can often be reduced due to poor root systems (Hooker *et al.* 1994).

Among the environmental factors involved in root development (for example, soil structure, temperature, water, nutrient availability), communities of soil microbiota must be considered. Soil microbiota interactions, especially with those organisms that colonize the rhizosphere (the soil zone influenced by roots through the release of substrates that affect microbial activity), have also been reported to affect plant health and soil quality. Root-associated microbiota help the host plant under limiting conditions caused by abiotic (water, nutrition) and/or biotic (soil-borne pathogens) factors. Arbuscular mycorrhizal fungi (AMF) and plant-growth promoting bacteria (PGPBs) are among these beneficial rhizosphere microbes. Mycorrhizal symbiosis significantly improves plant nutrition under low soil fertility. Mycorrhizal hyphae are more efficient than roots alone in nutrient uptake, especially of elements with low mobility in soil such as phosphorus (P). Some studies have also reported changes in phytohormone balance (Drüge and Schönbeck 1992). Recently, it has been reported that AMF are even able to change root architecture. These changes lead to more efficient nutrient uptake in mycorrhizal plants (Hooker and Atkinson 1992).

Additionally, some rhizosphere bacteria promote plant development and seed germination. This ability should be given serious attention, because micropropagated material is being used increasingly in commercial crops. PGPBs, as well as AMF, are able to enhance biomass production during the first stages of crops and can contribute to plant adaptation from the *in vitro* to the *post vitro* phase (Carletti 2000). Direct mechanisms such as nutrient solubility or fixation and siderophore or phytohormone production have been reported for some bacterial strains. Siderophores are considered relevant factors in plant nutrition, since they can act as an Fe^{3+}-chelating agent. It is known that some auxin-type phytohormones (indol-acetic acid, IAA) produced by PGPB strains,

promote lateral and primary root elongation and production, with positive effects on root system development (Kloepper *et al.* 1989 & 1991).

Since they share common microhabitats, AMF and PGPBs must interact during the colonization process and/or as rhizosphere microorganisms (Barea 1997). It is accepted that soil microbial communities, in general and especially PGPBs can have a great influence on the establishment of mycorrhizal symbiosis. In the same way, AMF can affect PGPB populations in roots. Thus, microbial interactions should be taken into account in studies on both the single and cooperative effects of these organisms on root systems (Barea 1997, 2000). Banana (*Musa acuminata* Colla AAA), is a monocotyledonous herbaceous species, that shows a great ability to establish mycorrhizal symbiosis (Jaizme-Vega *et al.* 1991, 1998, 2002, Rizzardi 1990, Declerck *et al.* 1994, Yano-Melo *et al.* 1999). Banana-PGPB associations have also been reported as beneficial (Rodríguez-Romero *et al.* 2003, Jaizme-Vega *et al*. 2004). However, despite the great number of studies on banana, there are not many references concerning the effect of rhizosphere microbiota on banana root architecture (Jaizme-Vega *et al.* 1994; García-Pérez and Jaizme-Vega 1997) and their consequences on plant growth and health.

This study examines the effects of AMF and PGPBs and their interaction on the banana root system. Two different experiments were conducted. The first determines the effect of AMF on root morphology of 'Grande Naine'. The second analysed the interaction of both microorganisms (AMF and PGPBs), on three banana cultivars ('Grande naine', 'Dwarf Cavendish' and a somaclonal variant of SH 3436-9 with ITC1283).

Materials and methods

Experiment 1: AMF – 'Grande naine'

Host plants, AM fungi and experimental conditions

Micropropagated banana *(Musa acuminata* Colla) cv. 'Grande naine' plantlets were used. After washing with fresh water to remove agar, they were transplanted from *vitro* flasks to two 24 L black polyethylene plastic containers (20 plants/container) filled with a sterilized substrate (3:1) of quartz sand and soil with a low concentration of phosphorus (12.7 mg/kg Olsen). Half the plants were inoculated with *Glomus intraradices* Schenck & Smith, cultured under Sudan grass (*Sorghum bicolor* L. var. *sudanense* Moench). AMF inoculum consisted of 25 g per container of rhizosphere soil containing external mycelium and infected root fragments obtained from pot cultures. Plants were maintained under greenhouse conditions (24ºC, 70% RH), receiving 600 ml of nutrient solution without phosphorus, per week (Hewitt 1952).

Assessment of variables and analyses

Four plants from each of the two treatments were sampled at 30, 40, 50, 65 and 80 days after transplanting and assessed for changes in biomass and morphological development. At each harvest, mycorrhizal root colonization was evaluated microscopically after staining with 0.05% trypan blue in lactic acid (Phillips and Hayman 1970) using the procedure described by Koske and Gemma (1989). The percentage of root system colonization was quantified using the grid intersect method (Giovannetti and Mosse 1980). At each harvest the following parameters were determined: number and length

of adventitious roots, number and length of lateral roots, lateral root frequency (represented by the number of roots of order n, divided by the length of roots of order n-1) and the percentage of roots present in each order. All data were compared by ANOVA and means were separated by Tukey's test ($P \leq 0.05$). All statistical analyses were performed with Systat 7.0.

Experiment 2: AMF - PGPBs - 'Grande naine' / 'Dwarf Cavendish' / ITC1283

Host plants, AM fungi and plant growth promoting bacteria

Micropropagated banana plantlets from three cultivars ('Grande naine', 'Dwarf Cavendish' and a somaclonal variant of SH 3436-9 from Cuba with ITC1283) were used. After washing with fresh water to remove agar, plants were transplanted to 24 L black polyethylene (PE) plastic containers (24 plants/container) filled with a sterilized substrate (1:1:1) made of soil, volcanic ash and peat TKS®1-Instant (Sphagnum-Torf® Klasman-Deilmann GmbH, Germany). The AMF was *Glomus manihotis*, from Colombia, cultured under Sudan grass (*Sorghum bicolor* L. var. *sudanense* Moench), with a 78% colonization index. AMF inoculum consisted of 1.5 kg per container of rhizosphere soil containing external mycelium and infected root fragments obtained from pot-cultures. For each banana cultivar half plants were inoculated with AMF. A mix of *Bacillus* spp., three strains (INR 7, T4 and IN 937 b) isolated and identified by Dr. Kloepper (Alabama, USA), were kept in TSB (Tryptone Soy Broth) with 20% glycerol. Bacterial inoculums consisted of a sterilized saline (0.85% NaCl) suspension containing an equal amount of each strain. Colonies were obtained after culturing onto Petri dishes with TSA (Tryptone Soy Agar) for two weeks. Bacterial suspension, containing approximately 10^8 colony forming units (CFU)/ml was added 20 days after transplanting. For each cultivar and treatment (mycorrhizal and non mycorrhizal), 20 ml were added to half of the plants

Experimental conditions and assessment of variables

Plants were kept under controlled conditions during the 60-day hardening phase (90% RH and 25ºC). During this period, plants were watered properly. At the end of the hardening phase, plants were transferred to individual 3 L black PE pots filled with a sterilized substrate (1:1:1) made of soil, volcanic ash and peat TKS®1-Instant (Sphagnum-Torf® Klasman-Deilmann GmbH, Germany). Plants were arranged in a random design under greenhouse conditions (75% RH and 30ºC). Fertilization was conducted following a programme similar to those of commercial nurseries for banana. Twice a month a foliar fertilizer, Wuxal® Super AA-8-8-6 (3%), was added. Four assessments were made at 30, 85, 135 and 185 days after bacterial inoculation. At each assessment the following parameters were measured on 6 plants in each cultivar and treatment: number of adventitious roots and shoot fresh weight (g). Leaf area (cm^2) was measured using a leaf area meter (LiCOR, Inc Lincoln, Nebraska, USA. Mod. Li-3100). The mycorrhizal colonization index was determined at each assessment. All data were compared by ANOVA and means were separated by Tukey's test ($P \leq 0.05$). All statistical analyses were performed with Systat 7.0.

Results

Experiment 1: AMF - 'Grande naine'

All the micropropagated banana plants used in this experiment were similar in size at inoculation. Fresh weight of the aerial part of the mycorrhizal plants increased in most of the harvests. Differences between the inoculated and control plants were more marked at 30 and 80 days, when the values were significantly higher in *G. intraradices* inoculated plants (Figure 1). Mycorrhizal root infection was absent from control plants, but well established in the mycorrhizal plants. At the first assessment (30 days after inoculation) mycorrhizal colonization was 70%, at the second one (20 days later) colonization was 80%, and increased to 100% from 50 days after inoculation (Figure 2).

The root system of micropropagated *Musa* plants consists of a series of adventitious roots that develop directly from the corm (subterranean structure). These roots branched in first order laterals, from which second order laterals developed. Mycorrhizal banana plants showed a denser root system than the control plants. Adventitious root number increased over time in both mycorrhizal and non-treated plants, although values of mycorrhizal plants were always significantly higher (Figure 3). In the case of adventitious root length, mycorrhizal plants showed lower values than non-treated plants, between the second and the third assessment, although differences were not significant (Figure 4). The degree of branching of adventitious roots (the number of branches per primary axis) increased over time in AMF treatments. At 30, 65 and 80 days post inoculation there were significant differences between treatments. Adventitious root branching was highest for the AMF treatment at day 30. The intensity of branching of first order laterals was not determined in this study (Figure 5).

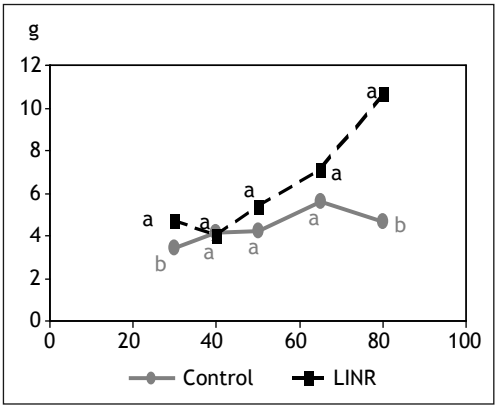


Figure 1: Effect of *Glomus intraradices* (LINR) on shoot fresh weight of micropropagated banana plants cv. 'Grande naine'. For each time, the data followed by the same letter are not significantly different according to Tukey's test (P≤0.050).

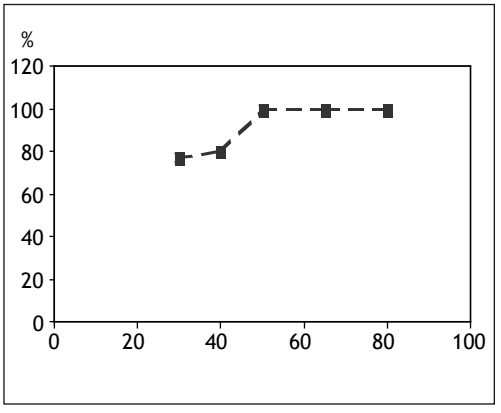


Figure 2: Variation with time of root infection percentage in *Glomus intraradices* (LINR) in micropropagated banana plants cv. 'Grande naine'.

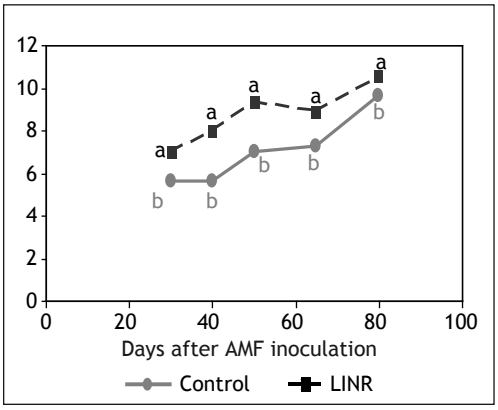


Figure 3: Variation with time of adventitious root number in *Glomus intraradices* (LINR) and control micropropagated banana plants cv. 'Grande naine'. For each time, the data followed by the same letter are not significantly different according to Tukey's test (P≤0.050).

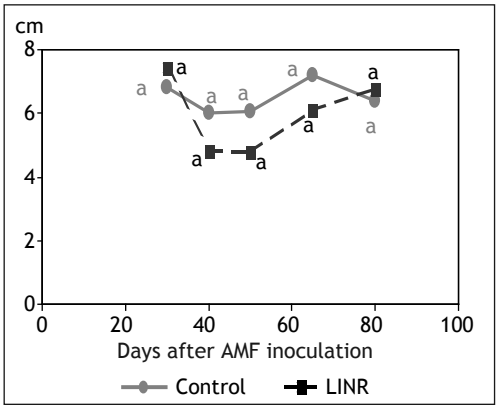


Figure 4: Variation with time of adventitious root length in *Glomus intraradices* (LINR) and control micropropagated banana plants cv. 'Grande naine'. For each time, the data followed by the same letter are not significantly different according to Tukey's test (P≤0.050).

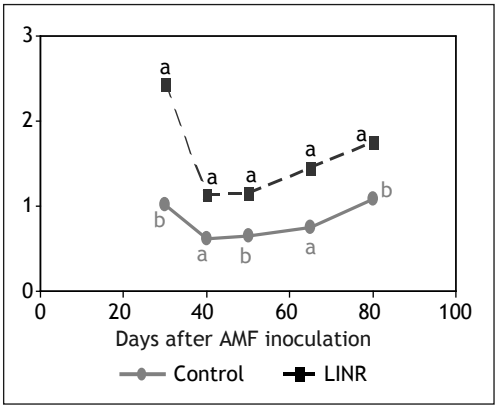


Figure 5: Variation with time of adventitious root branching in *Glomus intraradices* (LINR) and control micropropagated banana plants cv. 'Grande naine'. For each time, the data followed by the same letter are not significantly different according to Tukey's test (P≤0.050).

Experiment 2: AMF - PGPBs- 'Grande naine', 'Dwarf Cavendish', ITC1283

Combined inoculation (*G. manihotis*+ *Bacillus* spp.) of plants resulted in an increase in plant development compared with single inoculation of either AMF or PGPB. All physical parameters were higher in plants treated with both microorganisms. However, for some physical parameters single inoculation with *Bacillus* spp. or AMF were statistically identical with non-treated plants. Nevertheless, each banana cultivar showed a different trend.

In the case of 'Grande naine' cultivar, significant differences were highest 135 days after bacteria inoculation at which time, plants treated with AMF and PGPB, showed significant increases in physical development (Figure 6). For 'Dwarf Cavendish' plants, highest significant differences in adventitious root number were detected 135 days after *Bacillus* application when *Bacillus*-treated plants showed a greater number of adventitious roots. Significant increases in leaf area and fresh weight of the aerial parts were also registered for this treatment at the first and second assessments (Figure 7). INIBAP selection ITC1283 showed a generally good response after inoculation with both organisms. In this case, significant increases in plant development (leaf area and shoot fresh weight) could be detected at the first assessment. Plants from this cultivar colonised with *G. manihotis* were able to increase adventitious root number, leaf area and shoot fresh weight at the end of the experiment (Figure 8).

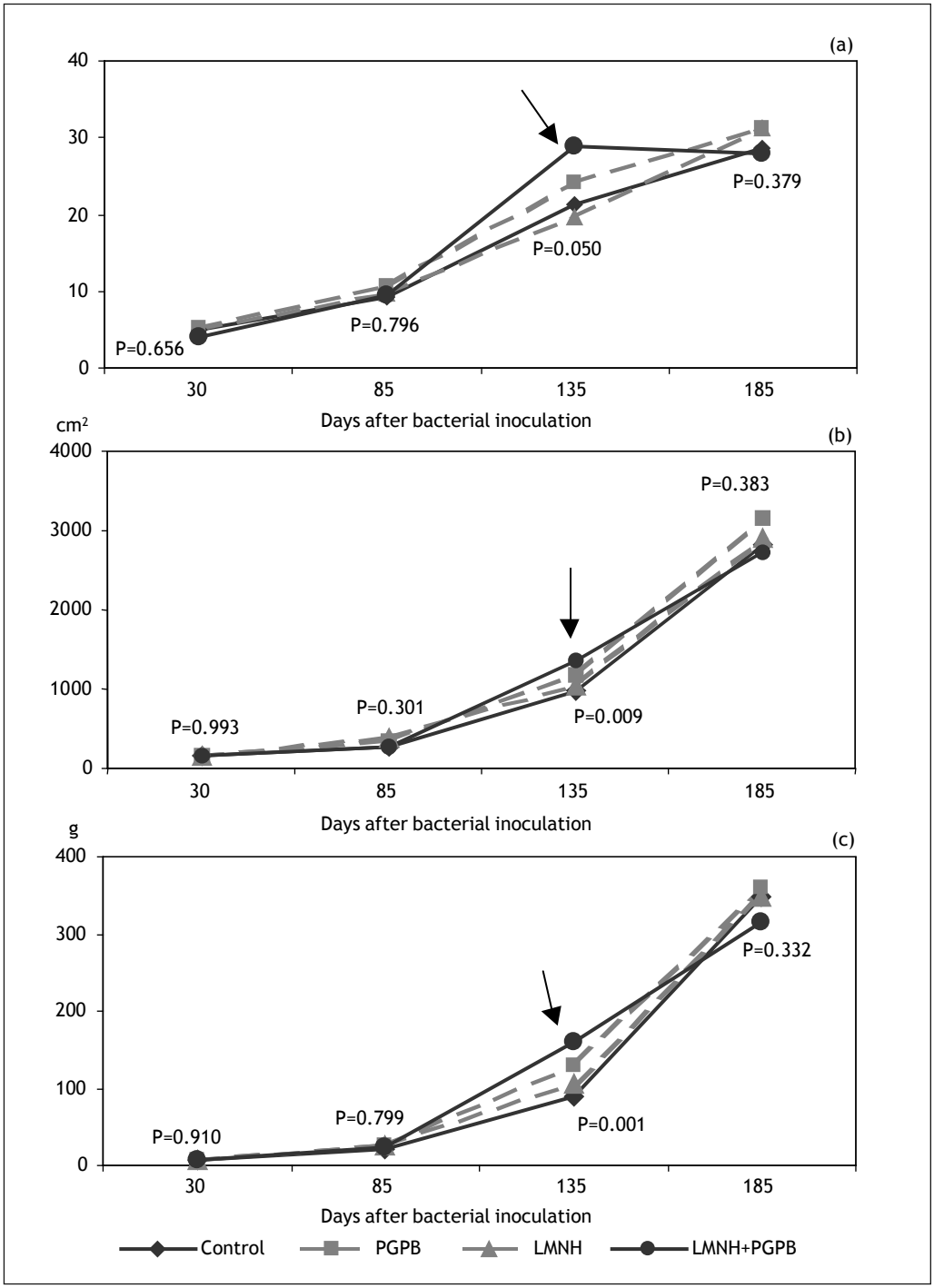


Figure 6: Effect of combined inoculation of *Glomus manihotis* (LMNH) and *Bacillus* (PGPB) on (a) adventitious root number, (b) leaf area and (c) shoot fresh weight on 'Grande naine' micropropagated plants.

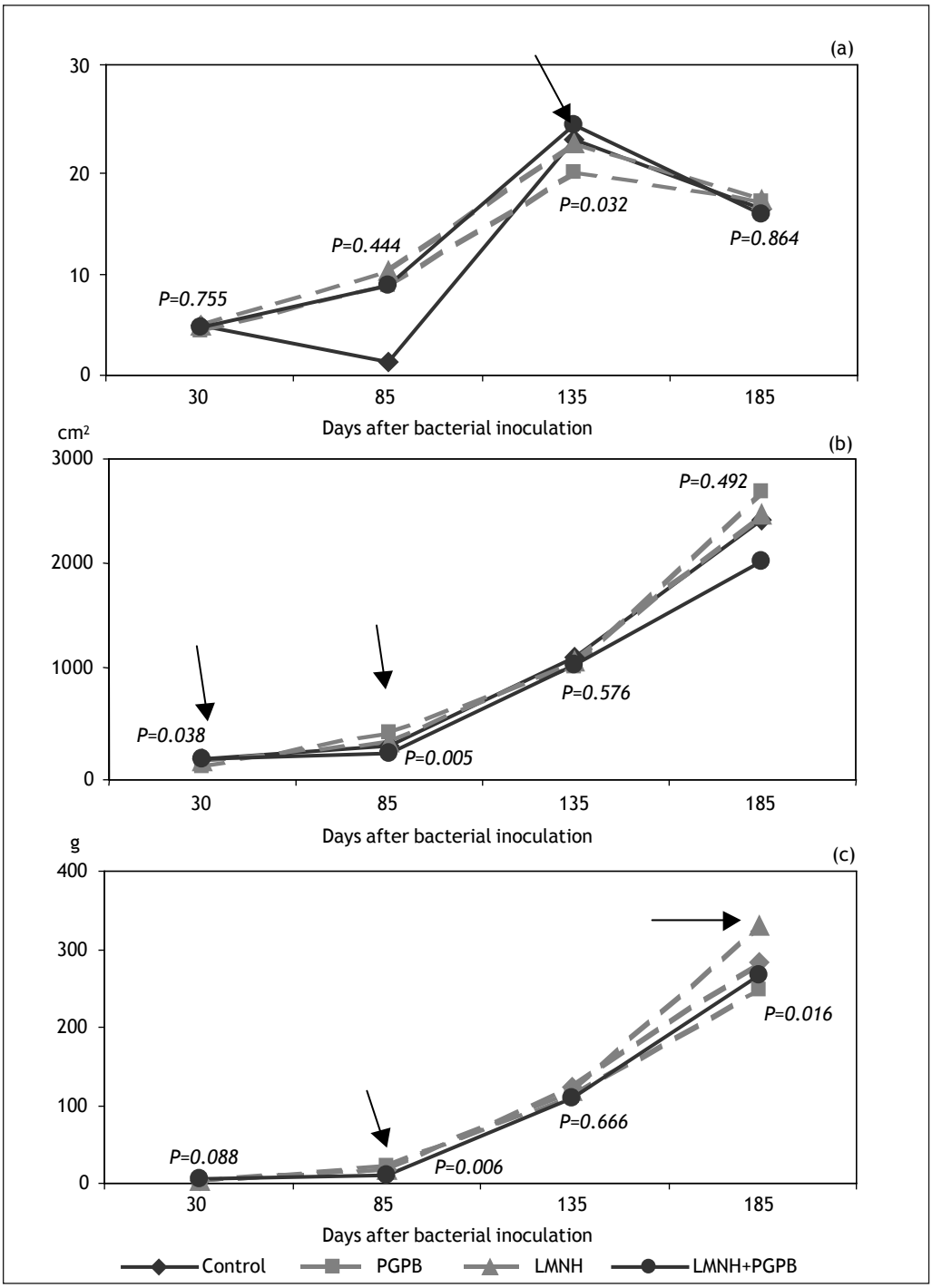


Figure 7: Effect of combined inoculation of *Glomus manihotis* (LMNH) and *Bacillus* (PGPB) on (a) adventitious root number, (b) leaf area and (c) shoot fresh weight on 'Dwarf Cavendish' micropropagated plants.

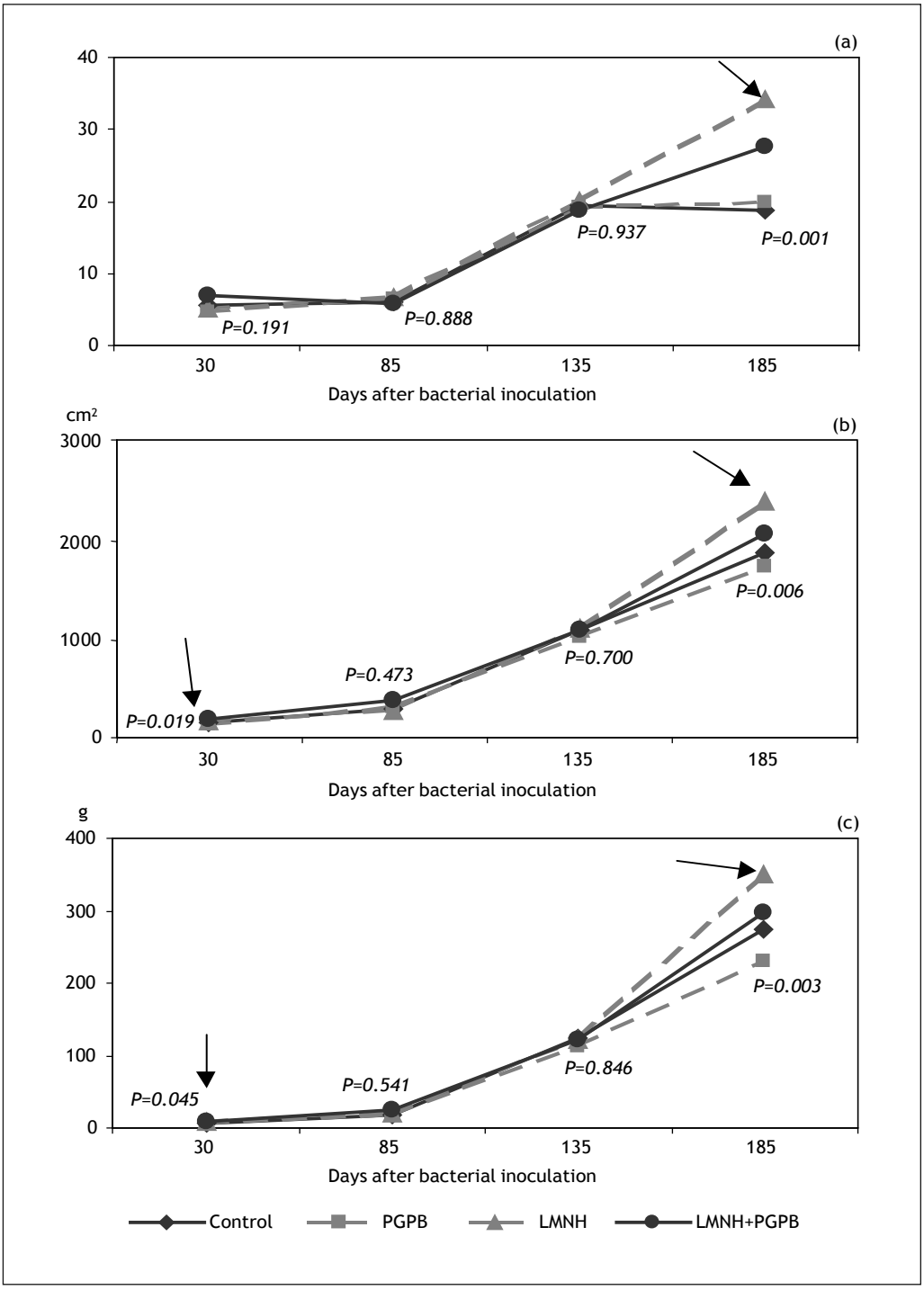


Figure 8: Effect of combined inoculation of *Glomus manihotis* (LMNH) and *Bacillus* (PGPB) on (a) adventitious root number, (b) leaf area and (c) shoot fresh weight on ITC1283 micropropagated plants.

It can be said in general, that all cultivars, except ITC1283, increased adventitious root number after the inoculation with both microorganisms. Concerning mycorrhizal colonization, all banana cultivars showed an acceptable root colonization index. No significant difference due to bacterial inoculation could be detected (Figures 9, 10 and 11).

Discussion

Mycorrhizal banana plants had root systems with more numerous and branched adventitious roots than those of the control plants. No significant differences between adventitious root length of mycorrhizal and control plants were observed at the first assessment, 30 days after transplanting, when the degree of colonization was still relatively low (about 30%). Later on, when infection increased, adventitious root length was always lower in mycorrhizae, and significantly lower at 40 and 50 days after transplanting. At 65 days after transplanting, mean adventitious root length was about the same in mycorrhizal and control plants. The lack of difference in adventitious root length between mycorrhizae and control plants at the last sample, 80 days after transplanting, could be partly explained by senescence processes in both treatments.

The reduction in length of adventitious roots was accompanied by an increase in their number, as observed in another endomycorrhizal system in which a monocotyledon was involved i.e. *Allium porrum* + *Glomus E3, Ornithogalum umbellatum* + *G. fasciculatum* (Berta *et al.* 1990, 1993). Lateral root length did not change in mycorrhizal banana plants, even if there was a trend towards an increase. The same occurred in *Platanus acerifolia* (Tisserant *et al.* 1992), in *Populus* sp. and *Prunus cerasifera.* Lateral roots were longer in mycorrhizal than in the control plants (Hooker *et al.* 1992, Berta *et al.* 1995) whereas in *Vitis vinifera* and *AIIium porrum* lateral roots were shorter in the mycorrhizae plants (Schellenbaum *et al.* 1991, Berta *et al.* 1993).

The most important effect of AMF infection on the root system of banana plants was an increase of adventitious root branching. This increase, together with the increase in number of adventitious roots, led to a denser root system, as observed in other endomycorrhizal systems, though effects may be different (Berta *et al.* 1993). It is generally assumed that a denser root system has a greater absorbing power than an elongated one and is typical of plants growing in nutrient rich soils (Glinski and Lipiec 1990). The extensive network of external mycelium, with its absorbing power and explorative functions, in addition to the denser root system, could improve the "growth effect" characteristic of mycorrhizal plants. Moreover, a very branched root system is particularly useful for banana plants, as they are easily uprooted by winds, which are a frequent problem in many cropping areas of the world.

Inoculation with both microorganisms lead to a positive effect on banana growth in all cases. Significant increases were detected compared with single inoculated treatments or non-treated plants. It can be assumed then, that under our experimental conditions, this association should be considered a case of synergism. Each banana cultivar showed a particular trend (Table 1). 'Grande naine' plantlets showed significant effects due to the combined treatment, at 135 days after inoculation. Those effects were mainly detected in adventitious root number. 'Dwarf Cavendish' plants had a similar response to the 'Grande naine' cultivar. On the other hand, ITC1283 showed significant increases in

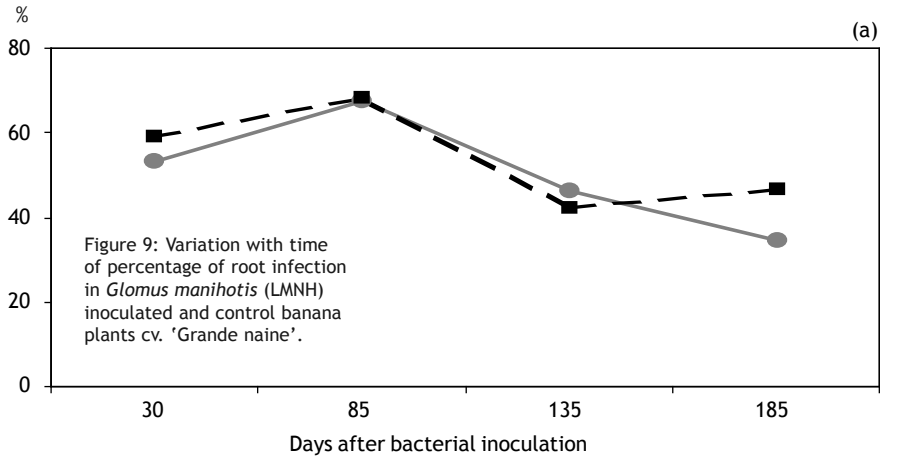


Figure 9: Variation with time of percentage of root infection in *Glomus manihotis* (LMNH) inoculated and control banana plants cv. 'Grande naine'.

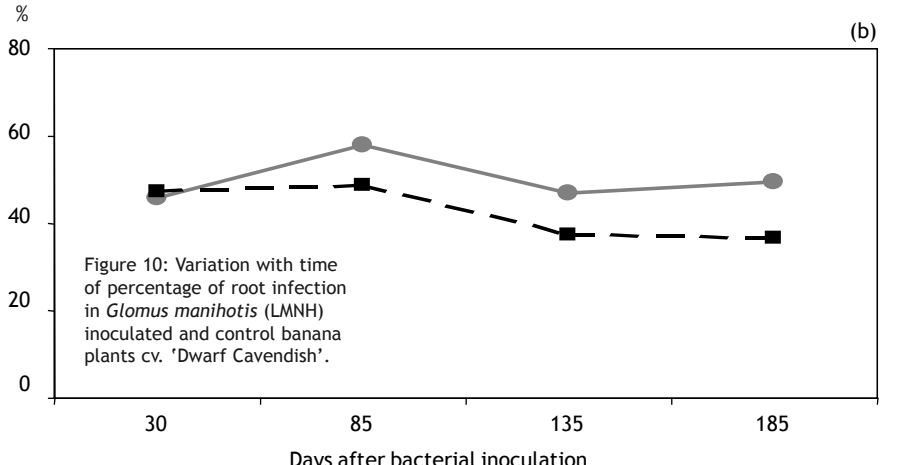


Figure 10: Variation with time of percentage of root infection in *Glomus manihotis* (LMNH) inoculated and control banana plants cv. 'Dwarf Cavendish'.

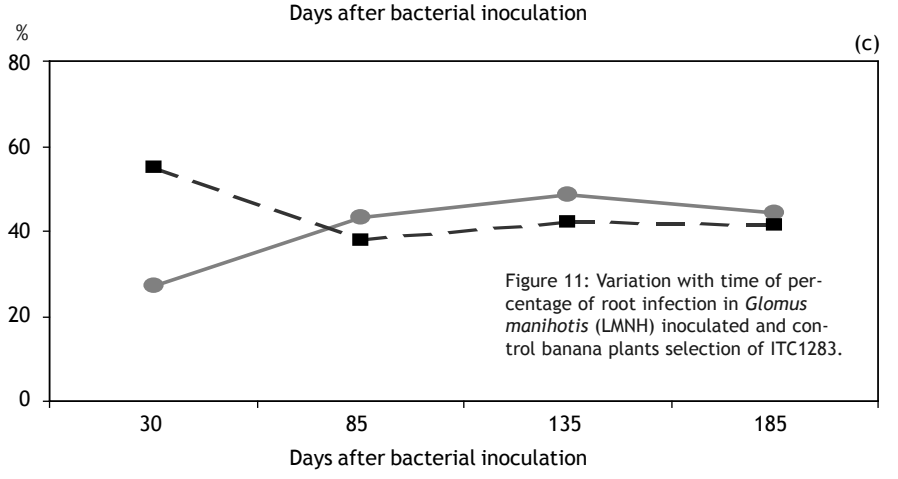


Figure 11: Variation with time of percentage of root infection in *Glomus manihotis* (LMNH) inoculated and control banana plants selection of ITC1283.



Table 1. The significant (p<0.05) responses of young banana plants, grown *post vitro*, to either the inoculation of *Glomus manihotis* (LMNH), or the addition of a mix of *Bacillus* spp. plant growth promoting bacteria (PGPB), or to a combination of *G. manihotis* and *Bacillus* spp. (LMNH+PGPB) during the first 185 days after inoculation.

Cultivar	Root number/plant	Leaf area	Shoot fresh weight
		30 days after bacterial inoculation	
Grande naine	-	-	-
Dwarf Cavendish	-	LMNH+PGPB	-
INIBAP ITC1283	-	LMNH+PGPB	LMNH+PGPB
		85 days after bacterial inoculation	
Grande naine	-	-	-
Dwarf Cavendish	-	PGPB	PGPB
ITC1283	-	-	-
		135 days after bacterial inoculation	
Grande naine	LMNH+PGPB	LMNH+PGPB	LMNH+PGPB
Dwarf Cavendish	LMNH+PGPB	-	-
ITC1283	-	-	-
		185 days after bacterial inoculation	
Grande naine	-	-	-
Dwarf Cavendish	-	-	LMNH
ITC1283	LMNH	LMNH	LMNH

- = no significant response in this combination of age and cultivar.

adventitious root number at the end of the experiment and just for plants with mycorrhizae alone.

Our results did not detect a direct effect of PGPBs on banana root morphology. Significant increases in adventitious root number only occur in mycorrhizal treated plants (mycorrhizae alone or combined with PGPB) in all cultivars. There are few references concerning the effects of PGPB on root morphology. Williamson and Jones (1973) found certain changes in root morphology of maize after inoculation with *Bacillus subtilis*. Other works (Loper and Schroth 1986) have detected a positive effect on root hair elongation in sugar beet, after inoculation with rhizosphere bacteria. Recently, Lippmann *et al.* (1995) have described the beneficial effects of some IAA-producing *Pseudomonas* strains on root elongation and lateral root production in maize seedlings. These effects were consequently related to plant shoot growth.

Microbial relationships in the rhizosphere have high specificity (Kloepper 1996). Interactions between beneficial microorganisms also confirm this specificity (Azcón 1989, Paulitz and Linderman 1989). Because most previous work concerns other crops, comparisons cannot be made with the same plant species. Other authors have already mentioned the beneficial use of these associations (Dihillion 1992, Singh and Kapoor 1998, Ravnskov and Jakobsen 1999, Ratti *et al.* 2001). Most described increases in plant biomass and nutrient contents (Dihillion 1992, Singh and Kappor 1998, Potty and Pillai 1996). The potential use of both AMF and P-solubilizing bacteria to reduce phosphorus fertilizer inputs has also been considered (Potty and Pillai 1996). In other cases, the diversity of the effects of different microbial associations has been mentioned (Toro *et al.* 1996, Ravnskov and Jakobsen 1999).

There are also some references concerning the effect of PGPBs on AMF (Burla *et al.* 1996, Germida and Walley 1997, Attia 1999). Some describe negative effects on mycorrhizal colonization development (Burla *et al.* 1996, Germida and Walley 1997). Our results confirm what Attia (1999) described: the absence of any negative effect on AMF, since the colonization root indices of double inoculated plants were identical to those with just AMF. Results from this experiment show that combined inoculation has positive effects on plant development and adventitious root number. However, due to the lack of references concerning the effect of PGPB on the banana root system, further experiments should be conducted to achieve a better approach.

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Biological control of nematodes in banana

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Abstract

Several species of nematodes are associated with banana and plantain in Cuba; however, the most important are *Radopholus similis, Meloidogyne incognita, Pratylenchus coffeae* and *Helicotylenchus multicinctus*. These parasites have been dealt with for several years using integrated management systems. These systems include legal, cultural, genetic, biological and even chemical measures that have been adapted to the different development stages in this crop.

Biological control has shown to be an effective alternative that can be combined with others within an Integrated Management System. The base for biological control is the use of fungi such as *Paecylomices lilacinus* and bacteria such as *Bacillus thuringiensis* var. *kurstaki*. More recently, *Corynebacterium paurometabolum* bacterium has been added to this group as well as mycorrhiza from the *Glomus* genus.

P. lilacinus was the first bioregulator of banana parasitic nematodes researched in the country. Its effectiveness was demonstrated under semicontrolled, *in vitro* conditions, and in the field. *B. thuringiensis* var. *kurstaki* (LBT 3 strain) is a bacterium effective against insects that has also nematicidal effects, mainly against *R. similis*. It was possible to determine that its applications under pot and field conditions significantly reduced nematode attack. Evaluation of its effectiveness in more than 185 ha of production fields revealed average reductions of 87% in plantations with different populations. Studies with *C. paurometabolum* (C-294 strain) showed that it has effects on eggs and juveniles, manifested both under laboratory and field conditions. Reduction of populations under controlled conditions exceeded 85%, while in the field, *R. similis* populations started to decrease after the application and stayed low during the experiment, showing results comparable with the nematicide used as control.

With regards to mycorrhiza, early inoculation of *in vitro* plants at the hardening stage, with several species of the *Glomus* genus, minimized damage caused by *R. similis* and *M. incognita*.

Resumen - Control biológico de nematodos en banano

Varias especies de nematodos se encuentran asociadas al banano y el plátano en Cuba, no obstante las más importantes son *Radopholus similis, Meloidogyne incognita, Pratylenchus coffeae y Helicotylenchus multicinctus*. Estos parasitos se han combatido desde hace varios años, mediante sistemas de manejo integrado. Estos incluyen medidas legales, culturales, genéticas, biológicas e incluso químicas que se han adecuado a las distintas fases de desarrollo del cultivo.

El control biológico ha demostrado ser una alternativa efectiva, que permite ser combinada con el resto de las que componen el Sistema de Manejo Integrado. La base para el sistema de control biológico es el empleo de hongos como *Paecylomices lilacinus* y bacterias como *Bacillus thuringiensis* var. *kurstaki*. De forma mas reciente han entrado en este grupo la bacteria *Corynebacterium paurometabolum* (en fase acelerada de introducción) y micorrizas del género *Glomus*.

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P. lilacinus fue el primer bioregulador de nematodos parásitos del banano que se estudió en el país. Su efectividad fue demostrada en condiciones *in vitro*, semicontroladas y de campo. *B.thuringiensis* var. *kurstaki* (cepa LBT 3), bacteria efectiva contra insectos tiene efectos nematicidas, principalmente contra *R. similis*. Se pudo determinar que su aplicación tanto en condiciones de macetas como de campo reducía significativamente los niveles de ataque de los nematodos. La valoración de su efectividad en mas de 185 ha de campos de producción, reveló reducciones de 87% como promedio, en plantaciones con diferentes niveles poblacionales. Los estudios con *C. paurometabolum* (cepa C-294) revelaron que tiene efectos sobre huevos y juveniles, que se manifestaron tanto en condiciones de laboratorio como de campo. La reducción de los niveles poblacionales en condiciones controladas superó el 85%, mientras que a nivel de campo las poblaciones de *R. similis* comenzaron a disminuir a partir de la aplicación y se mantuvieron bajas durante todo el ensayo, con resultados comparables a la sustancia nematicida utilizada como control.

Con relación a las micorrizas, se ha determinado que la inoculación temprana de varias especies del género *Glomus* en la fase de endurecimiento de las vitroplantas, permite atenuar el daño por *R. similis* y *M. incognita*.

Introduction

Several species of nematodes are associated with banana and plantain in Cuba. The most important are *Radopholus similis, Meloidogyne incognita, Pratylenchus coffeae* and *Helicotylenchus multicinctus*, which have a varied distribution in Cuba.

These parasites have been controlled for several years using integrated management systems that combine preventive and curative alternatives in a harmonious manner. These systems include legal, cultural, genetic, biological and even chemical measures, adapted to the different developmental stages present in the crops. Some examples are: limited chemical nematicides treatments on commercial banana plantations, which were used until the end of the eighties when they gave way to other environmentally friendly practices; massive *in vitro* plant production as healthy planting material; and more recently, utilization of new black Sigatoka (*Mycosphaerella fijiensis)* and *R. similis* resistant cultivars developed by the *Fundación Hondureña de Investigación Agrícola* (FHIA) in Honduras.

Biological control has been shown to be an effective alternative that can be combined with other measures. The base for biological control has been the use of the fungus *Paecilomyces lilacinus* and the bacterium *Bacillus thuringiensis* var. *kurstaki.* More recently, the bacterium *Corynebacterium paurometabolum* has been added to this group as well as mycorrhizae from the *Glomus* genus. This paper deals with the main results obtained using biological control over several years in Cuba.

Materials and methods

Paecilomyces lilacinus

This fungus was the first biocontrol agent studied in the country. Its effectiveness was evaluated under *in vitro* and semi-controlled conditions and also in the field. *In vitro* spore suspensions were tested at different concentrations (10^5 to 10^9 conidia/g), using small Petri dishes with egg masses of *M. incognita* and larvae and adults of *R. similis*. *In vitro* plants, planted individually in plastic bags filled with sterilized soil, were used under semi-controlled conditions. Plants were first infected with 10 g of the bioproduct

of *P. lilacinus* and one week later, 1500 *Meloidogyne* juveniles were added per plant. Root evaluation was performed using Taylor and Sasser's method (1978).

Under field conditions, tests were carried out in two phases: at the start of a new plantation and in a recently established one during two growth cycles. Fields, naturally infested with *M. incognita* and *R. similis,* respectively, were used. In the first phase, the *in vitro* plants were inoculated with the bioproduct of *P. lilacinus*, 20 days before planting. The nematode population on the roots was evaluated every two months using the maceration and sieving method. The bioproduct was applied around the plants (as a nematicide) on the recently established plantations (with 2000 *R. similis*/100 g of roots), and nematode population fluctuations were recorded every two months by the same method. The yield was evaluated over two crop cycles.

Bacillus thuringiensis (Bt)

This biocontrol agent was also evaluated under various conditions. Different strains were screened under *in vitro* conditions against *M. incognita* using the same method described above. Under field conditions, the bioproduct containing the strain LBT-3 was applied on a large scale in more than 15 fields of different sizes. The product was deposited around the plant. The nematode populations were evaluated every two months by the same method.

Corynebacterium paurometabolum

This bacterium was evaluated under *in vitro* conditions, semi-controlled and field conditions using the same methodology.

Mycorrhyzae (Arbuscular Mycorrhizal Fungi, AMF)

After a survey of natural populations of mycorrhyzae in banana and plantain fields, some species of the *Glomus* genus were selected to be evaluated under semi-controlled and natural conditions. The inoculum of mycorrhyzae was applied to *in vitro* plants at the hardening stage in both experiments. The nematode populations were evaluated with the same methodology and some growth indicators and yields were recorded.

Results and discussion

P. lilacinus showed a positive effect, reducing the colonization and hatching of *Meloidogyne* egg masses (Table 1). *R. similis* treated with this fungus showed complete immobility, malformations of the digestive system and also vacuoles 48 hours

Table 1. Effect of *P. lilacinus* on *M. incognita* under *in vitro* conditions.

Concentration conidia/g	Egg masses colonized (%)	Hatching (%)	Observations on second stage juveniles (J_2)
100 (Control)	0	71	J_2 with motility
105	40	40	J_2 with motility
106	40	45	J_2 with motility
107	100	24	J_2 with poor motility, growth of hyphae
108	100	5	J_2 without movement
109	100	3	J_2 without movement

after treatment. A toxin seems to be involved. *P. lilacinus* influenced the motility of nematodes in both cases and also affected the hatching of *M. incognita* eggs and the morphology of *R. similis.* This behaviour has important implications for root infection by nematodes. Under semi-controlled conditions, the preventive treatment of *P. lilacinus* in hardened *in vitro* plants reduced the number of *M. incognita* nematodes from 8900 to 820 /50 g roots. According to these results, it is recommended that biological control begin before nematode infestation in order for the fungus to colonize the rhizosphere. This type of preventive treatment has shown good and practical results in banana production systems. The preventive use of *P. lilacinus* on *in vitro* plants showed encouraging results in plantations with low initial nematode populations. During one year, the populations of *M. incognita* and *R. similis* did not increase significantly with respect to the control (Table 2). Also under these conditions, yields were 25% higher in treated plants.

Table 2. The effect of *P. lilacinus* on the number of *M. incognita* and *R. similis* over 15 months under field conditions. *P. lilacinus* increased yield by 25%.

Treatment	Nematode	Months				
		3	6	9	12	15
Control		460	990	2 500	4 700	8 900
	M. incognita					
P. lilacinus		150	320	450	818	1 560
Control		520	1 000	3 100	5 200	9 200
	R. similis					
P. lilacinus		100	250	410	790	1 700

Under production conditions, in recently established plantations with low initial nematode populations, the *P. lilacinus* treatments produced remarkable reductions in *R. similis* and *M. incognita*, between 75-85%, over a period of more than one year. Therefore, this fungus was used on a commercial scale in more than 5500 ha. This fungus showed good results in nematode control in different crops. Segers and Butt (1994) reported the use of the bionematicide BIOSTAT (with *P. lilacinus* base) to control species of *Meloidogyne, Pratylenchus, Scutellonema* and *Helicotylenchus* while Holland (2001) reports the efficiency of another bio-pesticide with the same fungus on banana nematodes. However, *P. lilacinus* is not currently being used in Cuba pending the completion of toxicology tests.

There are more than 80 strains in the Bt collection at the *Instituto de Investigaciones de Sanidad Vegetal* (INISAV). Of the 37 most-studied strains, 16 showed some nematicide activity. Strains LBT-1, LBT-3, LBT-4, LBT-25 and LBT-47 produced irreversible effects on egg hatching of *M. incognita* and have been selected for further study. LBT-3 strain is currently used to control some Lepidoptera and its large-scale reproduction methodology is well known. For this reason, it was selected for application under production conditions in the Camaguey province that suffers from significant nematode problems. An average nematode reduction of 87% was obtained two months after the treatments on more than 165 ha (Table 3). This strain is normally reproduced in

Table 3. Technical effectiveness (TE) of the *B. thuringiensis* var. *kurstaki* strain LBT-3 under production conditions in the Camaguey province, Cuba.

Location	Field (number)	Area (ha)	TE
Empresa Cultivos Varios Florida	53	4.3	100
(UBPC Celia Sánchez)	54	2.5	100
	55	3.0	100
Empresa Pecuaria Céspedes	6	4.0	80
(UBPC 10 de Octubre)	7	3.4	100
	9	9.4	100
	11	6.7	91
	12	9.4	90
	14	3.4	100
	15	3.4	88
	18	5.4	100
(Distrito Angel del Castillo)	31	5.0	64
Empresa Pecuaria Esmeralda	34	9.0	100
(UBPC Lidia and Clodomira)	41	10.7	80
Empresa Cultivos Varios Camalote	18	9.1	84
(Distrito Manuel Boza)	19	9.1	57
	20	4.3	62
	21	5.4	100
	22	3.4	83
	23	3.0	94
	24	6.3	70
	26	5.3	84
(Distrito Las Flores)	2	4.2	80
	6	3.7	80
Empresa Cultivos Varios Camagüey	11-B	4.7	92
(UDCT Victoria 1)	4	4.0	97
	1	5.9	91
	2-B	5.4	100
(UBPC Aguacate)	28	6.7	94
(UBPC 1ro de Enero)	3	5.4	100
TOTAL		165.4	87

specialized centers (CREE) and applied under production conditions in Eastern provinces such as Camaguey. Our results are similar to those obtained by Zuckermann *et al.* (1993) and Sharma (1995), who reported different degrees of nematode control with Bt strains. Also, very efficient strains were mentioned in Current Drugs Patents (2002). The effects of Bt against nematodes are attributed to the activity of toxins produced by the sporulated bacteria (Rodriguez *et al.* 1991).

Studies on *C. paurometabolum* showed that it affects eggs and juveniles under laboratory and field conditions. An almost total inhibition of *M. incognita* egg hatching (98%)

was observed in the former. Its mode of action is due mainly to the combined effect of the culture media where the bacteria grew (chitinases) and the gases it produced (sulphides). Testing under controlled conditions with *R. similis* indicated an almost 85% reduction in the population compared with the control (Table 4). According to the mode of action, the gases and metabolites could penetrate inside the roots through cavities formed by nematodes. Under field conditions, it was noticed that *R. similis* decreased after the treatments with the bacteria or phenamiphos. While this behaviour was maintained throughout the experiment (12 months) in the fields treated with bacteria, populations in the phenamiphos treated fields started to increase at the seventh month (Figure1). The yields of treated plants were significantly higher than those of the control plants, with increases of 106% for

Table 4. Effectiveness of *C. paurometabolum* and *B. thuringiensis* on *R. similis* under controlled conditions.

Treatment	Nematodes/plant
C. paurometabolum 100 ml	5 b
B .thuringiensis 100 ml	50 b
Control	2345 a

Means of nematodes/plant followed by the same letter are not different (P=0.05) according to Duncan multiple range test.

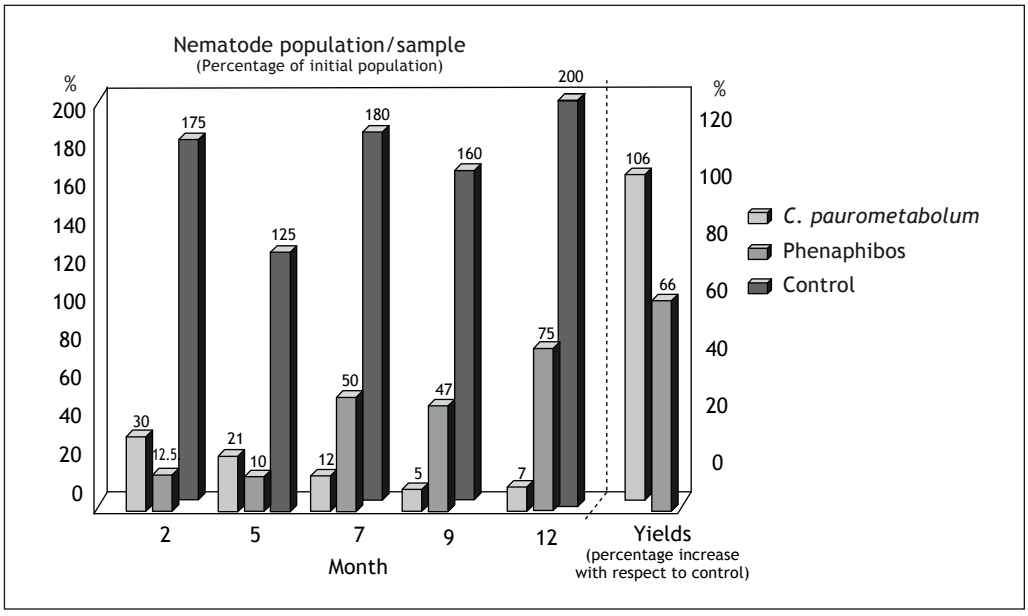


Figure 1. Behaviour of *R. similis* populations in plantain 'Macho 3/4' over time from planting. Right hand axis is yield, expressed as percentage increase with respect to control.

the bacterium and 66% for phenamiphos. There are no reports in the literature of this bacterium acting as a nematicide. Currently, a large scale reproduction methodology is available and a bio-nematicide product is in the registration and patent phase.

Regarding mycorrhyzae, early inoculation of *in vitro* plants during the hardening stage with *Glomus* species attenuated damage caused by *R. similis* and *M. incognita* and also reduced the nematode population. Testing under controlled conditions demonstrated that populations of both species were reduced to different degrees, with *G. intraradices,*

G. manihotis and *G. mosseae* the most promising. Field tests in plantations with low initial infestation have shown that plants inoculated early with AMF developed better than non-inoculated ones and that nematode populations grew more slowly than in control plots. Also, in one test using the FHIA-18 variety (resistant to *R. similis*), there was a tendency in plants with AMF to have better plant growth indicators and yields (Table 5). Jaizme-Vega (2001) and Sarah (2001) have reported similar results with banana nematodes and different arbuscular mycorrhizal fungi. These researchers suggest the possibility of including this alternative in management systems.

Table 5. Effect of colonization with mycorrhizae on plant growth and yields of the FHIA-18 variety in the Villa Clara province.

Treatment	Plant height (m)	Circumference (cm)	Number of leaves	Bunch weight (kg)
Mycorrhizae	2.18	41.8	7.33	17.1
No mycorrhizae	2.14	40.0	6.33	14.1
Significance	NS	NS	NS	NS

NS = no significant difference between means.

Conclusions

Biological control of plant parasitic nematodes in banana and plantain showed great potential for use under field conditions. However, it is advisable to perform local tests to study the necessary adaptations according to the different agro-ecosystems. *P. lilacinus* is an effective biocontrol agent of *R. similis* and *M. incognita*. The best results were achieved with the preventive inoculation of healthy *in vitro* plants during the hardening phase.

The strain LBT-3 of *B. thuringiensis* has nematicidal activity on *R. similis* and *M. incognita* under field conditions. Nevertheless, other strains have shown promising effects and will be studied in the near future. *C. paurometabolum* has a good nematicidal activity on the main banana and plantain parasitic nematodes. Its effectiveness has been demonstrated under a range of conditions. Mycorrhyzae of the genus *Glomus* reduced nematode damage caused by *R. similis* and *M. incognita*. The species *G. intraradices, G. manihotis* and *G. mosseae* have shown the most stable results.

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Parasitic nematodes on *Musa* AAA (Cavendish subgroup cvs 'Grande naine', 'Valery' and 'Williams')

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Abstract

Among the biotic factors affecting yield, banana-root nematodes are second only to black Sigatoka (*Mycosphaerella fijiensis*). The three commercial cultivars, 'Grande naine', 'Valery' and 'Williams' are equally susceptible, and in plantations in Costa Rica usually only polyspecific communities occur, consisting of a mixture of the migratory endoparasitic *Radopholus similis* and *Pratylenchus coffeae*, the ecto-endoparasitic *Helicotylenchus multicinctus*, and the sedentary endoparasitic *Meloidogyne incognita*, or rarely *M. javanica*. Based on their frequencies and population densities the relative importance of nematode genera in Costa Rica was established in decreasing order as follows: *R. similis* > *Helicotylenchus* spp. > *Meloidogyne* spp. > *Pratylenchus* spp. *R. similis* is the most abundant nematode, accounting for 82 to 97% of the overall root population. High populations of *R. similis* are found throughout the year and in all counties producing bananas. The nematodes damage the root and corm tissue. *R. similis* enters the root mainly by the root tip, but any portion of the entire root length may be invaded. Adults and juveniles occupy an intercellular position in the cortical parenchyma, in which they move actively, causing damage as they feed on the cytoplasm of the surrounding cells. The four nematode genera develop and complete their life cycle inside the banana roots. In highly infected roots, *R. similis* sometimes crosses the endodermis and invades the stele. Reddish brown lesions appear throughout the cortex. In some Costa Rican banana growing areas, crop losses on nematode infected plantations can be high, up to 30-50%. Infected plants have poor root anchorage and the ability of the root system to take up water and nutrients is reduced, which results in losses in bunch weight and crop longevity, and a lengthening in the plant production cycle. Pathogenicity studies have shown that *R. similis* restricts banana root system growth and reduces the concentration of K in the root dry matter. All the phenological stages can be infected by any of the four genera, but again, *R. similis* is the most frequent and the most abundant at any stage. Even the roots of very small peepers (suckers 10 cm high) can be infected, and in the case of *R. similis,* it is common to find nematodes in the corm tissue also. This suggests that root infection of these young suckers in infected plants is caused by either *R. similis* coming from the corm or from the soil.

Resumen - Nematodos parásitos de *Musa* AAA (subgrupo Cavendish cvs 'Grande naine', 'Valery' y 'Williams')

Entre los factores bióticos que afectan el rendimiento en banano, los nematodos son el segundo en importancia después de la Sigatoka negra (*Mycosphaerella fijiensis*). Los tres cultivares comerciales 'Grande naine', 'Valery' y 'Williams', son igualmente susceptibles y en las plantaciones locales, usualmente solo comunidades poliespecíficas ocurren, consistiendo de una mezcla de los endoparásitos migratorios *Radopholus similis* y *Pratylenchus coffeae*, el ecto-endoparásito *Helicotylenchus multicinctus* y el endoparásito sedentario *Meloidogyne incognita* o raramente *M. javanica*. Basado en las frecuencias y densidades poblacionales, la importancia relativa de los géneros de nematodos en Costa Rica se estableció en orden decreciente como sigue: *R. similis* > *Helicotylenchus* spp. > *Meloidogyne* spp. > *Pratylenchus* spp. *R. similis* es el nematodo más abundante y representa de un 82-97% de la población total en las raíces. Altas poblaciones de *R. similis* se encuentran durante todo el año en todos los cantones productores de banano. El daño

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se localiza en las raíces y cormo. *R. similis* penetra las raíces principalmente por la parte terminal (caliptra), pero cualquier parte de la raíz puede ser invadida. Adultos y juveniles ocupan una posición intercelular en el parénquima cortical donde ellos se mueven activamente causando daño conforme se alimentan del citoplasma de las células vecinas. Los cuatro géneros de nematodos se desarrollan y completan su ciclo de vida dentro de las raíces de banano. En raíces altamente infectadas, *R. similis* algunas veces pasa la endodermis e invade el cilindro vascular. Coloraciones café rojizas aparecen a través de toda la corteza. En algunas plantaciones locales infectadas las pérdidas en rendimiento alcanzan hasta un 30-50%. Plantas infectadas carecen de buen anclaje y la habilidad de las raíces para absorber agua y nutrientes se reduce, lo que resulta en pérdida de peso del racimo y longevidad de la planta y se alarga los intervalos entre ciclos de producción. Estudios de patogenicidad muestran que *R. similis* restringe el crecimiento del sistema radical y reduce la concentración de K en las raíces. Todos los estados fenológicos de la planta de banano pueden ser infectados por cualquiera de los cuatro géneros, pero nuevamente *R. similis* es el más frecuente y abundante en cualquier estado de desarrollo de la planta. Aún raíces de hijos muy pequeños (10 cm de altura) pueden ser infectadas y en el caso de *R. similis* es común también encontrarlo en el cormo. Esto sugiere que la infección de las raíces en hijos nuevos de plantas infectadas, ocurre igualmente de *R. similis* procedente del cormo o del suelo.

Introduction

Banana is an important crop in Costa Rica accounting for almost 17% of the agricultural gross national product. In 2003, 1.85 million tonnes were exported, produced on 42,000 ha, generating a total income of US $541 million FOB (Sánchez and Zuñiga 2004). Besides the constraints of banana market requirements and demands, there are other limiting factors. Among the biotic factors affecting yield, banana-root nematodes are second only to black Sigatoka (*Mycosphaerella fijiensis*). Nematodes reduce bunch weight and plant longevity, and increase the crop cycle duration (Quénéhervé 1991).

In Costa Rican plantations (Araya *et al*. 1995, 2002) usually only polyspecific communities occur, consisting of a mixture of *Radopholus similis*, *Helicotylenchus multicinctus*, *Meloidogyne incognita*, *M. javanica*, and *Pratylenchus* spp. Here we report some research results related to the parasitic behaviour and nematode damage under controlled conditions on commercial banana plantations in Costa Rica.

Host suitability

The commercial cultivars planted are ‘ Grande naine’, ‘Valery’ and ‘Williams’, which are part of the *Musa* AAA Cavendish subgroup. All these cultivars are equally susceptible to *R. similis* (Figure 1) and their reaction to each of the other three most important

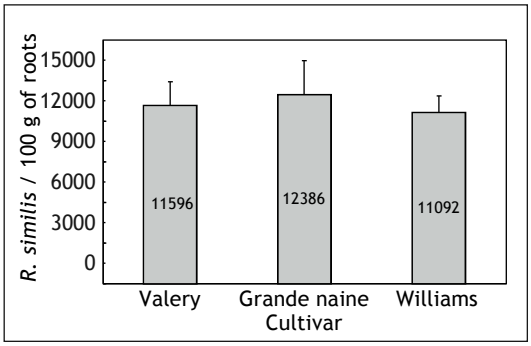


Figure 1. *Radopholus similis* numbers in banana (*Musa* AAA subgroup Cavendish cvs ‘Valery’, ‘ Grande naine’ and ‘Williams’). Each bar is the mean ± standard error of 250 root samples. Each sample contains roots of 5 plants.

Musa parasitic nematodes is similar. This reaction agrees with pot experiments, carried out under our conditions with *R. similis* (Moens *et al*. 2003) and with the other nematodes (Araya *et al*. 2003). Also, other researchers found similar results, inoculating Cavendish subgroup cultivars with *R. similis* (Stoffelen *et al*. 2000, Viaene *et al*. 2000 and 2003), *M. incognita* (Pinochet *et al*. 1998, Van den Bergh *et al*. 2002a, b), *P. coffeae* (Viaene *et al*. 1998, Stoffelen *et al*. 1999a, 2000, Viaene *et al*. 2000, Van den Bergh *et al*. 2002a) and *H. multicintus* (Barekye *et al*. 2000).

Nematode frequencies and populations

In surveys in Costa Rica from 1994 to 1999, looking at root samples extracted from five plants on each occasion, *R. similis* was the most abundant nematode, ranging from 82 to 86%, while *Helicotylenchus* spp., *Meloidogyne* spp. and *Pratylenchus* spp. varied respectively from 8 to 10%; 5 to 9% and < 1% of the root population (Araya *et al*. 1995, 2002). The four nematode genera detected are well known pathogens in banana roots (McSorley and Parrado 1986, Sarah 1989, Gowen 1995, Sarah *et al*. 1996, Bridge *et al*. 1997, De Waele and Davide 1998, Marin *et al*. 1998).

Nematode frequency was very stable in the different years (Table 1). The highest frequency, above 95%, was always found for *R. similis*, followed by *Helicotylenchus* spp., ranging from 52 to 60%. The four nematode genera counted were detected in all counties and all months of the year. The favorable climatic conditions (Figure 2), without a dry season and only small variations in temperature, promote adequate plant growth throughout the year. This may explain the low variation observed in nematode population densities and frequencies.

Table 1. Absolute frequency by year (1994-1999) of the banana (*Musa* AAA) root parasitic nematodes in Costa Rica as a percentage of the total number of samples.

	Year						
	94	**95**	**96**	**97**	**98**	**99**	**Total**
No. of samples	11 688	10 618	11 253	10 929	12 707	14 525	71 720
	Percentage of samples with nematode species						**Mean**
R. similis	95	96	96	99	98	97	97
Helicotylenchus	56	56	52	54	56	60	56
Meloidogyne	68	59	51	57	48	47	56
Pratylenchus	15	13	11	13	13	14	13

The distribution of the root samples per nematode population density interval clearly indicated that *R. similis* accounted for the highest population (Figure 3). From the 71 720 recorded root samples, only 2324 (3%) were free of the nematode and 37 489 (52%) contained more than 10 000 individuals per 100 g of roots. These high populations and frequencies were probably encouraged by the long-term banana monoculture and the affinity between this nematode and the type of commercial banana planted (*Musa* AAA) (Orton and Siddiqi 1973). The high populations of *R. similis* agree with its high reproductive fitness *in vitro* on carrot discs (Fallas and Sarah 1995, Stoffelen *et*

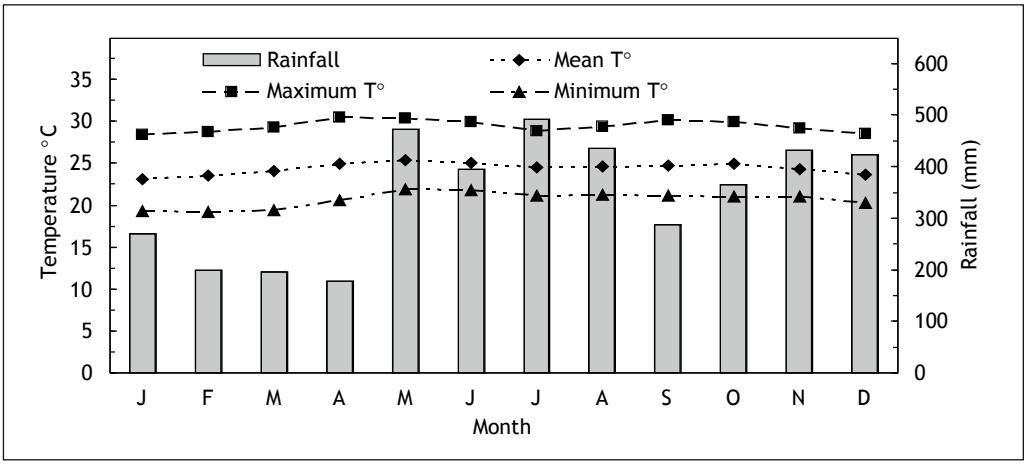


Figure 2. Average of 15 years (1989-2003) of the monthly mean, maximum and minimum temperature (°C) and rainfall (mm) in a Costa Rican export banana-growing area.

al. 1999b) and on banana plants under controlled conditions (Fallas *et al*. 1995, Binks and Gowen 1997, Stoffelen *et al*. 1999c).

The high *R. similis* populations and frequencies are consistent with other local studies (Jiménez 1972, López 1980, Figueroa 1989) and with observations from the Philippines (Boncato and Davide 1992), Colombia (Gómez 1980), and Ecuador (Gómez 1997). The behavior of *R. similis* as a main banana root nematode agrees with the results of Fargette and Quénéhervé (1988), Speijer and Fogain (1999), and Kashaija *et al*. (1999) in African countries, Stanton (1994) in Australia, Davide (1994) in the Philippines, Pone (1994) in the Pacific Islands, Jiménez *et al*. (1998) in Ecuador and Gómez (1980) in Colombia.

Helicotylenchus spp. was absent in 31,608 (44%) of the samples and in only 1,779 (2%) reached levels above 10 000 nematodes per 100 g of roots (Figure 3). *Helicotylenchus* spp. populations were lower than *R. similis*, in agreement with other results (Gómez 1980). More likely, this is because this nematode does not reproduce as fast as *R. similis* and the life cycles of the nematodes differ. *H. multicinctus* was found to have a life cycle of 42 days at 28ºC on *Arabidopsis thaliana* and the adult females laid 4 eggs per day for a period of 10-12 days (Orion and Bar-Eyal 1995). In contrast, the *R. similis* life cycle was completed in 20-25 days at 24-32ºC on banana roots and the adult females laid 4-5 eggs per day for 15 days (Loos 1962). This means that *R. similis* could be expected to have more generations and more individuals per generation in the same period of time.

More than 33,564 (46%) samples were free of *Meloidogyne* spp. and only 1113 (2%) showed densities higher than 10,000 nematodes per 100 g of roots (Figure 3). This low population density and frequency could be related to the feeding behavior of *R. similis*. Pinochet (1977) and Santor and Davide (1992) found that the presence of *R. similis* on the galls, induced by *M. incognita,* caused deterioration and disintegration of the giant cells, which, in turn, affected the development and reproduction of *M. incognita*.

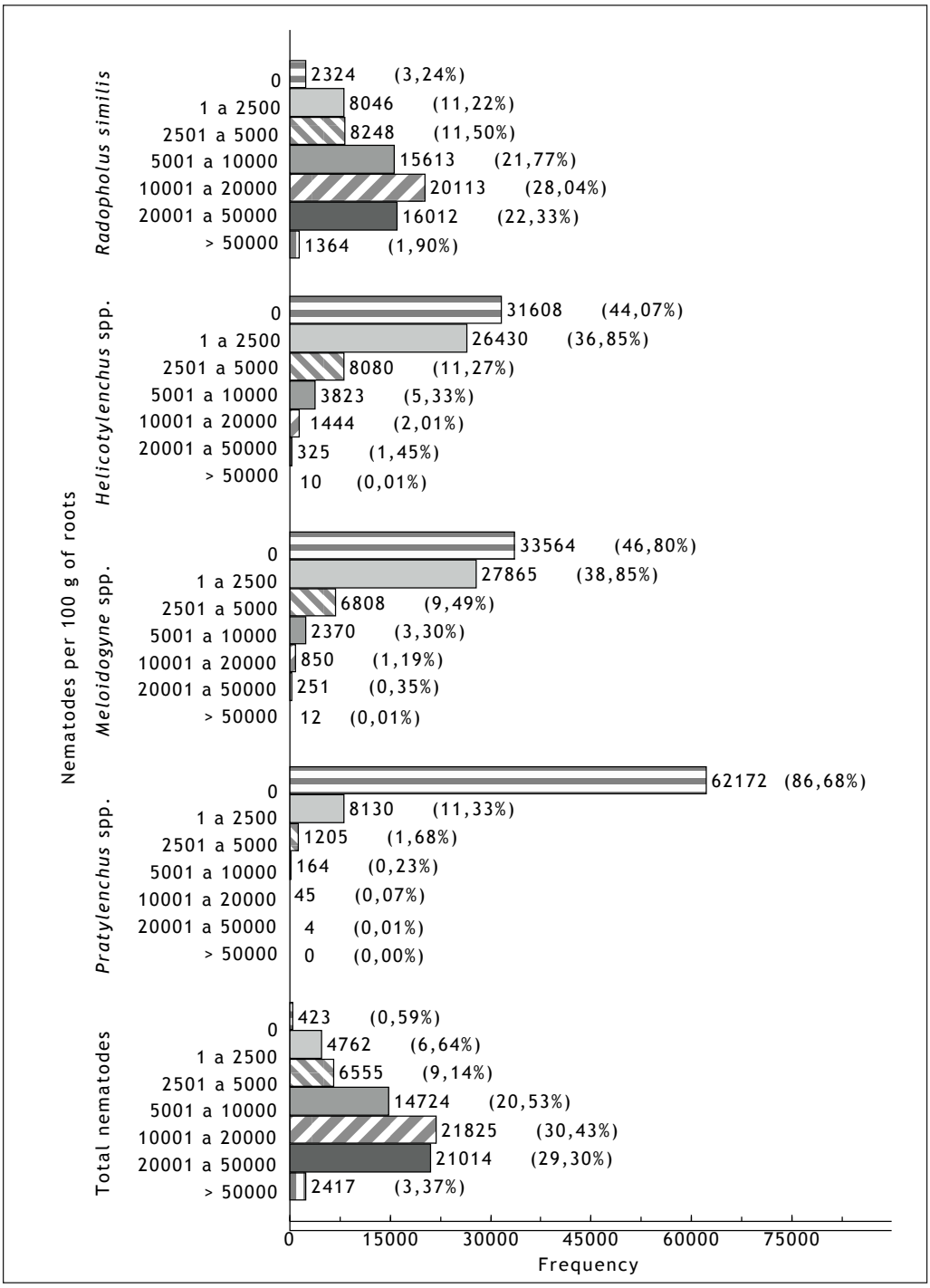


Figure 3. Frequency of nematodes according to the specific ratios per 100 g of fresh roots in 71 720 banana (*Musa* AAA) root samples recorded from 1994 to 1999. Total nematodes = *R. similis* + *Helicotylenchus* spp. + *Meloidogyne* spp. + *Pratylenchus* spp.

Pratylenchus spp. were only present in 9548 (13%) samples, with just 49 (0.08%) above 10,000 nematodes per 100 g of roots (Figure 3). This is reasonable, because *Pratylenchus* spp. has the same habitat as *R. similis* and a longer life cycle (Siddiqi 1972). This means that while they compete for the same feeding site, *R. similis,* with its higher reproduction rate, suppresses the growth of *Pratylenchus* spp.

When all nematodes were pooled (total nematodes), only 423 samples (1%) were nematode free and 45,256 (63%) samples contained more than 10,000 nematodes per 100 g of roots (Figure 3). Similar frequency, abundances and distributions were observed when sampling was done at flowering and harvest of individual plants on three experiments (Figures 4, 5 and 6). Only in the experiment carried out on the newest farm (Figure 6), which was planted about nine years ago, produced samples free (4%) of any parasitic nematode (Araya *et al*. 2003).

Nematode populations according to sucker height and phenological stage of the plant

The suitability of different phenological stages of the plant for parasitic nematodes was evaluated in five experiments by sampling roots of suckers of different heights and by sampling plants at flowering, harvest and 30, 60 and 90 days after harvest (Araya *et al*. 2003). On three farms, Anabel, Calinda, and Esmeralda, no difference in the *R. similis* population was found among suckers from 10 to 350 cm height or even with recently flowered or harvested plants (Figure 7). The lowest *R. similis* population found on any of the farms and at any sucker height or plant stage, was higher than 14,000 nematodes per 100 g of roots.

Helicotylenchus spp. populations were low with the exceptions of those found on the Anabel and Nueva Esperanza farms. On Anabel, the highest populations were observed in suckers of 340-350 cm height, while on Nueva Esperanza, populations increased up to the flowering stage (Figure 8). When individual plants were sampled five times progressively (at flowering, at harvest, and 30, 60 and 90 days after harvesting), the *R. similis* population decreased as plants aged on the three farms. The lowest population was consistently found to be at 90 days after harvest (Figure 9). Nevertheless, the nematodes that remain in the harvested plants act as a reservoir and can become a source of inoculum for the other members of the plant production unit.

Pathogenicity and symptoms of *Radopholus similis*

Moens *et al*. (2003) found a linear reduction of root weight when *R. similis* was inoculated at densities increasing from 0.14 to 2.24 nematodes per mL of substrate, corresponding to 254 to 2128 *R. similis* per pot, respectively. Root weight decreased by 3.9 g (16%) with each successive inoculation of 1000 nematodes (Figure 10A). Sarah *et al*. (1993) found that after exposing 'Valery' plants in 1.8 L pots to *R. similis* populations from different places around the world, root weights decreased from 19 to 80%, 8 weeks after inoculation with 300 individuals. Also, Marin *et al*. (1999), using 'Grande naine' plants in 1.4 L pots inoculated with 200 *R. similis* from different countries, observed root weight reductions of up to 21% after 8 weeks. Hahn *et al*. (1996) found decreases in root weight ranging from 8 to 26% in 'Valery' plants in 0.8 L pots 8 weeks after inoculation with 100 *R. similis*, and up to 30% 12 weeks after inoculation

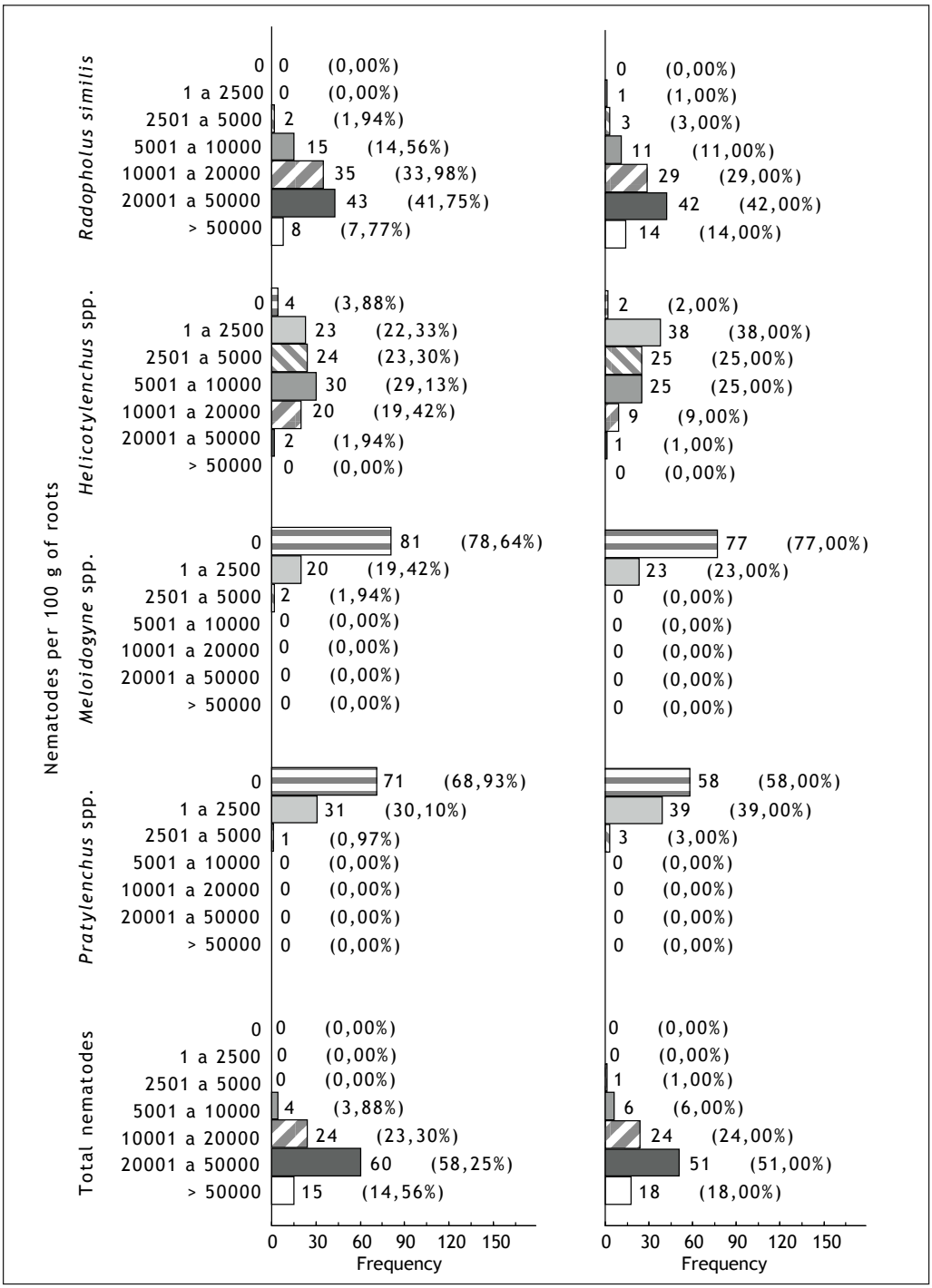


Figure 4. Frequency of nematodes according to the specific ratios in 103 individual banana (*Musa* AAA) root samples recorded on the Productora Tropical farm. Total nematodes = *R. similis* + *Helicotylenchus* spp. + *Meloidogyne* spp.+ *Pratylenchus* spp.

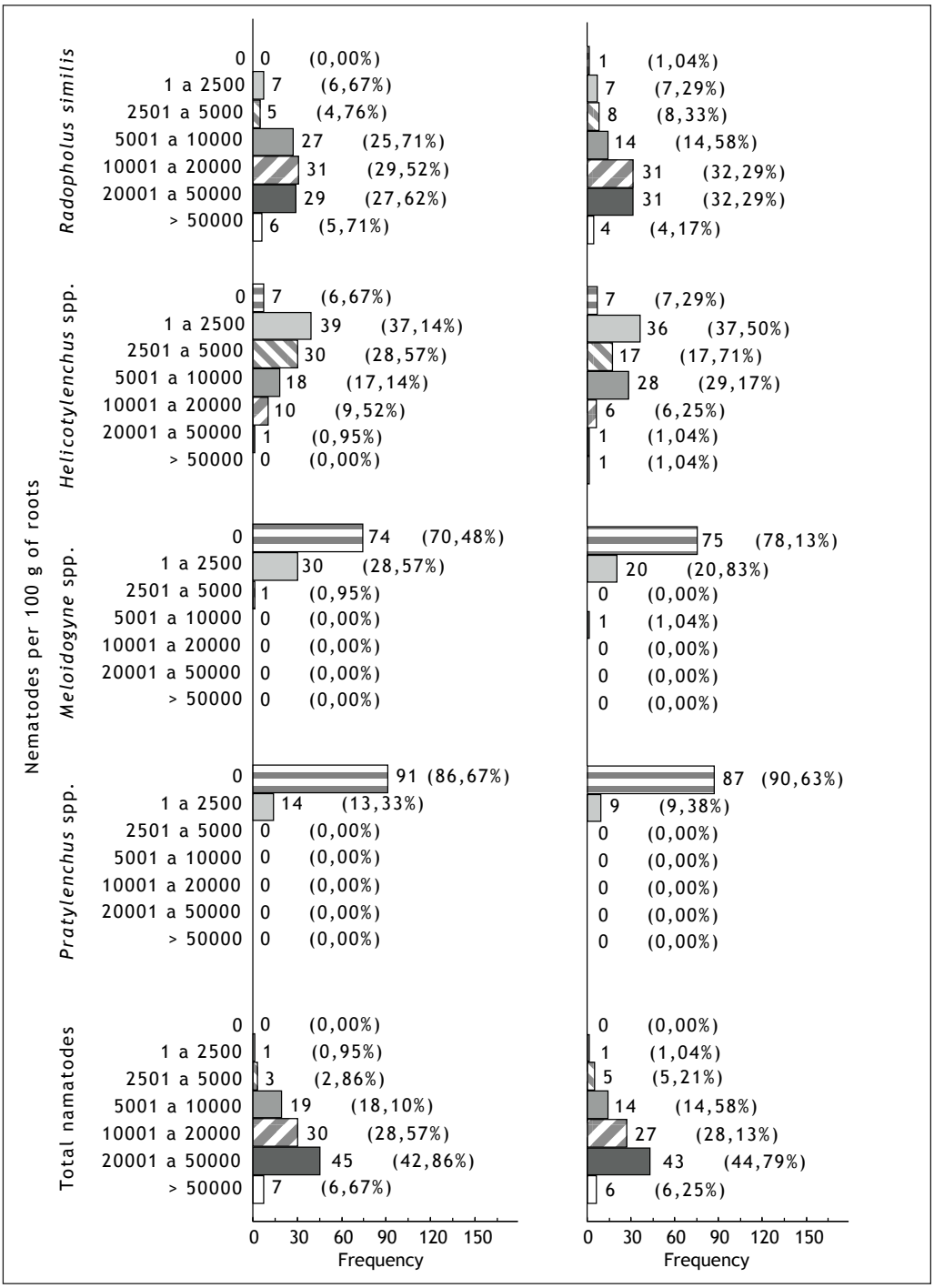


Figure 5. Frequency of nematodes according to the specific ratios in 105 individual banana (*Musa* AAA) root samples recorded on the San Pablo farm. Total nematodes = *R. similis* + *Helicotylenchus* spp. + *Meloidogyne* spp. + *Pratylenchus* spp.

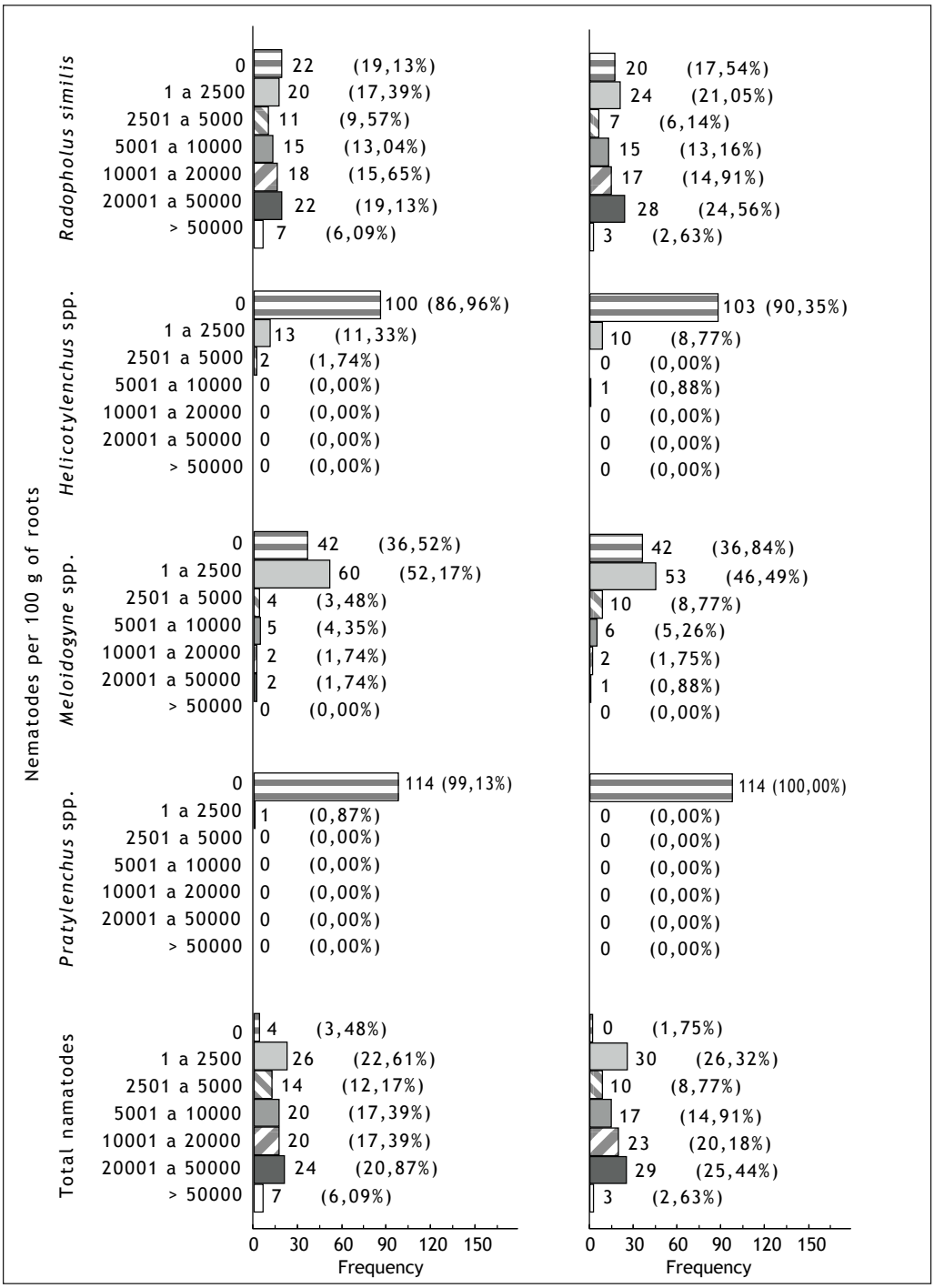


Figure 6. Frequency of nematodes according to the specific ratios in 115 individual banana (*Musa* AAA) root samples recorded on the La Rebusca farm. Total nematodes = *R. similis* + *Helicotylenchus* spp. + *Meloidogyne* spp. + *Pratylenchus* spp.

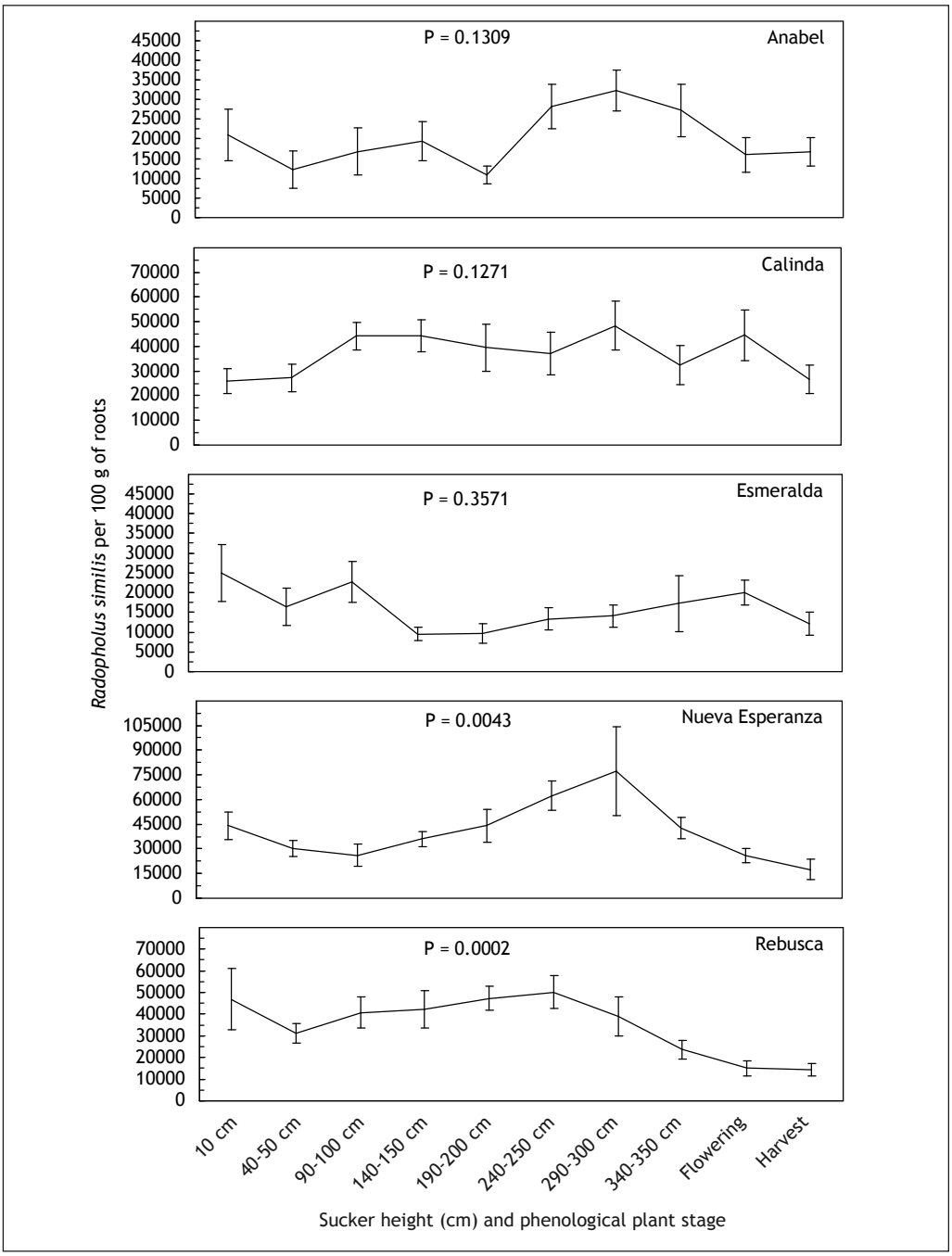


Figure 7. *Radopholus similis* according to sucker height (cm) or phenological banana (*Musa* AAA cv. 'Grande naine') plant stage.

Each point is the mean ± standard error of 15 samples. All the samples were taken in a maximum of 3 days. Each sample was composed of the roots of 5 plants. The p values correspond to the comparison among the means of the different sucker heights or plant stages. The names in the upper right corner are the farms where the experiment was done.

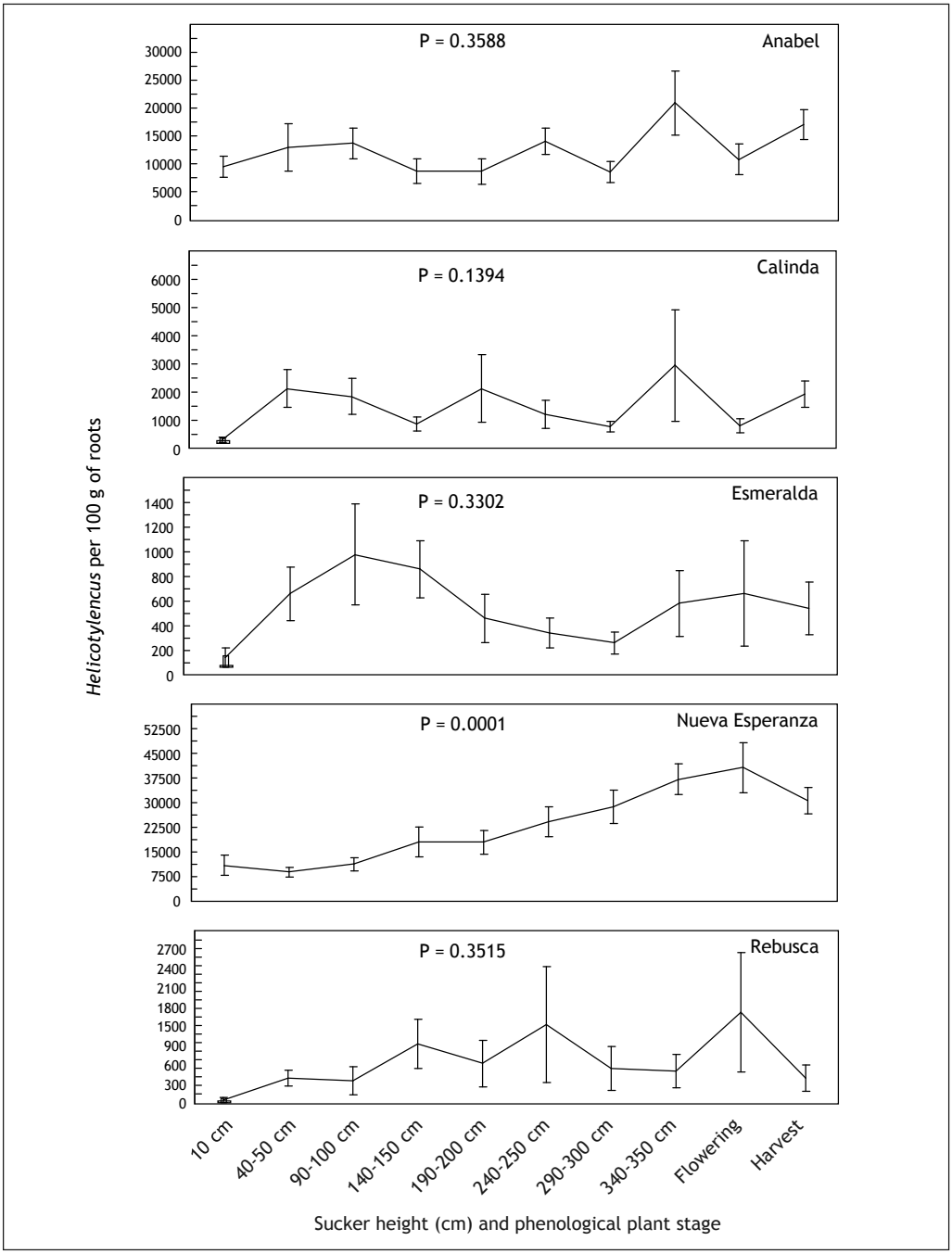


Figure 8. *Helicotylenchus* spp. according to sucker height (cm) or phenological banana (*Musa* AAA cv. 'Grande naine') plant stage.

Each point is the mean ± standard error of 15 samples. All the samples were taken in a maximum of 3 days. Each sample was composed of the roots of 5 plants.

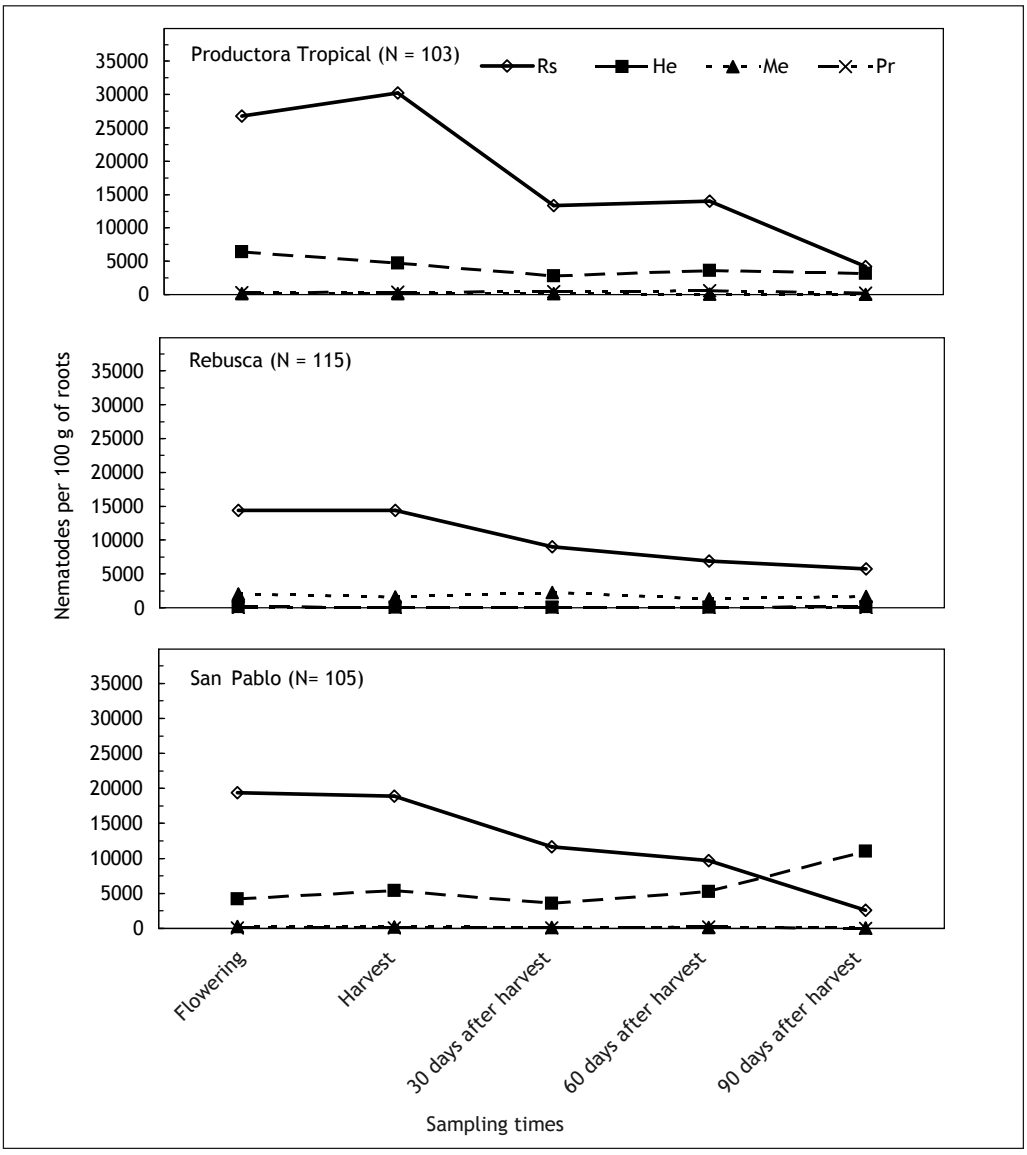


Figure 9. Nematode numbers in individual plants sampled 5 times progressively (at flowering, at harvest, and 30, 60 and 90 days after harvest). Rs = *Radopholus similis*, He= *Helicotylenchus* spp., Me = *Meloidogyne* spp. and Pr = *Pratylenchus* spp.

with 300 *R. similis*. Fallas *et al*. (1995), evaluating 'Valery' plants in 0.8 L pots inoculated with 100 *R. similis*, found decreases in root weight of 11 to 53% after 12 weeks. A reduction in the K concentration in the root dry matter was observed when 'Grande naine' plants were inoculated with different initial *R. similis* populations (Figure 10B). Other nutrients that varied significantly were N, S, Ca and Cu.

Fogain and Gowen (1995) found root necrosis of 3 to 12%, 6 weeks after inoculating ' Grande naine' plants in 1 L pots with 300 *R. similis*. Fogain *et al*. (1996) observed

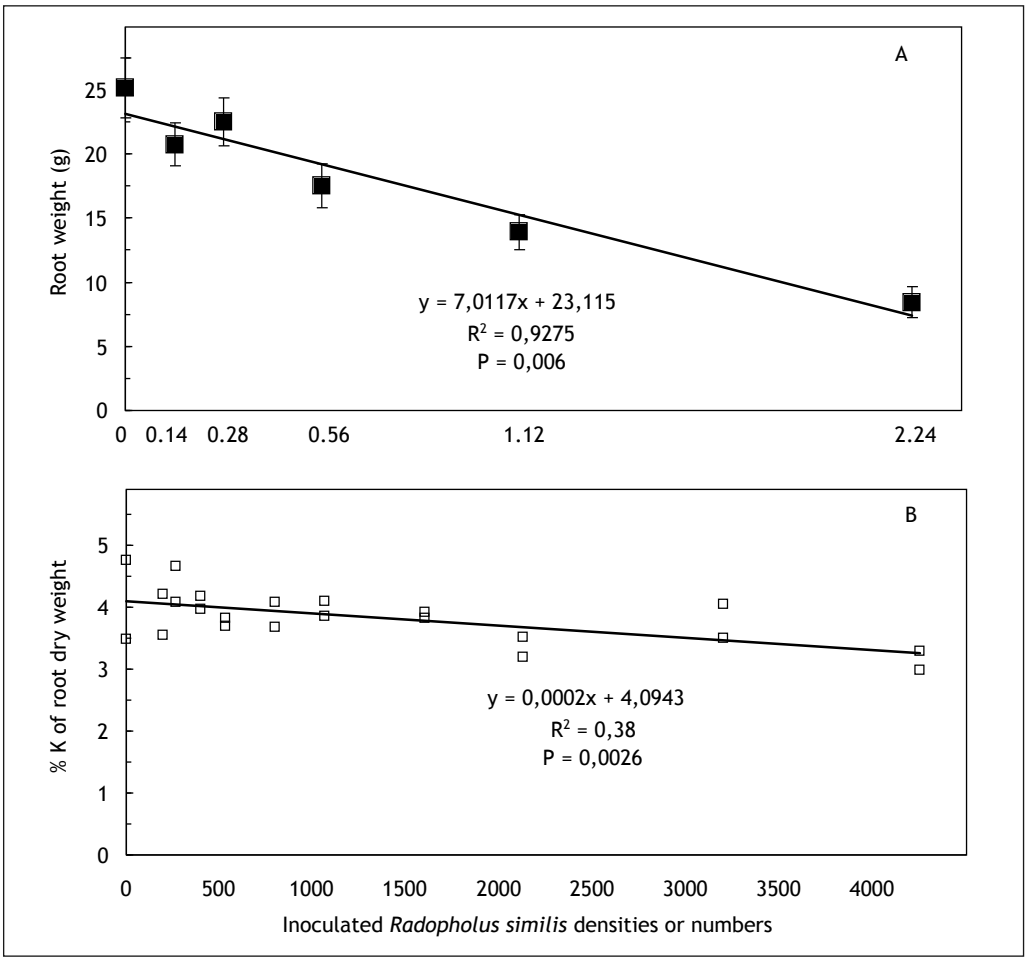


Figure 10. Effect of initial *Radopholus similis* inoculation densities per ml of substrate or numbers per 1.8 L pots on *Musa* AAA cv. Grande naine. A) root weight.
Each point is the mean ± standard error of 12 repetitions over 8 weeks of exposure. B) % K of the dry root weight. Each point is the mean ± standard error of 12 repetitions, with an exposure time of 12 weeks.

a high root lesion index in follower suckers of plantain cultivars in 10 L pots inoculated with 1000 *R. similis*. Moens *et al*. (2001) found a significant correlation between *R. similis* and root necrosis or damage, ranging from 0.62 to 0.75, in root samples from commercial banana plantations.

'Giant Cavendish' bananas inoculated with 1000, 2000, 3000 or 4000 *R. similis* suffered bunch weight reductions of 17, 42, 51, and 61% respectively (Davide and Marasigan, 1985). In a local study, ' Grande naine' plants, initially grown in 1.8 L pots, were inoculated with 1000 *R. similis* or *M. incognita* or *P. coffeae* or *H. multicinctus*. The *R. similis* and *P. coffeae* were cultured on carrot disks and *M. incognita* and *H. multicinctus* on potted banana plants. Three weeks later, plants were transferred to 200 L drums containing sterilized soil and allowed to develop until harvest, when root content, damage

and bunch weight were recorded. Plants inoculated with *R. similis* had 3.6 kg (66%) less root weight, 6.4 kg (27%) less bunch weight and 262% more root damage than non-inoculated plants (Figure 11A-B).

The root and corm symptoms (Figure 12A-D) agree with those reported in the literature (Tarté and Pinochet 1981, Gowen and Quénéhervé 1990, Gowen 1995, Sarah 2000). Black and brown discoloration was observed in roots and corm after washing the surface free of soil. However, in early infections pre-symptomatic roots (Figure 12C) hold a lot of nematodes and when there is excess soil water, symptoms are easily confused with those caused by waterlogging. When the corm was lightly peeled, a purple, reddish-brown discoloration was easily seen, similar to that found in longitudinally split roots, where lesions extended from the epidermis towards the vascular cylinder.

Pathogenicity and symptoms of *Meloidogyne incognita*

In pot experiments with 22 Vietnamese banana genotypes, fresh root weight increased significantly in 2 of the 3 experiments in plants inoculated with 500 to 4000 *Meloidogyne*

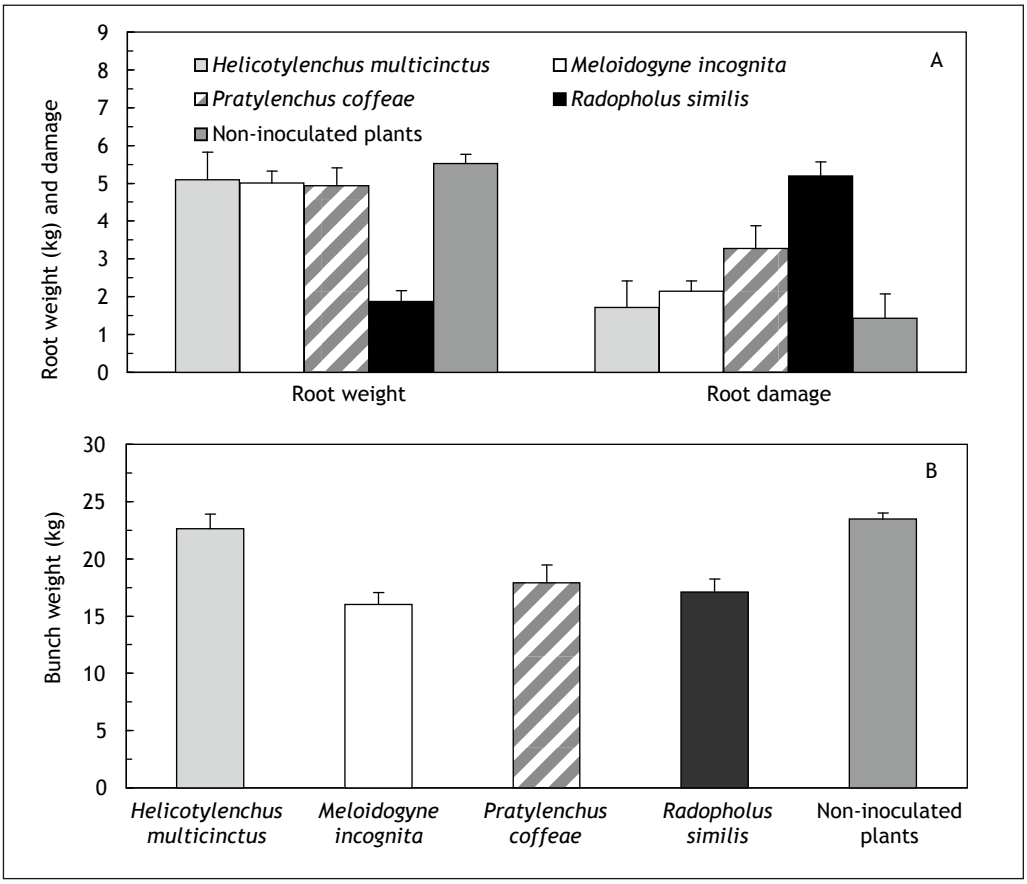


Figure 11. Root fresh weight, root damage and bunch weight at harvest of *Musa* AAA cv. 'Grande naine' plants inoculated with 1000 nematodes compared with plants without nematode inoculation.
Each bar is the mean ± standard error of 10 observations. The scale used for root damage was from 0 to 10.

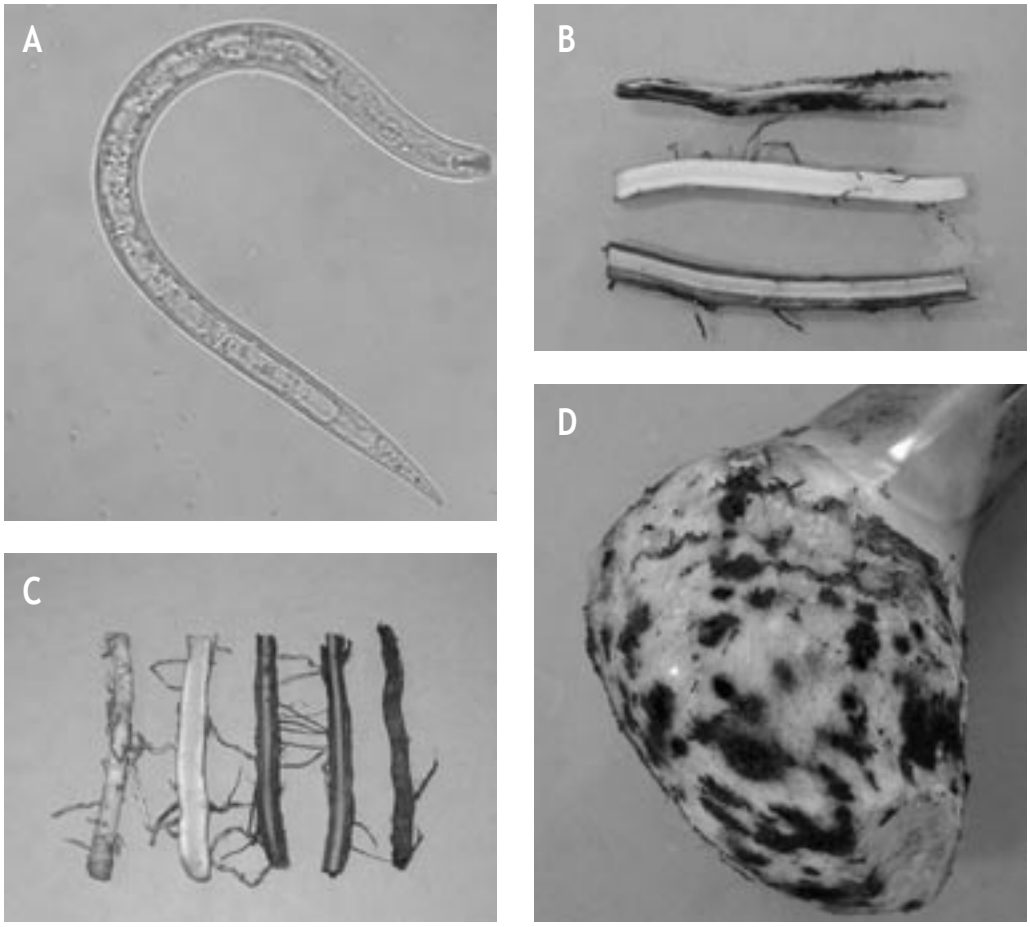


Figure 12. *Radopholus similis* and infection-induced symptoms in banana roots and corm. A) Adult female of *R. similis* at 20x magnification. B) In the center a healthy root (cream-white color) and on either side, roots with purple, reddish-brown discoloration extending from the epidermis to the vascular cylinder, C) On the right, two apparently healthy, asymptomatic roots containing 19 240 *R. similis* per 100 g of roots. On the right, three roots completely damaged first by *R. similis* (88 560 / 100 g of roots) and later by waterlogging, and D) Reddish-brown discoloration on the corm tissue.

spp. (Van den Bergh *et al*. 2002a). Also, in very young banana roots under *in vitro* conditions, *M. incognita* can penetrate the roots and cause damage (Coosemans *et al*. 1994). Jonathan and Rajendran (2000a) found a significant reduction in root weight for the higher initial inoculations in their study working with increasing inoculations from 0 to 10 000 individuals in pots of 105 kg soil capacity. In contrast, no negative effect on growth was observed in *Musa* AAB plants, inoculated with *M. incognita* and cultivated in 10 L pots in Ivory Coast (Adiko 1989).

In Malaysia, Razak (1994) reported stunted growth and small bunches due to the infection of *M. incognita* in 'Pisang nangka' and 'Pisang mas'. Similar effects on plant growth have been reported in India (Patel *et al*. 1996) where a delay in flowering was also observed. Van den Bergh *et al*. (2000) reported that *Meloidogyne* spp. had the most negative effect on the bunch characteristics of banana plants in Vietnam. High

Meloidogyne spp. populations, up to 66,000 per 100 g of roots, have been reported in ' Grande naine' vitroplants in field conditions in Cameroon (Fogain 1994).

'Giant Cavendish' bananas, inoculated with 1000, 10 000 or 20 000 *M. incognita,* suffered bunch weight reductions of 26, 45 and 57% respectively (Davide and Marasigan 1985). In our experiment, carried out in 200 L drums, *M. incognita* (Figure 13A-C) did not significantly reduce root weight, 0.5 kg (9%), and did not significantly increase root damage, but it did significantly suppress bunch weight by 7.5 kg (32%) (Figure 11A-B). This reduction in yield coincides with Jonathan and Rajendran's results (2000b), which found bunch weight increases of 31% when controlling this nematode with nematicide. The observed root symptoms (Figure 13D) are close to those reported by Sikora and Schlösser (1973), Pinochet (1977), Tarté and Pinochet (1981), De Waele and Davide (1998) and De Waele (2000). Deformation, bifurcation, swellings and stunting on primary and secondary roots are the most common symptoms where fine roots are rare. Sometimes gall formation is observed close to the root tip.

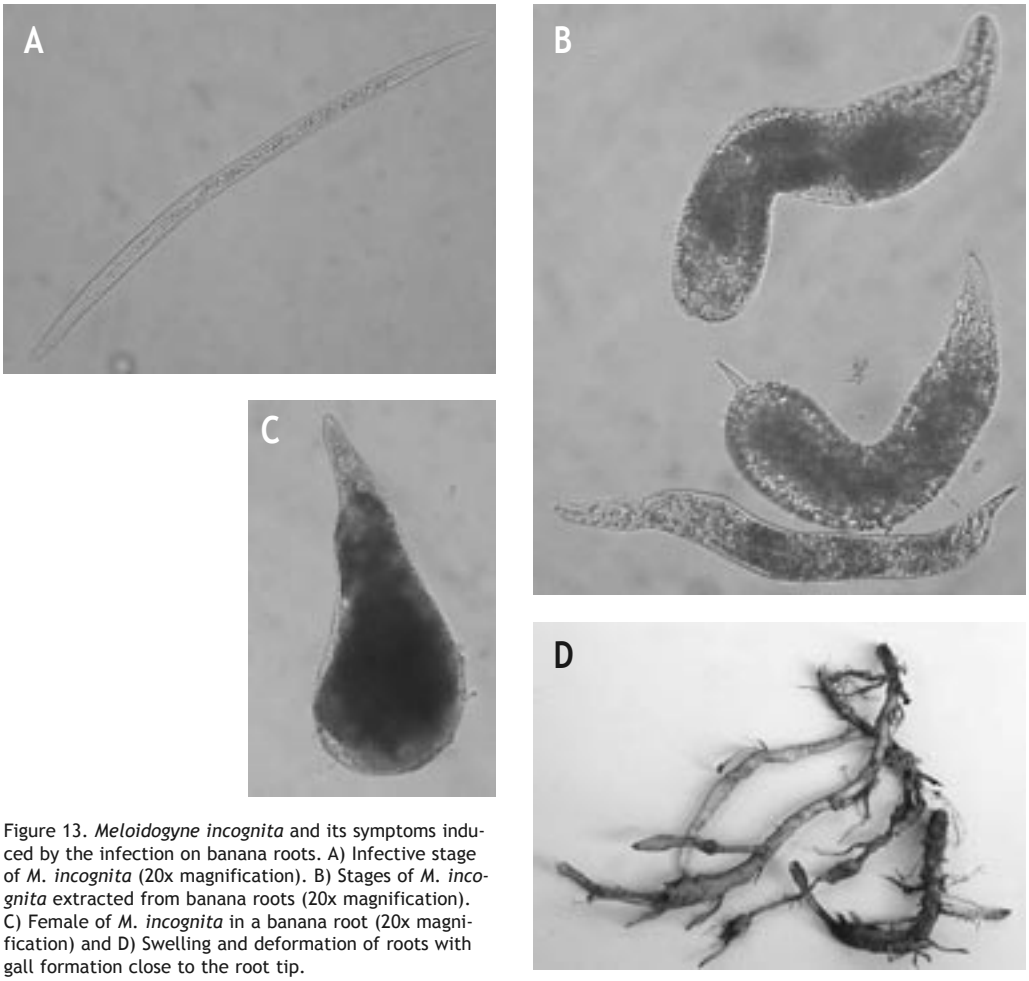


Figure 13. *Meloidogyne incognita* and its symptoms induced by the infection on banana roots. A) Infective stage of *M. incognita* (20x magnification). B) Stages of *M. incognita* extracted from banana roots (20x magnification). C) Female of *M. incognita* in a banana root (20x magnification) and D) Swelling and deformation of roots with gall formation close to the root tip.

Pathogenicity and symptoms of *Pratylenchus coffeae*

Van den Bergh *et al.* (2002a) observed a reduction in fresh root weight in 3 experiments with 24 Vietnamese genotypes of banana inoculated with 1,000 *P. coffeae*. Pinochet (1978), Tarté (1980), Rodríguez (1990), Bridge *et al*. (1997) also found that *Pratylenchus* spp. damaged banana roots and reduced yield. In our experiment, carried out in 200 L drums, *P. coffeae* (Figure 14A) did not significantly reduce root weight -0.58 kg (11%), but it did significantly increase root damage by 129%, and significantly suppressed bunch weight by 5.6 kg (24%) (Figure 11A-B). Symptoms (Figure 14B) induced by *P. coffeae* infection were very similar to those caused by *R. similis* and coincided with those described by Pinochet (1978), Bridge *et al*. (1997) and Gowen (2000a). Purple or black necrosis of the epidermis and cortical root parenchyma with surface cracks occurred.

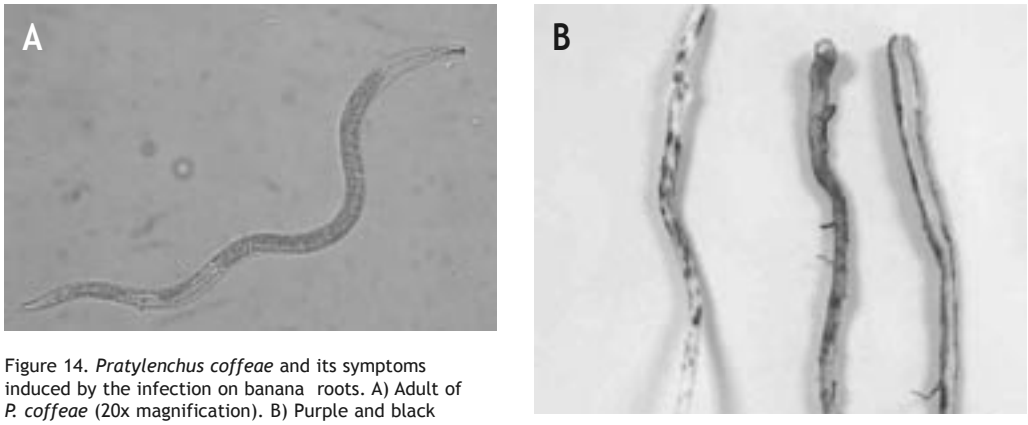


Figure 14. *Pratylenchus coffeae* and its symptoms induced by the infection on banana roots. A) Adult of *P. coffeae* (20x magnification). B) Purple and black necrosis extending from the root epidermis to the vascular cylinder.

Pathogenicity and symptoms of *Helicotylenchus multicinctus*

Helicotylenchus multicinctus and *H. dihystera* (McSorley and Parrado 1986, Davide 1996, Mani and Al Hinai 1996, Chau *et al*. 1997) damage the banana root system and reduce yield by 19% (Speijer and Fogain 1999) to 34% (Reddy 1994). There are mixed reports on the effect of *H. multicinctus* in potted plants. Barekye *et al*. (1999) found a root weight reduction in some *H. multinctus* inoculated plants compared with plants without nematodes. In Uganda, a non-significant reduction in root weight was observed in *Musa* AAA-East Africa cultivar 'Kisansa' plants inoculated with 1000 *H. multicintus* (Barekye *et al*. 2000). In greenhouse experiments, we observed fresh root weight reductions in *Musa* AAA 'Grande naine' plants inoculated with 515 *H. multicinctus*.

In Florida, *H. multicinctus* can cause severe root damage resulting in the toppling of mature plants (McSorley 1986, Gowen 1995). According to McSorley and Parrado (1986), this nematode is more important in subtropical banana production areas. In Lebanon, *H. multicinctus* is considered the most important banana root parasitic nematode (Sikora and Schlösser 1973). The same authors felt that this nematode, together

with *M. incognita,* was associated with the general decay of the banana root system observed.

In our experiment carried out in 200 L drums, *H. multicinctus* (Figure 15A) did not significantly reduce either root weight, 0.42 kg (8%), or increase root damage, 19%, or suppress bunch weight, 0.9 kg (4%) (Figure 11A-B). However, in Israel, bunch weight increased by 18% when controlling this nematode with nematicide (Minz *et al*. 1960). The symptoms (Figure 15B) in the plants infected with *H. multicinctus* in drums coincide with those observed by McSorley (1986) and Gowen (2000b). Tertiary roots appeared necrotic and fell off when the roots were handled. Thicker and larger roots showed small black-brown surface lesions and larger necrotic areas.

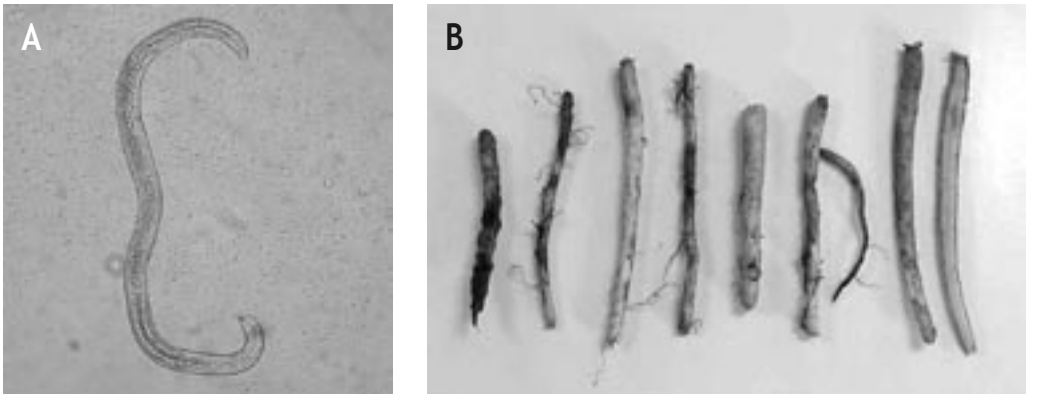


Figure 15. *Helicotylenchus multicinctus* and its symptoms induced by the infection on banana roots. A) Adult of *H. multicinctus* (20x magnification). B) Small black-brown root surface lesions and larger necrotic areas.

Practical implications of mixed nematode populations

The different parasitic habits of the nematode genera present - migratory endoparasites (*R. similis* and *Pratylenchus* spp.), sedentary endoparasites (*Meloidogyne* spp.) and ecto-endoparasites, feeding on subsurface tissue (*H. multicinctus*) - are likely to exacerbate root damage, because of lesions at feeding sites in the root cortex and throughout the root tissue. Usually control is recommended when *R. similis* population density exceeds a specific number per 100 g of roots, but the other nematodes also reduce the root system and yield. Therefore, development of nematode management tactics requires consideration of the damage caused by the total phytonematode population.

In current breeding programmes, resistance to black Sigatoka is, together with a high yield and good postharvest qualities, the most important factor in the screening process. Nevertheless, some programs could also incorporate resistance to *R. similis*. This is the case in different FHIA hybrids. Part of the 'Pisang jari buaya' group (*Musa* AA) demonstrated resistance (Wehunt *et al*. 1978, Viaene *et al*. 2000 and 2003), and this trait was, through the SH-3142 improved diploid (Pinochet and Rowe 1979), successfully incorporated into a series of FHIA hybrids. Other potential sources of resistance to *R. similis* are 'Kunnan' and 'Paka' (*Musa* AA section Eumusa) (Collingborn and Gowen 1997), and the Fe'i varieties 'Menei' and 'Rimina' (section Australimusa) (Stoffelen

et al. 1999a). Even if this resistance was identified, isolated and incorporated into commercial cultivars, this would not resolve the problem, because of the existence of polyspecific nematode communities. Changes in the nematode composition will occur, favouring root parasitic nematodes to which these hybrids are not resistant. Also, differences in the aggressiveness of *R. similis* have been reported (Sarah *et al*. 1993, Fallas *et al* 1995, Marin *et al*. 1999) when comparing populations. Therefore, broad-spectrum resistance should be sought, conferring resistance to a wide range of known *R. similis* biotypes, and to the other important parasitic nematodes. Up to now, 'Yangambi km5' shows resistance to *R. similis* (Sarah *et al*. 1992, Price 1994) and *P. coffeae* (Viaene *et al*. 1998), but its progeny produce abnormal leaves and/or erect and semi-erect bunches (Stoffelen *et al*. 1999a). Another source of resistance to these two nematodes is *Musa acuminata* spp. *burmannicoides* 'Calcutta 4' (Viaene *et al.* 2000). This variety has already been used in the IITA breeding programme (Swennen and Vuylsteke 1993, Tenkouano *et al*. 2003), and experiments are on-going.

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The effect of arbuscular mycorrhizal fungi (AMF)-nematode interactions on the root development of different *Musa* genotypes

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Abstract

In this study, the effect on *Musa* plant growth, with focus on the root system, of two arbuscular mycorrhizal fungi (AMF), *Glomus mosseae* and *G. intraracides*, and two migratory endoparasitic nematodes, *Radopholus similis* and *Pratylenchus coffeae*, were examined. In addition, the AMF-nematode interaction was studied. Ten *Musa* genotypes with different root systems were selected. Based on their relative mycorrhizal dependency and their host plant response, two genotypes 'Obino l'ewai' and 'Calcutta 4') were selected for AMF-nematode interaction studies. The experiments were performed under greenhouse conditions.

Mycorrhizal colonization of the roots resulted in significantly better plant growth, even in the presence of nematodes. The effect of AMF on the root system was genotype-dependent and seemed to be related to the relative mycorrhizal dependency of the genotype. Genotypes with a proportionally high secondary and tertiary root weight (like 'Calcutta 4' and 'Kayinja') had a rather low mycorrhizal dependency and a high fresh root weight. For those genotypes, AMF had no influence on the branching of roots. Genotypes with a proportionally high weight of primary roots (like 'Obino l'ewai', 'Igitsiri', 'Mbwazirume', 'Pisang lilin' or 'Pisang jari buaya') had a medium to high mycorrhizal dependency and the presence of AMF increased root branching. The nematodes also affected the root system, especially by decreasing branching. Nematode population densities were significantly reduced in the presence of AMF, except for *P. coffeae* in 'Obino l'ewai'.

In this study, the effect of the interaction between AMF and nematodes on root morphology was studied for the first time. The analysis is rather complex since many factors are involved. The three factors: genotype, AMF and nematode influence the root system; making firm conclusions very difficult. All together, there is no net effect, since the reduced branching caused by the nematodes, is counter balanced by the increased branching caused by AMF. This could be a possible strategy to reduce the negative impact of nematode infection.

Resumen - Efecto de las interacciones entre hongos micorrícicos arbusculares (HMA) y nematodos en el desarrollo radical de diferentes genotipos de *Musa*

En este estudio, se investigó el efecto de dos hongos micorricicos arbusculares (AMF por sus siglas en inglés). *Glomus mosseae* y *G. Intraradices*, y de dos nematodos endoparásitos migratorios, *Radopholus similis* y *Pratylenchus coffeae*, sobre el crecimiento de plantas de *Musa*, con énfasis en su sistema radical. Adicionalmente, se estudió la interacción AMF-nematodo. Se seleccionaron 10 genotipos de *Musa* con diferentes sistemas radicales. Basado en su dependencia relativa a las micorrizas y su respuesta como planta hospedera, se seleccionaron dos genotipos ('Calcutta 4' and 'Obino l'ewai') para estudiar la interacción AMF-nematodo. Los experimentos se efectuaron bajo condiciones de invernadero.

La micorrización resultó en un crecimiento significativamente mejor de la planta, aún en presencia de nematodos. El efecto de la AMF sobre el sistema radical dependió del genotipo y pareció estar relacionado con la dependencia relativa del genotipo a las micorrizas. Los genotipos con un peso proporcionalmente alto de raíces secundarias y terciarias (como 'Calcutta 4' y 'Kayinja') tuvieron

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una dependencia bastante baja a las micorrizas y un alto peso de raíces frescas. Para estos genotipos, la AMF no influyó en las ramificaciones. Los genotipos con un peso proporcionalmente alto de raíces primarias (como 'Obino l'ewai', 'Igitsiri', 'Mbwazirume', 'Pisang lilin', o 'Pisang jari buaya') mostraron una dependencia de mediana a alta a las micorrizas y la presencia de la AMF incrementó las ramificaciones. Los nematodos también afectaron el sistema radical, reduciendo el número de ramificaciones. Las densidades de población de los nematodos se redujeron significativamente en presencia de la AMF, con excepción de *P. coffeae* en 'Obino l'ewai'.

En este estudio, se investigó por vez primera, el efecto de la interacción AMF - nematodos en la morfología radical. Este análisis es bastante complejo pues involucra muchos factores. Los tres factores - genotipo, AMF y los nematodos - influenciaron el sistema radical, lo que dificulta establecer conclusiones definitivas. En resumen, no existe un efecto neto, porque la reducción en las ramificaciones causadas por los nemátodos se equilibra con el aumento de las mismas causado por la AMF. Esta podría ser una estrategia para reducir el impacto negativo de la infección por nematodos.

Introduction

Roots function both as a support system and as the nutrient uptake organ of plants. Root morphology changes in response to the soil environment to minimize the metabolic cost of maintaining the root system. In response to nutrient-limiting conditions, plants may increase root fineness, root/shoot ratio or the number or length of the root hairs (Hetrick 1991). Each of these adaptations involves a different metabolic cost. Mycorrhizae are another alternative to such changes.

Several studies have shown that colonization by arbuscular mycorrhizal fungi (AMF) can influence root system morphology of host plants (Tisserant *et al.* 1992). Most plants infected with AMF develop a denser root system, with a higher number of shorter primary roots of a greater diameter (Berta *et al.* 1993). In most plants, the branching of roots increased after AMF colonization (Schellenbaum *et al.* 1991, Tisserant *et al.* 1992). However, less-branched root systems were observed in mycorrhizal plants of *Andropogon gerardii* (Hetrick *et al.* 1988) and *Gossypium hirsutum* (Price *et al.* 1989).

Different mechanisms have been suggested for the alteration of root systems following AMF colonization (Berta *et al.* 1993). In physiological aspects, it is well recognized that AMF can increase nutrient absorption, especially for elements with low mobility in the soil such as phosphorus (P). Other studies have reported changes in phytohormone balance in association with AMF (Dannenberg *et al.* 1992). Anatomically depressed meristimatic activity of mycorrhizal root apices was found (Berta *et al.* 1993).

Arbuscular mycorrhizal fungi are able to alter the rooting strategy of plants not only in response to soil fertility but also in response to other micro-organisms in the rhizosphere (Hetrick 1991). The rhizosphere comprises both beneficial and pathogenic micro-organisms. Migratory endoparasitic nematodes are pathogens infecting roots of many different hosts. Especially in the tropics, they cause huge yield losses (Sasser and Freckman 1987). The infected roots become necrotic due to the nematode, thereby inhibiting nutrient and water uptake and weakening the anchorage of the plant. Until now, the most commonly used approach to control these pathogens is the use of nematicides. However, nematicides are expensive and toxic both for the user and the environment. The application of AMF could be a possible approach to nematode management, as a part of an integrated pest management strategy.

In *Musa*, there are good indications that genotypes that are more resistant to migratory endoparasitic nematodes have a larger and denser root system than the susceptible

genotypes (Blomme 2000, Stoffelen 2000). Until now, only one study reported the effect of AMF on root system morphology of banana plantlets (Jaizme-Vega *et al.* 1994). The most important modification in root morphology induced in banana plants by AMF consisted of increased branching and increased total root length, which led to a dense rooting pattern. The influence of AMF on the root system of *Musa* genotypes differing in root morphology and the influence of the AMF/nematode interaction on the root system and vice versa has not been studied.

In this paper, we examine whether AMF can be used as a strategy to manage nematodes, by inducing a larger and denser root system. The first objective was to investigate whether the effect of AMF on the root system differed for Musa genotypes with initially different root systems. The second objective was to study the interaction between AMF and two plant-parasitic nematodes, *R. similis* and *P. coffeae*, on two *Musa* genotypes with a different root system structure and different responses to AMF (high and low mycorrhizal dependency). The influence of the AMF on the root system and the influence of the altered root system on the nematode reproduction were studied.

Materials and methods

Musa tissue culture plants were obtained from the International *Musa* germplasm collection at the INIBAP Transit Centre (ITC) at K.U.Leuven, Belgium (Table 1). The plant material was proliferated, regenerated and rooted in test tubes on Murashige and Skoog (MS) medium (Murashige and Skoog 1962).

The *Glomus mosseae* isolate, used in this study, was originally recovered from Pome banana (*Musa* AAB, Pome sub-group) grown on a biological farm in Los Realejos, Tenerife, Canary Islands, Spain. The *Glomus intraradices* isolate was recovered from banana in Martinique (MUCL 41833). The isolates were maintained and propagated on

Table 1. Information on *Musa* genotypes differing in root morphology.

Accession name	ITC number1	Genome, group
Calcutta 4	0249	AA, burmannicoides
Grande naine	1256	AAA, Cavendish
Igitsiri	0081	AAA, Mutika/Lujugira
Kayinja	/	ABB, Pisang Awak
Mbwazirume	0084	AAA, Mutika/Lujugira
Obino lewai	0109	AAB, Plantain
Pisang lilin	1400	AA
Pisang jari buaya	0690	AA, Pisang jari buaya
Yangambi km5	1123	AAA, Ibota
Gros Michel	1122	AAA, Gros Michel

1 ITC number = accession number at the International Musa Germplasm collection at the INIBAP Transit Centre at KULeuven.

sorghum cultures. Two *R. similis* populations differing in pathogenicity were selected: a highly pathogenic population from Uganda and a less pathogenic population from Indonesia. The *P. coffeae* population was isolated from banana roots in Ghana. They were maintained in monoxenic conditions on carrot discs at 27±1°C in the dark. Prior to inoculation, the nematodes were isolated using the Baermann funnel technique (Hooper 1990).

In the first three experiments, the micropropagated banana plants were transplanted, after deflasking, to germination trays (60 x 40 cm) for early mycorrhizal colonization during the hardening phase. The substrate consisted of a sterilized 2:1 peat-quartz mixture. Arbuscular mycorrhizal inoculum consisted of 1.5 kg rhizosphere soil from 6-months-old sorghum pot cultures of *G. mosseae* containing spores, hyphae and heavily infected root fragments. The inoculum was spread as a layer between two layers of substrate. The plants not receiving mycorrhizal inoculum received a filtrate of soil inoculum free from AMF propagules. Ten plants were included, per treatment. A period of 6 weeks allowed the establishment of the mycorrhizal symbiosis. After these 6 weeks, eight plants per treatment were transplanted to 1-L containers filled with sterilized 2:1 peat-quartz substrate. For each plant, 1 g Osmocote®, a slow release fertilizer, was added to the substrate. During 16 weeks, i.e. 6 weeks in the germination trays followed by 10 weeks in individual containers, the plants were maintained in the greenhouse at an ambient temperature of 20-27°C, with a 12-hour photoperiod (170-190 $\mu mol\ m^{-2}s^{-1}$ PAR) and a relative humidity of 50-70%.

In the second part, we studied the interaction between AMF and banana nematodes and the selected genotypes were colonized with mycorrhizae as described in the previous paragraph. In the treatments with nematodes, the plants were inoculated with 1000 vermiform (juvenile and adult) nematodes per plant, 8 weeks after planting (2 weeks after transplanting to individual containers). After nematode inoculation, the plants were kept in the greenhouse for 8 weeks (for *R. similis*) or 10 weeks (for *P. coffeae*) to allow nematode reproduction.

In the first three experiments, plant growth was assessed 16 weeks after planting. Plant height, number of leaves, foliar surface, fresh and dry shoot weight and fresh root weight were measured for each plant. The relative mycorrhizal dependency (RMD) was determined by expressing the difference between the dry weight of the mycorrhizal plant and the average dry weight of the non-mycorrhizal plant as a percentage of the dry weight of the mycorrhizal plant (Plenchette *et al.* 1983). Root growth was characterized by the total root weight, the weight of the primary roots, weight of the secondary and tertiary roots and weight of the *in vitro* roots. The roots present at time of deflasking (i.e. beginning of the experiment) and thus formed under *in vitro* conditions are considered as *in vitro* roots.

The AMF infection was determined in the mycorrhizal plants. For assessing the mycorrhizal colonization, secondary and tertiary root samples were collected and stained with 0.05% trypan blue in lactic acid (Koske and Gemma 1989). After clarifying, staining and destaining, 20 1-cm fine root segments were mounted on slides and observed under a light microscope. The frequency of AMF colonization (F %) was calculated as the percentage of root segments colonized by either hyphae or arbuscules or vesicles. In the experiments where the interaction between AMF and nematodes was studied, plant growth and mycorrhizal colonization were assessed as described above. In the treatments inoculated with nematodes, nematode reproduction was assessed (Speijer and De Waele 1997).

The data were analyzed with the STATISTICA® package (Statsoft, 1997). All plant parameters were analyzed by two-way ANOVA, while the mycorrhizal data and nematode data were analyzed by one-way ANOVA. Before analysis, data on nematode reproduction were log(x+1) transformed. Data for frequencies of mycorrhizal colonization were arcsine(x/100) transformed. Means were separated by the Tukey test ($P \leq 0.05$).

The relative proportions of the *in vitro*, primary and secondary and tertiary roots were compared in a Chi-square test ($P \leq 0.05$).

Results

Effect of two AMF on the root development of 10 *Musa* genotypes

Ten genotypes were tested in three experiments with 'Grande naine' as a reference. Overall, the root colonization with both *G. mosseae* (experiments 1 + 2) and *G. intraradices* (experiment 3) had a beneficial effect on root growth (Table 2). The presence of AMF increased the total fresh root weight by increasing the weight of the first order

Table 2. Influence of *Glomus mosseae* and *G. intraradices* on the root growth of *Musa* genotypes differing in root morphology, 16 weeks after planting.

	Root fresh weight, g			
	Total	1st order	2nd and 3rd order	*In vitro* roots
		Experiment 1		
Without *G.mosseae*				
Grande naine	16.9 A	4.7 AB	11.7 A	0.4 A
Calcutta 4	18.3 A	5.8 B	12.4 A	0.2 A
Kayinja	22.0 B	6.2 B	15.4 B	0.5 B
Obino l'ewai	15.7 A	6.0 A	8.9 A	0.8 AB
With *G. mosseae*				
Grande naine	39.3 A	10.7 AB	28.5 A	0.1 A
Calcutta 4	36.2 A	10.9 B	25.3 A	0 A
Kayinja	46.3 B	12.5 B	33.2 B	0.6 B
Obino lewai	37.2 A	7.7 A	29.5 A	0 AB
	***	***	***	NS
		Experiment 2		
Without *G. mosseae*				
Grande naine	12.6 a	5.4 bc	6.7 ab	0.53 abc
Igitsiri	5.1 a	1.8 a	3.0 a	0.29 a
Mbwazirume	5.4 a	2.5 ab	2.6 a	0.26 a
Pisang lilin	10.0 a	4.9 abc	4.8 ab	0.29 a
With *G. mosseae*				
Grande naine	45.1 c	13.2 d	31.5 e	0.44 ab
Igitsiri	29.1 b	5.6 bc	21.5 d	2.01 c
Mbwazirume	23.5 b	6.2 c	17.1 cd	0.16 a
Pisang lilin	23.7 b	10.5 d	11.7 bc	1.53 bc
		Experiment 3		
Without *G. intraradices*				
Grande naine	5.75 a	3.16 a	2.59 a	/
Pisang jari buaya	7.25 a	3.79 a	3.46 a	/
Yangambi km5	7.50 ab	4.59 a	3.66 a	/
Gros Michel	6.75 a	3.62 a	3.12 a	/
With *G. intraradices*				
Grande naine	15.75 bc	6.49 b	9.26 bc	/
Pisang jari buaya	18.88 c	7.44 b	11.44 c	/
Yangambi km5	15.12 c	6.50 b	8.62 b	/
Gros Michel	15.87 c	6.31 b	9.56 c	/

Within a column in an experiment, means followed by the same letter, are not significantly different at P=0.05. Small letters refer to an interaction effect, capital letters refer to a main effect by cultivar. *, **, *** indicate significant differences at P < 0.05; 0.01; 0.001 for a main effect by AMF. NS indicates no significant differences.

roots and of the secondary and tertiary roots. The weight of *in vitro* roots (only measured in experiment 1 and 2) was not altered by the presence of AMF, except for 'Igitsiri' and 'Pisang lilin'. The number of primary roots tended to increase when AMF were present (data not shown). In general, the AMF had a positive influence on root growth, but the impact differed among genotypes.

After 16 weeks, the proportion of *in vitro* roots was very small in both mycorrhizal and non-mycorrhizal treatments (Figure 1). The proportion of secondary and tertiary roots was larger than the proportion of primary roots, but some variation among genotypes was observed. The non-mycorrhizal 'Pisang lilin' and 'Mbwazirume' had the largest proportion of primary roots (49% and 46%, respectively), while the mycorrhizal 'Igitsiri' had the smallest proportion of primary roots (19%). The presence of *G. mosseae* did not influence the root proportions of 'Calcutta 4', 'Kayinja' or 'Pisang lilin' (Figure 1). For 'Grande naine', the results were not very clear. In the first experiment, the AMF did not influence the root proportions, while in the second experiment, the presence of the AMF significantly decreased the proportion of primary root weight. For 'Obino l'ewai', 'Igitsiri' and 'Mbwazirume', the AMF significantly increased branching of the root system as indicated by a proportional decrease of the primary root weight in favour of an increase of the secondary and tertiary root weight.

The presence of *G. intraradices* significantly increased the proportion of secondary and tertiary roots of all four genotypes tested (Figure 2). In the non-mycorrhizal plants the proportion of primary roots ranged from 52% ('Pisang jari buaya') to 61% ('Yangambi km5'), while in the mycorrhizal plants the proportion of primary roots ranged from 39% ('Pisang jari buaya') to 43% ('Yangambi km5').

Mycorrhizal colonization with *G. mosseae* and *G. intraradices* was successful, as indicated by the high frequencies (Table 3). Differences in relative mycorrhizal depen-

Table 3. Root colonization by *Glomus mosseae* (exp. 1 and 2) and G. intraradices (exp. 3) and the relative mycorrhizal dependency (RMD) of *Musa* genotypes differing in root morphology, 16 weeks after planting.

Genotype	F%	I%	RMD (%)
		Experiment 1	
Grande naine	50 a	17 a	66 bc
Calcutta 4	61 a	20 a	50 a
Kayinja	56 a	21 a	58 ab
Obino l'ewai	54 a	15 a	75 c
		Experiment 2	
Grande naine	72 b	22 b	62 a
Igitsiri	70 b	16 ab	83 c
Mbwazirume	50 a	14 a	70 b
Pisang lilin	33 a	13 a	70 b
		Experiment 3	
Grande naine	88 a	28 a	37 a
Pisang jari buaya	88 a	29 a	60 a
Yangambi km5	89 a	28 a	48 a
Gros Michel	93 a	35 a	62 a

F% = frequency of the mycorrhizal colonisation in the roots and I% = intensity of the mycorrhizal colonisation in the roots. Within a column in an experiment, means followed by the same letter, are not significantly different at P=0.05.

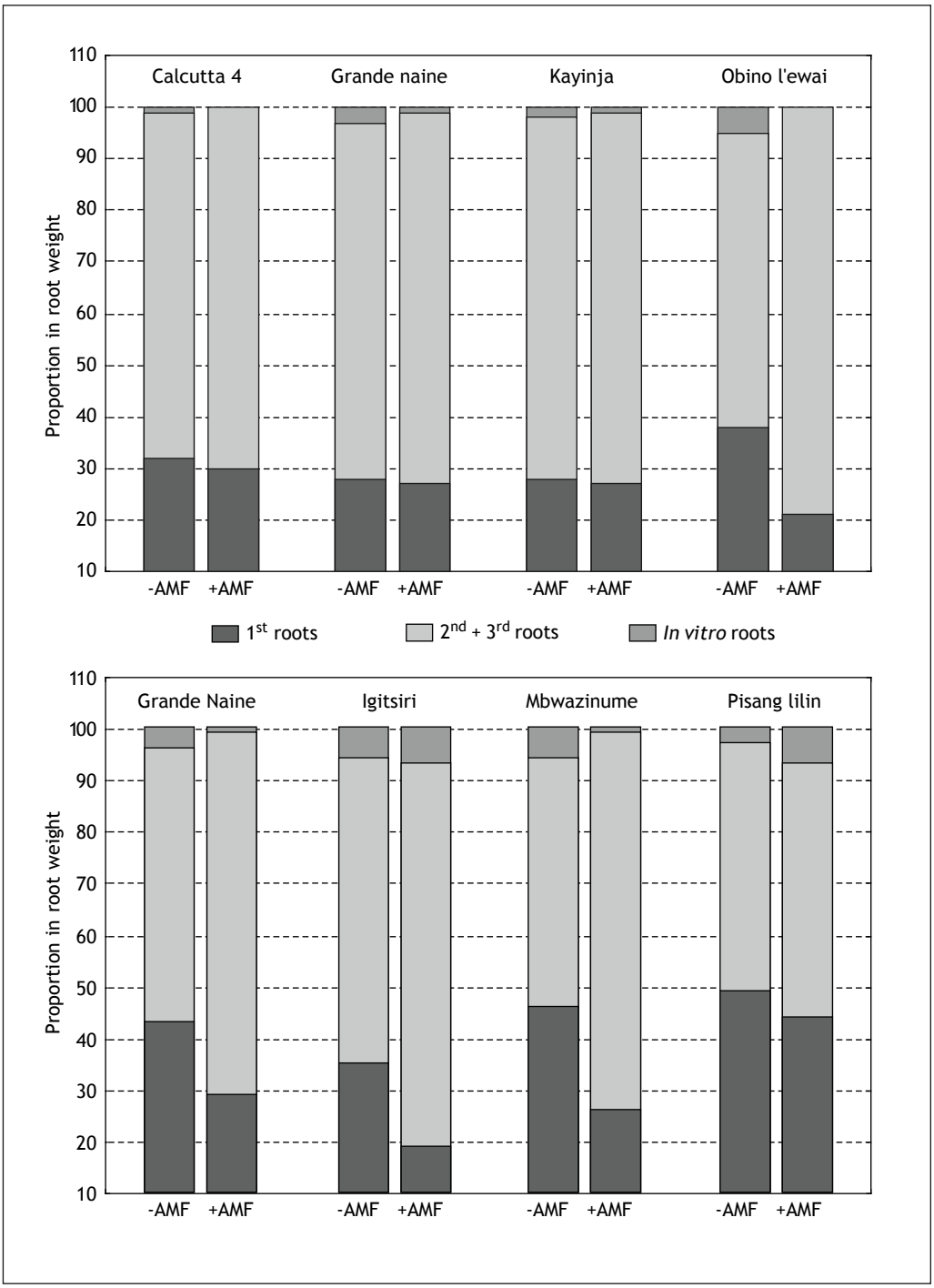


Figure 1. Effect of *Glomus mosseae* (AMF) on the proportional root weight of primary (1st), secondary (2nd) and tertiary (3rd) and *in vitro* roots of four different *Musa* genotypes 16 weeks after planting (top = experiment 1, bottom = experiment 2)

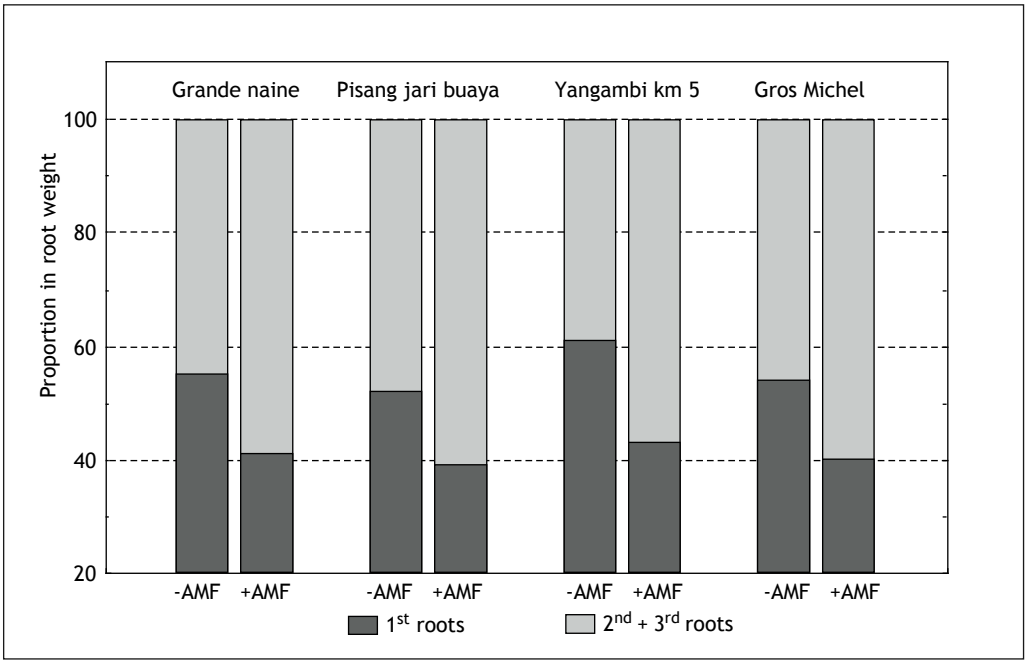


Figure 2. Effect of *Glomus intraradices* (AMF) on the proportional root weight of primary (1st), secondary (2nd) and tertiary (3rd) and *in vitro* roots of four different *Musa* genotypes 16 weeks after planting.

dency (RMD) were observed in the first and second experiment. 'Obino l'ewai' and 'Calcutta 4' were selected for further experiments based on their RMD, which were high and low respectively.

Effect of AMF-nematode interactions on root development of two selected *Musa* genotypes

In experiments 4 and 5, 'Obino l'ewai' showed a significantly better plant growth when colonized by *G. mosseae* (data not shown). The presence of the AMF had a positive influence on root growth, while the presence of *R. similis* or *P. coffeae* did not affect root growth in general (Table 4). 'Obino l'ewai' colonized with AMF had significantly higher primary, secondary and tertiary root weights. The presence of *P. coffeae* did not reduce mycorrhizal colonization. The *R. similis* population density was significantly reduced when AMF were present, while the *P. coffeae* population density was not affected.

In experiments 6 and 7, 'Calcutta 4' showed significantly better plant growth when colonized with *G. mosseae* (data not shown). The presence of AMF influenced root growth positively, except when plants were infected with *R. similis* from Indonesia (Table 5). Mycorrhizal 'Calcutta 4' plants had significantly higher primary, secondary and tertiary root weights than 'Obino l'ewai' (except for plants infected with *R. similis* from Indonesia). Mycorrhizal colonization was not influenced by the presence of *R. similis* or *P. coffeae*, while the population densities of all nematodes tested were significantly suppressed by *G. mosseae*.

Table 4. Influence of two plant-parasitic nematodes, *Radopholus similis* and *Pratylenchus coffeae*, and the AMF, *Glomus mosseae*, on the root growth of 'Obino l'ewai', 16 to 18 weeks after planting.

	Root fresh weight (g)				AMF (F%)	Nematodes per g roots
	Total	1st order	2nd + 3rd order	*In vitro*		
			Experiment 4			
-AMF/-rs	9.5 AB	4.2 B	4.7 B	0.6	/	/
-AMF/+rs Uganda	4.2 A	2.3 A	1.4 A	0.5	/	1336 B
-AMF/+rs Indonesia	10.0 B	4.5 B	4.8 B	0.7	/	218 A
+AMF/-rs	17.6 AB	6.1 A	10.8 B	0.7	53 b	/
+AMF/+rs Uganda	16.3 A	6.9 A	7.6 A	1.7	31 a	314 B
+AMF/+rs Indonesia	20.1 B	8.7 B	10.4 B	1.3	58 c	74 A
	***	***	***	**		***
			Experiment 5			
-AMF/-pc	4.6	1.2	2.8 B	0.6	/	/
-AMF/+pc	3.7	1.5	1.5 A	0.7	/	100
+AMF/-pc	11.5	3.8	7.5 B	0.2	89	/
+AMF/+pc	10.8	3.5	6.6 A	0.7	89	74
	**	***	***	NS	NS	NS

Within columns and experiments, means followed by the same letter are not significantly different at P=0.05. Lower case letters refer to an interaction effect, upper case letters refer to a main effect by nematodes. *, **, *** indicate significant differences at P < 0.05; 0.01; 0.001 for a main effect by AMF. NS indicates no significant differences.

Table 5. Influence of two plant-parasitic nematodes, *Radopholus similis* (rs) and *Pratylenchus coffeae* (pc), and the AMF, *Glomus mosseae*, on the root growth of 'Calcutta 4', 16 to 18 weeks after planting.

	Root fresh weight (g)				AMF	Nematodes
	Total	1st order	2nd + 3rd order	*In vitro*		
			Experiment 4			
-AMF/-rs	5.4 ab	2.5 ab	2.5 ab	0.4	/	/
-AMF/+rs Uganda	1.6 a	0.6 a	0.6 a	0.4	/	252 B
-AMF/+rs Indonesia	7.6 bc	3.2 b	3.9 ab	0.6	/	171 A
+AMF/-rs	13.0 c	4.2 b	8.5 c	0.3	39	/
+AMF/+rs Uganda	12.6 b	5.3 b	6.8 bc	0.6	40	142 B
+AMF/+rs Indonesia	8.6 bc	4.2 b	3.9 ab	0.5	33	79 A
				NS	NS	*
			Experiment 5			
-AMF/-pc	2.3	0.6	1.6	0.1	/	/
-AMF/+pc	2.1	0.8	1.1	0.2	/	234
+AMF/-pc	9.5	2.2	6.4	0.9	64	/
+AMF/+pc	8.6	2.5	5.3	0.8	48	57
	***	***	***	***	NS	***

Within columns and experiments, means followed by the same letter are not significantly different at P=0.05. Lower case letters refer to an interaction effect, upper case letters refer to a main effect by nematodes. *, **, *** indicate significant differences at P < 0.05; 0.01; 0.001 for a main effect by AMF. NS indicates no significant differences.

For 'Obino l'ewai', the presence of *R. similis* (Ugandan population) significantly reduced the branching of the root system in non-mycorrhizal plants, while mycorrhizal colonization significantly increased root branching in both control plants and plants infected with *R. similis* (Ugandan population) (Figure 3). In the non-mycorrhizal 'Obino l'ewai'

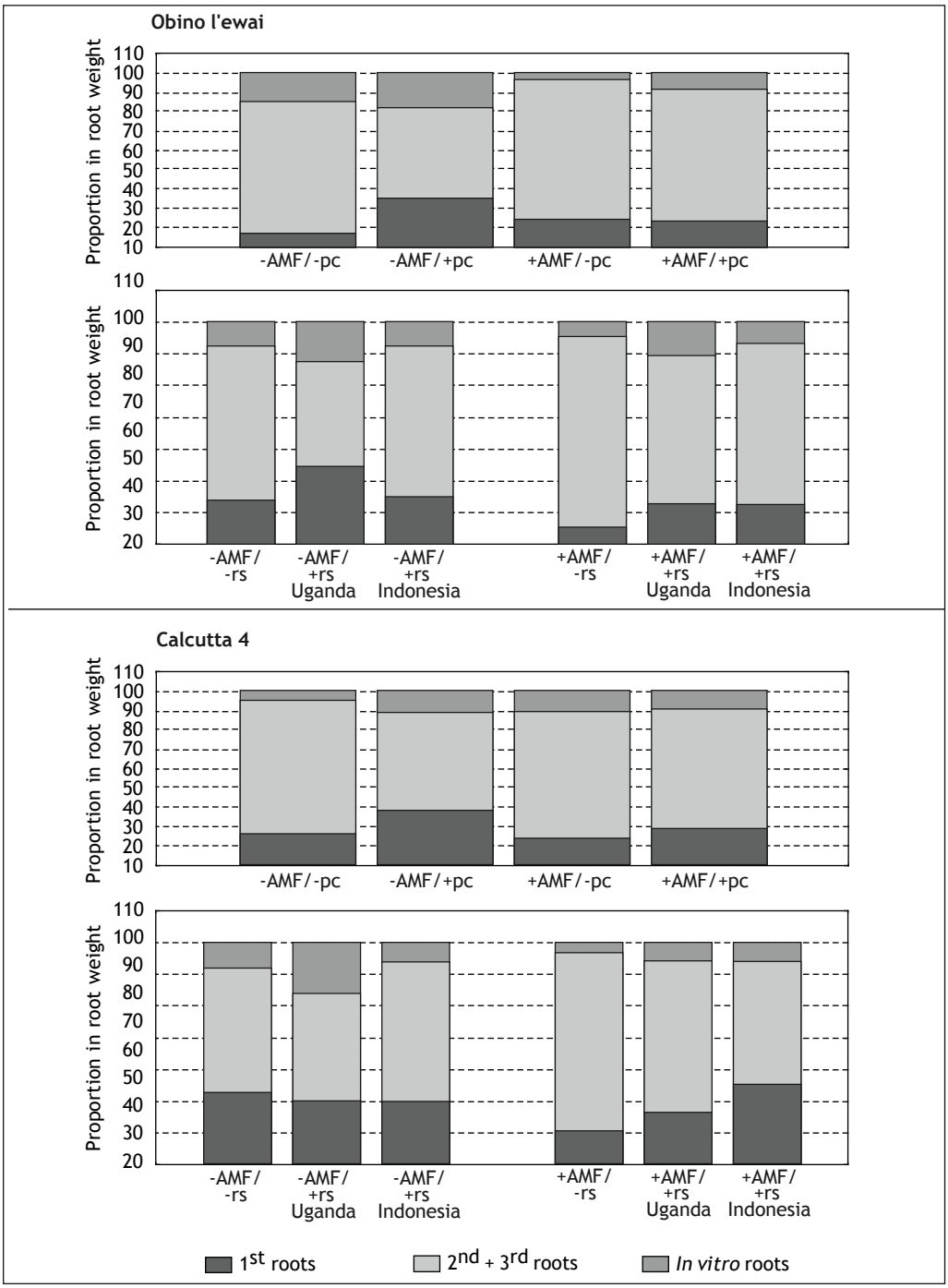


Figure 3. Effect of *Glomus mosseae* (AMF) and *Radopholus similis* (rs) or *Pratylenchus coffeae* (pc) on the proportional root weight of primary(1st), secondary (2nd) and tertiary (3rd) and *in vitro* roots of 'Obino l'ewai' (graphs on the top) and 'Calcutta 4' (graphs on the bottom) 16 (when inoculated with *R. similis*) or 18 weeks (when inoculated with *P. coffeae*) after planting.

plants, the presence of the *P. coffeae* caused a significant decrease in the proportion of secondary and tertiary root weight in favour of an increase in the proportion of primary root weight while in the mycorrhizal plants, no shift in proportions of root weight was observed. In absence of nematodes, the proportion of secondary and tertiary root weight remained the same while proportionally the *in vitro* root weight decreased in favour of the primary root weight. When inoculated with *P. coffeae*, the AMF significantly increased branching of the root system.

For 'Calcutta 4', the presence of *R. similis* (Ugandan and Indonesian population) did not influence the branching of the root system. Mycorrhizal colonization significantly increased the proportion of secondary and tertiary roots in control plants and plants infected with *R. similis* (Ugandan population). For *R. similis* (Indonesian population), no significant effect of the nematode on root morphology was observed. The presence of *P. coffeae* significantly reduced branching in the non-mycorrhizal treatments but not in the mycorrhizal treatments. The presence of AMF did not alter the proportions of the different root types of 'Calcutta 4'.

Discussion

Each of the ten *Musa* genotypes included in our study responded positively to colonization with *G. mosseae* or *G. intraradices*. Our findings are similar to the results obtained by Jaizme-Vega and Azcon (1995), Pinochet *et al.* (1997) and Yano-Melo *et al*. (1999) on *Musa* species with different *Glomus* species and under different experimental conditions. Our study confirms the beneficial effect of colonization with mycorrhizae in the initial phase of plant growth. However, the magnitude of the response varied among genotypes.

A great variation in dependency on mycorrhizal colonization has previously been observed among *Musa* spp. (AAA group; Declerck *et al.* 1995). In our study, RMD also differed among genotypes when colonized with *G. mosseae*: the lowest RMD was observed for 'Calcutta 4' and the highest RMD for 'Obino l'ewai'and 'Igitsiri'. When colonized with *G. intraradices*, no differences in RMD were observed. However, for 'Grande naine' the RMD appeared to be different depending on the AMF. This illustrates that RMD is not only genotype dependent, but also AMF dependent.

The presence of *R. similis* or *P. coffeae* did not influence root growth. Previous studies in *Musa* indicate that *R. similis* and *M. javanica* do not influence plant growth at the early stages of infection (Umesh *et al*. 1988, Pinochet *et al*. 1997, Elsen *et al*. 2003). These root pathogens destroy the root system, hampering water and nutrient uptake. Normally, this results in poorer growth of the infected plant, but under these experimental conditions, the short time of the experiment was probably not sufficient to detect these negative effects on plant growth.

Glomus mosseae reduced nematode population build-up for both nematode species, regardless of the pathogenicity of the population (with the exception of *P. coffeae* in 'Obino l'ewai'). Many reports have demonstrated a decrease in nematode population development resulting in a increased resistance and/or tolerance of *R. similis* and *Pratylenchus* spp. (Smith and Kaplan 1988, Vaast *et al.* 1998). Previous studies in

Musa reported a suppressive effect of AMF on the reproduction of *R. similis* and *P. coffeae* (Elsen *et al.* 2003, Umesh *et al.* 1988).

Based on our results, it appears that the effect of the AMF on the branching of the root system is genotype-dependent. Genotypes with a proportionally high secondary and tertiary root weight (like 'Calcutta 4' and 'Kayinja') have a rather low mycorrhizal dependency and a high fresh root weight. These findings corroborate the study by Declerck *et al.* (1995). In addition, the AMF has no influence on the branching of the roots of genotypes with this type of root system. Therefore, it appears that genotypes with a well-developed root system (large, well-branched, good development of root hairs) have no need to establish a mycorrhizal symbiosis. Genotypes with a proportionally high root weight of primary roots (like 'Obino l'ewai', 'Igitsiri', 'Mbwazirume' or 'Pisang lilin') have a high to medium mycorrhizal dependency and the presence of AMF increases branching. In this study, the genotypes representing this type of root system (i.e. high proportion of primary roots), have been cultivated for a long time and are known for their poor anchorage and root growth. It is possible that these genotypes use the AMF symbiosis as a strategy to improve their root growth and the development of their root system.

It is generally assumed that a denser root system has a greater absorbing power than an elongated one. Therefore, not only the network of extra-root mycelium, with its absorbing power and explorative functions, but also the type of root system could improve the beneficial growth of mycorrhizal plants. Moreover, a much branched root system is particularly useful for *Musa*, as they are easily uprooted by strong winds, especially when the root system is weakened by the presence of nematodes.

The presence of a highly pathogenic *R. similis* or a *P. coffeae* population influenced the root system of both 'Obino l'ewai' and 'Calcutta 4' as evidenced by reduced branching. Thus the proportion of primary roots increased in mycorrhized plants. However, the total root weight was not affected by the nematodes. The tested *R. similis* population with a low pathogenicity did not influence root branching. In *Musa*, Stoffelen (2000) showed that nematodes can infect all root types, including *in vitro* roots, but they have a preference for the primary roots. In that study, 70 to 90% of the nematodes were extracted from the primary roots, but no reduction of primary root weight was observed. However, the nematode infection caused a significant reduction of the secondary and tertiary root weight (Stoffelen, 2000). Our findings confirm this for *P. coffeae* infection in 'Obino l'ewai' and 'Calcutta 4' and for Ugandan *R. similis* infection in 'Obino l'ewai'.

In our study, the effect of the interaction between AMF and nematodes on root morphology was studied for the first time. The analysis is rather complex since there are many factors involved. The three factors: genotype, AMF and nematode influence the root system, making conclusions very difficult. All together, there is no net effect, since the reduced branching caused by the nematodes is counterbalanced by the increased branching caused by AMF. This could be a possible strategy to reduce the negative impact of nematode infection.

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Secondary metabolites in roots and implications for nematode resistance in banana (*Musa* spp.)

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Abstract

Secondary metabolites and more specifically phenylpropanoids, in roots of *Musa* have been related to nematode resistance based on the differential presence of these compounds in the roots of resistant and susceptible cultivars. However, a strong biochemical basis for resistance has not yet been elucidated. The current study demonstrated biochemical differences in the phenylpropanoid pathway of secondary metabolism between cultivars resistant to the banana nematode *Radopholus similis*, 'Yangambi km5' and 'Pisang jari buaya', and the susceptible 'Grande naine'. Unlike previously reported results, lignification and preformed phenolic cells were not found to be specific features of the resistant cultivars. Accumulation of sinapic acid in the thickened cell walls of the endodermis and vascular elements was induced by nematode infection in both the resistant and the susceptible cultivars, while flavonoid-containing cells in the vascular cylinder were only found in resistant cultivars after infection. 'Grande naine' roots contained the highest total phenolic content, which could be related to high amounts of proanthocyanidins. In 'Yangambi km5' roots, the proanthocyanidin and total phenolic content was the lowest, but mean amounts of total phenols increased after infection, unlike in the other cultivars.

Resumen - Metabolitos secundarios en raíces y sus implicaciones para la resistencia a nematodos en banano (*Musa* spp.)

Metabolitos secundarios y más específicamente los fenilpropanoides, en sistemas radicales de *Musa*, han sido relacionados a la resistencia a nematodos, basados en la presencia diferencial de estos compuestos en las raíces de cultivares resistentes y susceptibles. Sin embargo, todavía no se cuenta con una fuerte base bioquímica que explique esta resistencia. El presente estudio muestra diferencias bioquímicas en la vía del metabolismo secundario del fenilpropanoide entre cultivares resistentes al nematodo barrenador del banano *Radopholus similis*, 'Yangambi km5' y 'Pisang jari buaya', y el susceptible 'Grande naine'. A diferencia de reportes anteriores, no se encontró que la lignificación y las células fenólicas preformadas estén específicamente relacionadas con los cultivares resistentes. La acumulación de ácido sinapico en el engrosamiento de las paredes celulares de la endodermis y elementos vasculares, fue inducido por la infección de nematodos tanto en los cultivares resistentes como susceptibles, mientras que células conteniendo flavonoides en el cilindro vascular fueron encontradas únicamente en cultivares resistentes después de la infección. Las raíces de 'Grande naine' mostraron el mayor contenido de fenoles, lo que pudo haber estado relacionado con altos niveles de proantocianidinas. En las raíces de 'Yangambi km5', la proantocianidina y el contenido total fenólico fue el mas bajo, pero los niveles totales promedio fenólicos aumentaron después de la inoculación, a diferencia de los otros cultivares.

Introduction

In the past fifteen years, various sources of resistance and tolerance to parasitic nematodes have been identified within banana. However, the underlying mechanisms, which make it possible for these plants to suppress nematode reproduction or suffer little

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injury are, as in many other plant species, poorly understood. Knowledge of these mechanisms is nevertheless of critical importance to develop strategies for the control of nematodes, especially when one wants these strategies to be environmentally-safe and suitable for subsistence banana growers. Such insights can provide 'resistance markers' to facilitate screening of *Musa* germplasm and provide *Musa* breeders and molecular biologists with the necessary principles to create nematode resistant plants.

Plants interact with their environment through secondary metabolism. Within this part of the metabolism, the phenylpropanoid pathway is of critical importance as its products (phenolic compounds) protect the plant against abiotic and biotic factors (reviewed by Dixon and Paiva 1995). To date, resistance against nematodes in *Musa* has been correlated with phenylpropanoids, *i.e.* lignification in 'Pisang jari buaya' (AA, 'Pisang jari buaya' group) (Fogain and Gowen 1996), preformed phenolic cells and infection-induced accumulation of phenolics in 'Yangambi km5' (AAA, Ibota group) (Fogain and Gowen 1996, Valette *et al.* 1998), phenylphenalenone phytoalexins in *Musa acuminata* (Binks *et al.* 1997, Luis 1998) and high levels of proanthocyanidins in 'Kunnan' (AB) (Collingborn *et al.* 2000). However, these metabolites were not characterized to a sufficient biochemical level and/or no reference was made to their physiological relevance in nematode resistance. Research on secondary metabolites in banana roots has been very limited and provides no guidance for crop improvement.

The results presented here deal with the biochemical nature of nematode resistance encountered in 'Pisang jari buaya' and 'Yangambi km5', in comparison with the susceptible 'Grande naine' (AAA, Cavendish group). Various techniques were used, including histochemical staining of root sections and spectrophotometric detection of phenols in root extracts. Results obtained so far are not conclusive about the biochemical basis for resistance, but provide guidance for future research into the secondary metabolism of *Musa*.

Materials and methods

Plant material, nematodes and experimental set-up

Plant material was obtained from the International *Musa* germplasm collection at the INIBAP Transit Centre at KULeuven. It included 'Grande naine' (ITC1256) (GN), which was chosen as a susceptible cultivar (Stoffelen *et al.* 2000), and 'Yangambi km5' (ITC1123) (YKm5) and 'Pisang jari buaya' (ITC0312) (PJB), which were chosen as resistant cultivars. Micropropagated banana plants were planted in pots filled with 600 ml of a sterilized 2:1 peat-quartz mixture. To each plant 1 g Osmocote®, a slow release fertilizer, was added.

A highly virulent strain of *R. similis* from banana plants in Uganda was used in the experiment (Fallas *et al.* 1995). After ten weeks of growth in the greenhouse, eight plants of each cultivar were inoculated with 1000 vermiform (female and juvenile) nematodes per plant. Eight uninfected plants were included per cultivar. Histochemical staining of root sections and analysis of root extracts was performed two weeks after infection.

Histochemical staining of root sections

Root sections were hand cut from fresh root samples. For the detection of phenylpropanoids, sections were stained within 2 min with saturated (0.25%, w/v) diphenylboric

acid-2-aminoethyl ester (DPBA) (Sigma-Aldrich Inc., Bornem, Belgium) in MilliQ water containing 0.02% (v/v) Triton-X-100. The sections were visualized immediately with an epifluorescence microscope equipped with a DAPI filter (excitation 340-380 nm, suppression LP 430 nm) and a FITC filter (excitation 450-490 nm, suppression LP 520 nm). Identification was made by comparing colour and intensity to standard references (Peer *et al.* 2001).

For the histochemical staining of lignin in root sections, hand cut sections were fixed in 4% glutaraldehyde for 60 min and rinsed with water. For Mäule staining, fixed sections were immersed in 0.5% $KMnO_4$ for 10 min, rinsed with water and destained with 10% HCl for 5 min. After a final rinse they were mounted in concentrated NH_4OH and examined by bright-field microscopy. For Wiesner staining, fixed sections were stained with 10% phloroglucinol in ethanol/water (95/5, v/v) for 2 min, mounted in concentrated HCl (37%) and examined by bright-field microscopy (Strivastava 1966). No specific staining technique was used for the detection of suberin. However, as suberin has a lignin-like structure in its polyaromatic domain, it fluoresces and is stained by the Wiesner and Mäule reagents. Photographic documentation of root sections was achieved with a SPOT RT CCD camera and SPOT software version 3.3 (Diagnostic Instruments Inc., USA).

Extraction and analysis of phenols

For the extraction of phenols from roots, approximately 1-2 g of freshly harvested roots was ground in liquid nitrogen. Proanthocyanidin (condensed tannins) amounts were determined using the butanol/HCl assay described by Collingborn *et al.* (2000) for banana root samples. Ground samples (100 mg) were treated with 5 ml 1-butanol/HCl (95/5, v/v), mixed and incubated at 95°C. After 1 h, samples were thoroughly mixed and centrifuged at 3000 g for 10 min. The absorbance of the top phase was read at 550 nm against a blank sample using a Novaspec II spectrophotometer (Amersham Pharmacia Biotech Inc., Buckinghamshire, UK).

The total phenolic content of root samples was determined using the Folin-Ciocalteu assay (Singleton and Rossi 1965). Ground samples (1 g) were extracted by shaking continuously in a 2 ml aqueous methanol (50%) solution for 1 h at room temperature. Extracts were filtered through a 0.45 µm pore PTFE syringe filter (Merck, Darmstadt, Germany) and stored at -20°C until analysis. In glass tests tubes, 200 µl of the root extracts was mixed with 5 ml water. To each of the samples 500 µl of the Folin-Ciocalteu reagent (Merck, Darmstadt, Germany) was added. Samples were thoroughly mixed and after 3 min, 1 ml saturated sodium carbonate solution (35% in water, w/v) was added. Samples were further diluted to 10 ml with water and left in the dark at room temperature for 1 h. Absorbance was measured at 727 nm against water using a Novaspec II spectrophotometer. A standard calibration curve of gallic acid was determined and results were expressed as gallic acid equivalents/g fresh roots.

Statistical analysis

Data on the phenolic content of roots were analysed with the STATISTICA® package (Anonymous 2001). Since the number of samples was small (five per cultivar for each treatment) and variances not homogeneous (Levene's test for homogeneity of varian-

ces), the non-parametric equivalent of ANOVA, Kruskal-Wallis analysis of variance by ranks, was applied. If Kruskal-Wallis was significant, the significance of the differences between treatments and cultivars was pair wise calculated as described by Siegel and Castellan (1988).

Results and discussion

Histochemical staining of root sections

Lignified root cell walls

The DPBA-staining technique was used for the localization and identification of phenolic compounds in root sections. Syringyl lignin units (derived from sinapic acid) and guaiacyl lignin units (derived from caffeic acid) appeared blue and greenish-white respectively when viewed through a DAPI filter (Figure. 1A, F) and green and bright yellow respectively through a FITC filter (Figure 1B, C, D).

Various studies on resistance mechanisms in banana roots deal with the hypothesis that PJB constitutively contains higher amounts of lignin (Pinochet 1988, Binks 1996, Fogain and Gowen 1996, Elsen *et al. in press*). Among the cultivars tested earlier, PJB and 'Calcutta 4' had the highest lignification of the central cylinder, while in the susceptible cultivars (including GN) and YKm5, no or very few cell walls were lignified (Fogain and Gowen 1996, Elsen *et al. in press*). In the present experiment however, the level of lignification did not differ between the cultivars. In roots of the susceptible GN, cells of the endodermis and central cylinder showed the same degree of thickening of their walls as those of the resistant PJB and YKm5 (Figure 1A-D). In individual roots of the three cultivars, lignification of cell walls increased with the age of the root and the development of laterals. Roots that had recently emerged from the corm were not lignified (Figure 1E, F), while older roots showed the strongest cell wall thickening (Figure 1A-D). This observation might explain the contradictory reports on the occurrence of nematodes in the central cylinder of banana roots (Valette *et al.* 1997 and 1998, Elsen *et al. in press*). The lignified anticlinal walls of the endodermis prevent nematodes from penetrating the central cylinder and affecting the vascular elements (Blake 1961). But in young roots, nematodes can be found in the vascular tissue (Mateille 1994, Sarah *et al.* 1996) because the barrier – the lignified walls of the endodermis – is not developed yet.

In YKm5, the thickened endodermis was predominantly composed of guaiacyl units (yellow fluorescence) (Figure 1D), while in PJB and GN syringyl units (green fluorescence) prevailed (Figure 1A-C). This observation was confirmed by staining with the Wiesner and Mäule reagents which are specific for total lignin (guaiacyl and syringyl units) and syringyl units respectively. In the three cultivars, guaiacyl units were the dominant constituents of lignified cell walls inside the central cylinder. The suberized walls of the outer cortical cells contained predominantly sinapic acid in the case of PJB and GN and caffeic acid in the case of YKm5.

In response to nematode infection, syringyl lignin concentrations increased in the endodermis of YKm5 and in the central cylinder of GN, YKm5 and PJB. This reaction seems to be part of the general defence response of banana, as it occurred in both resistant and susceptible cultivars and in response to both nematodes and fungi

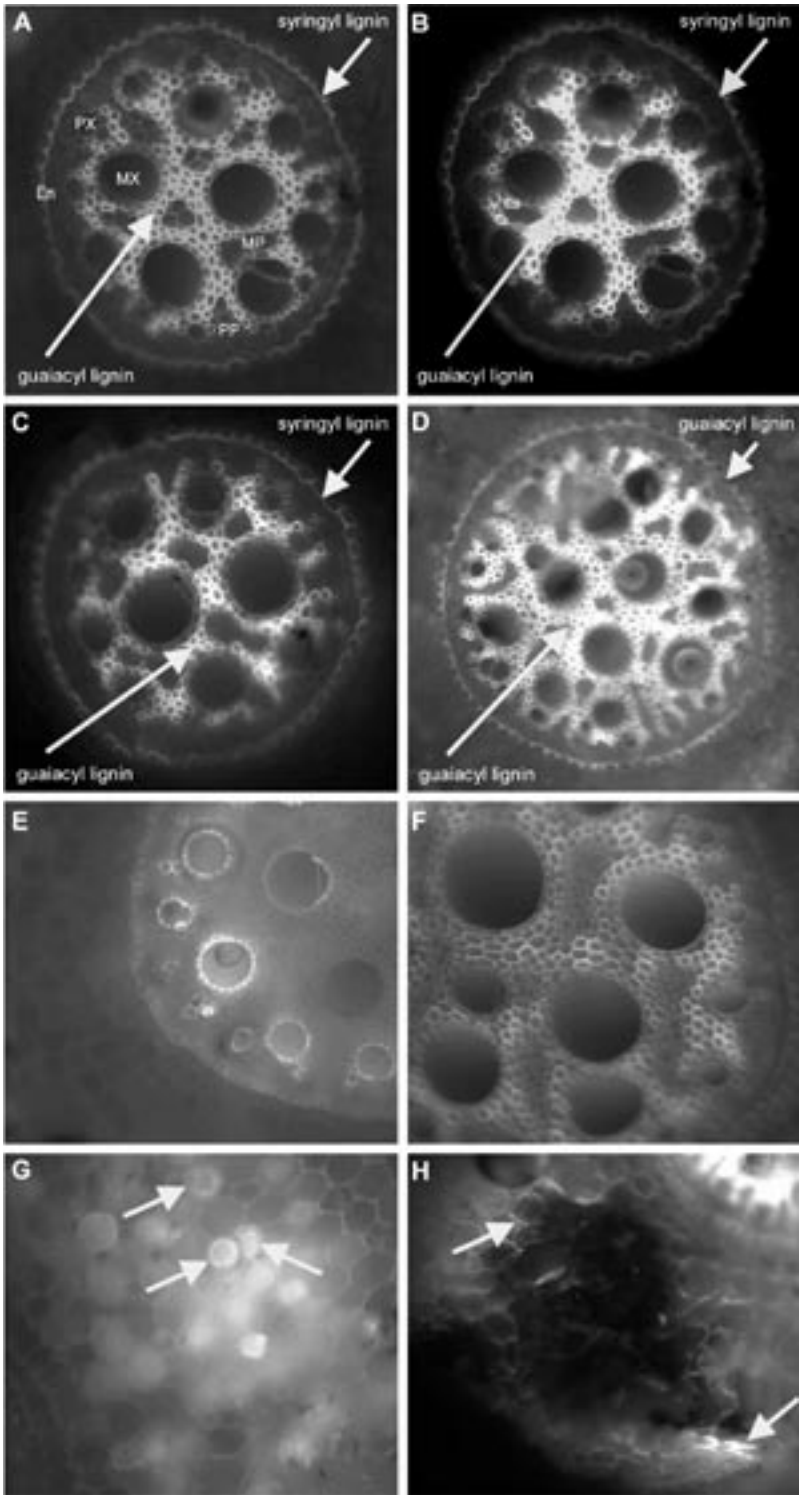


Figure 1. A-D - Cross sections of an older root of 'Grande naine' (A, B), 'Pisang jari buaya' (PJB) (C) and 'Yangambi km5' (D) showing the strong lignification of the endodermis and central cylinder (100x). E, F - Cross sections of young PJB roots showing the absence of, or weak lignification of, the endodermis and central cylinder (100x). G - Flavonol-containing cells (arrows) in the cortex of a PJB root (100x). H - Cross section through a nematode-damaged PJB root showing the presence of flavonols (arrows) in the tissue bordering the necrotic area (100x). Sections were stained with DPBA and viewed under a DAPI filter (A, F) or a FITC filter (B-E, G, H).
En: endodermis, PP: protophloem, MP: metaphloem, PX: protoxylem, MX: metaxylem.

(De Ascencao and Dubery 2000). However, the rate of increase and the total amount could be the decisive factor for resistance/tolerance, as was observed in Fusarium wilt-tolerant *Musa* (De Ascencao and Dubery 2000). Syringyl lignin could be more resistant to enzymatic degradation by pathogens; or compounds released after wall degradation could be toxic to the invaders. In *in vitro* bioassays, sinapic acid had a low toxicity and did not repel or inhibit egg hatch of *R. similis* (Wuyts, *unpubl. data*).

Phenol-containing root cells

Phenolic compounds were detected in cells as granules or as an amorphous mass (Figure 1G), as was described by Mueller and Beckman (1974). They were identified as the flavonols quercetin and kaempferol by their characteristic fluorescence, which was golden yellow and bright green when viewed with a FITC-filter. The lowest number of phenolic cells was found in the cortex of YKm5, while PJB contained the most. This is not in agreement with the proposed mechanism of constitutive resistance in YKm5 (Fogain and Gowen 1996). In the cortex of infected roots, the number of flavonol-containing cells did not increase in the three cultivars, which corresponds with the findings of Elsen *et al.* (*in press*) for YKm5 in *in vitro* screenings for resistance. In the central cylinder of YKm5 and PJB, however, flavonoid-containing cells were present when necrosis had developed in the cortex. Preliminary results of HPLC-analysis of root extracts, confirmed that infected roots of YKm5 and PJB contained higher concentrations of quercetin and kaempferol, while in GN a decrease was found. Flavonols could function in the central cylinder as protective agents or as regulators of physiological processes related to infection, or defence against infection.

Cells bordering the nematode-damaged tissue in the cortex contained flavonols in their walls and in the extracellular spaces in GN, PJB and YKm5 (Figure 1H). The accumulation of phenolic compounds, including flavonols, at the site of infection or wounding is a general feature of the plant response to biotic factors (Dixon and Paiva 1995). In *in vitro* bioassays quercetin and kaempferol were not toxic to *R. similis*, but they did repel the nematode at concentrations as low as 50 ppm (Wuyts N., *unpubl. data*). Flavonols may also act as phytoalexins against secondary infection by pathogenic soil organisms which use the damaged tissue as an 'easy' access to the root.

Analysis of phenol content in root extracts

Proanthocyanidins were analysed in roots of susceptible and resistant cultivars to determine their role in the response to nematode infection (Table 1). Amounts were not significantly different between cultivars, but the highest values were obtained for GN and the lowest for YKm5. Nematode infection had no significant effect on proanthocyanidin accumulation, although the increase was the highest in PJB. Total phenolic content of roots did not differ significantly between cultivars or between treatments. The high concentration in GN roots could be related to the high concentrations of anthocyanidin-related compounds. Only in YKm5 roots (with the lowest constitutive amounts of total phenolics) did the mean phenolic concentration increase in nematode infected roots, which cannot be related to the proanthocyanidins. HPLC-analysis of root extracts is necessary to determine the absolute amounts of the different phenolic compounds in roots.

Table 1. Amount of proanthocyanidins and total phenolic compounds determined by spectrophotometry in roots of three banana cultivars either uninfected or infected by *R. similis* (two weeks after inoculation).

	Proanthocyanidins[a] (A550 nm)			Total phenolic content[a] (µg GAE[b]/g FW)		
Cultivar	- *R. similis*	+ *R. similis*		- *R. similis*	+ *R. similis*	
Grande naine	0.471	0.486	(+ 3%)	230	224	(- 3%)
Yangambi km5	0.279	0.311	(+ 11%)	157	205	(+ 31%)
Pisang jari buaya[c]	0.335	0.446	(+ 33%)	246	240	(- 2%)

[a] results were not significantly different ($P < 0.05$) between cultivars and treatments (GN and YKm5) ($n = 5$) as calculated by the Kruskal-Wallis analysis of variance by ranks; [b] gallic acid equivalents; [c] $n = 1$, not included in the statistical analysis.

Collingborn *et al.* (2000) have suggested the butanol/HCl-assay as a rapid test in screening for resistance against *R. similis*, based on their observation that the resistant 'Kunnan' contained significantly higher amounts of proanthocyanidins pre- and post-infection compared with the susceptible 'Dwarf Cavendish'. However, in the current experiment as well as in the findings of Binks (1996), no correlation existed between resistance and proanthocyanidin amounts. Moreover, the amounts were not significantly higher in roots of infected plants compared with uninfected plants in either the resistant or the susceptible cultivar. However, in the experiment, a random sample of roots was taken from infected and uninfected plants, while Collingborn *et al.* (2000) specifically selected areas with lesions for extraction. In general, proanthocyanidins accumulate in response to wounding by the action of polyphenoloxidases (browning reaction). As a result, higher amounts of proanthocyanidins can be expected in roots with lesions than in undamaged ones. Furthermore, in susceptible cultivars the relative accumulation of proanthocyanidins is higher after nematode infection than in resistant ones (data of Collingborn *et al.* 2000). Proanthocyanidins have strong negative effects on herbivorous insects through their protein-binding capacity, which results in reduced efficiency of nutrient absorption in gut and midgut lesions (Hagerman and Butler 1991). To determine whether proanthocyanidins can be considered as phytoalexins against nematodes in banana roots, they need to be tested in bioassays with nematodes.

Conclusions

The aim of the study was to elucidate the biochemical basis for nematode resistance. Constitutive lignification of root cell walls, and induced cell wall strengthening upon nematode infection, were similar in susceptible and resistant cultivars. In resistant cultivars, the number of cells containing flavonols in the central cylinder was higher when the cortex was damaged by nematodes. The absolute amount of proanthocyanidins in roots cannot be considered as a 'biochemical' marker for nematode resistance, as the highest amounts were found in the susceptible cultivar. Future research includes the analysis of root extracts by HPLC and a search for the physiological relevance of flavonoids in nematode-infected roots.

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6

Recommendations

Recomendaciones

Recommendations

Future efforts in research and development should address the following issues:

- Biological, physical and chemical causes of soil fatigue and their long term implications.
- Key indicators to determine soil quality and health.
- Study the interactions in the rhizosphere among microorganisms and soil elements.
- Study the practical value of mycorrhizae, endophytes and other microorganisms in the field.
- Determine the potential use of organic amendments.
- Determine the strategies with collaborators for the development of these ideas.

Recomendaciones

Las iniciativas futuras en investigación y desarrollo deben enfocar los temas siguientes:

- Factores biológicos, físicos y químicos que ocasionan la fatiga del suelo y sus implicaciones a largo plazo.
- Principales indicadores para determinar la calidad y salud del suelo.
- Estudio de las interacciones a nivel de rizosfera entre los microorganismos y los elementos del suelo.
- Investigar el valor práctico de las micorrizas, endofitos y otros microorganismos en el campo.
- Determinar el uso potencial de las enmiendas orgánicas.
- Definir las estrategias con los colaboradores para el desarrollo de estas ideas.

7

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INIBAP – Red Internacional para el Mejoramiento del Banano y el Plátano

La Misión de INIBAP es aumentar de manera sostenible la productividad del banano y el plátano cultivados por pequeños productores para el consumo doméstico y mercados locales y de exportación. El programa tiene cuatro objetivos principales:

- Organizar y coordinar un esfuerzo global de investigación sobre banano y plátano para el desarrollo, la evaluación y la diseminación de cultivares mejorados y para la conservación y utilización de la diversidad de las Musaceas;
- Promover y fortalecer colaboraciones en la investigación relacionada con banano y plátano a los niveles nacional, regional e internacional;
- Fortalecer la capacidad de los SNIA para conducir actividades de investigación y desarrollo sobre banano y plátano;
- Coordinar, facilitar y apoyar la producción, recopilación y el intercambio de información y de documentación sobre banano y plátano.

INIBAP es una red del Instituto Internacional de Recursos Fitogenéticos (IPGRI), un centro '*Future Harvest*'.

*MUSA*LAC – Red de Investigación y Desarrollo de Plátano y Banano para América Latina y el Caribe

*MUSA*LAC surgió mediante un Acuerdo de Constitución en el ámbito de FORAGRO, firmado el día 6 de junio del 2000, en Cartagena de Indias, Colombia. Los socios de *MUSA*LAC son 15 instituciones nacionales de investigación y desarrollo en representación de sus respectivos países (Bolivia, Brasil, Colombia, Costa Rica, Cuba, Ecuador, Honduras, Jamaica, México, Nicaragua, Panamá, Perú, Puerto Rico, República Dominicana y Venezuela) y 4 instituciones regionales/internaciones (CATIE, CIRAD, IICA e INIBAP). El objetivo general de *MUSA*LAC es incrementar la productividad y competitividad en la cadena agroalimentaria del plátano y el banano a través del desarrollo científico y tecnológico, fortaleciendo los sistemas nacionales de investigación y desarrollo, integrando actores, priorizando y coordinando acciones en América Latina y el Caribe. *MUSA*LAC está dirigida por un Comité Directivo conformado por un representante de cada país miembro; un Presidente y dos Vice-Presidentes y una Coordinación Ejecutiva, actualmente coordinada por INIBAP-LAC, con sede en el CATIE, Turrialba, Costa Rica.

CORBANA – Corporación Bananera Nacional

CORBANA S.A. es una institución pública sin fines de lucro, cuyos objetivos son:

- Fortalecer la investigación en el cultivo del banano.
- Incrementar la productividad bananera con un mínimo de riesgo ambiental.
- Fomentar programas de reducción de costos.
- Brindar servicios de investigación, asistencia técnica e información sobre precios y mercados.
- Propiciar un régimen equitativo de relaciones entre productores nacionales y empresas comercializadoras.
- Establecer junto con el Gobierno, políticas bananeras que ayuden al mantenimiento de la industria a largo plazo.
- Centralizar la información sobre banano para promover y fomentar la participación en la investigación y en el desarrollo tecnológico del sector bananero.

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